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Resurrection of plants and their survival mechanism: Drought perspective

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Abstract

Drought is one of the dangerous hazards of environment. Drought stress impinge on growth, membrane integrity, osmotic adjustment, pigment content, photosynthesis and yield. Most of the plant can withstand drought for a short period of time *via* morphological, physiological and biochemical changes. However, plants are unable to recovery from drought condition when relative water content (RWC) falls below 40% and that condition called desiccation. Effect of desiccation on the survival ability of resurrection plants is low and have ability to withstand cellular water loss up to 95%. These plants assume a dormant state where they can withstand prolonged periods of drought by using morphological, biochemical and cellular mechanisms and resume active metabolism within 24 hours of rehydration. The population of resurrection plants is <2% of total flora and various mechanisms adapted for desiccation tolerance are dissected briefly in this review.

Keywords: Resurrection, drought tolerance, antioxidant, LEA protein and vitrification

Introduction

Drought is dangerous hazard of nature. It is related to a deficiency of precipitation over an extended period of time. Drought is also related to the timing of precipitation. Drought adversely affect growth and productivity and trigger a series of morphological, physiological, biochemical and molecular changes in plants. Drought, temperature extremes, and saline soils are the most common abiotic stresses that plants encounter. Globally, approximately 50% of the land is affected by drought. Drought stress is affected by climatic, edaphic and agronomic factors.

Almost 32 *per cent* of wheat culture face up to various types of drought stress during the growth season in developing Countries. Drought stress is the most important limiting factor of field crops in India. Most parts of India's cultivation land is placed in arid and semiarid regions, where erratic and insufficient rainfall during crop growth period is the major constraint. Hence, plants under go various kinds of stress and performance reduces severely in these regions.

Drought impacts include growth, yield, membrane integrity, pigment content, osmotic adjustment, water relations, and photosynthetic activity. The susceptibility of plants to drought stress varies in dependence of stress degree, different accompanying stress factors, plant species, and their developmental stages (Demirevska *et al.*, 2009) [7]. Exposure of plants to drought stress substantially decreased the leaf water potential, relative water content and transpiration rate, with a concomitant increase in leaf temperature.

Drought stress is a decrease of soil water potential so plants reduce their osmotic potential for water absorption by osmotic regulation. Therefore osmotic regulation will help to cell development and plant growth in water stress. Decrease of relative water content close stomata and also after blocking of stomata will reduce photosynthesis rate. It is reported that high relative water content is a resistant mechanism to drought, and that high relative water content is the result of more osmotic regulation or less elasticity of tissue cell wall.

Drying causes a number of subcellular stresses in plants

- **Mechanical stress:** Associated with turgor loss which occurs in the water potential range -1.5 to -3 Mpa and at RWC 60-50%
- **Oxidative stress:** By unregulated metabolism which occurs in the water potential range -11 to -3 Mpa or RWC 45-25%
- **The destabilization or loss of macromolecular integrity:** At low water contents which occurs in the water potential range -150 Mpa and < 10% RWC

Most plants can withstand drought for a short period, via physiological and morphological changes such as stomatal closure and architecture specialization to reduce water loss and modulate water up take, but will experience extensive cellular damage from which recovery is not possible when water content falls below 40% relative water content.

This kind of mechanism in crop plants only under drought not under desiccation. There is difference between drought and desiccation, drought means just deficiency of water but desiccation means extreme dryness. This drought will not affect the survival ability of resurrection plants.

“Resurrection” means returned to the life. Only a group of plants called resurrection plants have desiccation tolerance (DT), they can survive extreme dehydration, even over

months or years. The ability to withstand cellular water loss to 95% RWC and above. These plants assume a dormant state whereby they can withstand prolonged periods of drought and resume active metabolism when water become available again. Mechanical damage, destabilization, or loss of membrane integrity, and oxidative stress related to disruption of metabolism are the major challenge for plants to survive cellular desiccation. Unlike bryophytes and lichens, which can withstand rapid dehydration by the mechanism of rehydration induced repair process, resurrection angiosperms employ more complex DT pathways that require both short and long term genetic and biochemical reactions (Farrant *et al.*, 2009) ^[11].

Normal plants	Resurrection plants
Desiccation tolerance capacity is limited to seeds, pollens, dormant buds during maturation.	Desiccation tolerance capacity also present in vegetative tissue such as leaves, root and shoot.
Reduction of relative water content beyond 40% enough to kill the tissue.	Reduction of relative water content of the tissue up to 95%, tissue can have ability to restore its growth.
These plants cannot survive dried state, rehydration after drying is no effect on plants.	These plants can survive dried state and resume normal growth and metabolism within 24 h of rehydration.
Large number of population	Population is less. < 0.2% of the total flora (350 species).
Energy utilization more in growth and development.	Energy utilization more in protection and repair mechanism.

Types of resurrection plants

Poikilochlorophyllous resurrection plants

In poikilochlorophyllous resurrection plants, chlorophyll is degraded and thylakoid membranes are dismantled during desiccation.

EX: *Xerophyta humilis*.

Homoiochlorophyllous resurrection plants

Homoiochlorophyllous species retain chlorophyll, but use various mechanisms to prevent light-chlorophyll interaction while plants are dry.

EX: *Craterostigma wilmsii* and *Myrothamnus flabellifolius*

Plant strategies to survive in desiccation

1. Protection of cellular membranes and organelles during desiccation
EX: Angiosperms: *C. plantagineum* (Dicote), *S. stapfianus* (monocot)
2. Repair mechanisms in the damaged cell upon rehydration
EX: Mosses
3. Maintaining life in the dried state: These plants can persist in the air-dried state for months, and revive from the desiccated state even after several years.

Plants have different mechanism and processes to follow above strategies like different cellular mechanism, different plant morphology, different gene expression and different bio molecular synthesis

Cellular mechanisms

Cell wall changes during desiccation

When water availability to roots decreases, plants tend to limit water loss from transpiration by closing the stomata, and thereby reducing the water flux through the plant, and by reducing leaf growth, which results in a smaller transpiring leaf area (Tardieu 2005). The reduction of growth under water deficit is accomplished by a reduction in cell division rate and an increase in cell wall stiffening, which inhibits cell wall expansion (Cosgrove 2000) ^[5]. This stiffening of the cell wall poses a problem for drying cells. In order to tolerate

desiccation, any cell with a large, water-filled vacuole must overcome or limit the mechanical stress caused by its shrinking during drying. The cell walls of some resurrection plants have special adaptations that promote folding to reduce the mechanical stress caused by desiccation. In *C. wilmsii*, a significant increase in xyloglucans and unesterified pectins is observed in the cell wall during drying (Vicre *et al.*, 1999) ^[27]. Dehydration also induces a considerable reduction of glucose in the hemicellulosic fraction of *C. wilmsii* cell walls (Vicre *et al.*, 2004) ^[26]. These changes are thought to enhance the tensile strength of the *C.*

wilmsii cell wall, allowing it to contract and to fold without collapsing in the dried tissue. Thus, cell wall flexibility is an important factor in tolerance to injury caused by desiccation. In *C. plantagineum*, an increase in expansin activity during desiccation is associated with a rise in cell wall flexibility and folding (Jones and McQueen-Mason 2004) ^[16].

Lipid composition of cellular membranes

In the desiccation-tolerant mosses *T. ruralis* and *Selaginella lepidophylla*, the shrinking of cells caused by dehydration results in cells with highly convoluted walls and membranes that are similar in appearance to cells in dry seeds. In the resurrection plant *Boea hygrosopica* where increased unsaturation of fatty acids was observed in all lipid classes upon dehydration regardless of whether it was slow or rapid (Navari-Izzo *et al.*, 1995) ^[19]. High degree of polyunsaturation in phospholipids results in greater membrane fluidity. Increased cell wall and membrane fluidity may be an important protective mechanism for the survival of resurrection plants during desiccation. In *S. stapfianus* during desiccation, phospholipid content increased in leaves dried attached to the parent, but decreased in leaves that have been dried detached (Quartacci *et al.*, 1997). The fact that attached dried leaves develop desiccation tolerance, while detached dried leaves do not (Neale *et al.*, 2000) ^[20], may in part be due to the level of polyunsaturated lipids within the plasma membrane.

The leaves of resurrection plants contain a relatively high number of double bonds in their polar lipids, which is a general characteristic of chloroplasts (Hoekstra, 2005). There

is a negative correlation between the longevity of desiccation-tolerant tissues and the number of double bonds in the polar lipids of membranes, and that the lifespan of resurrection plants during prolonged desiccation is generally limited to several years maximally.

Upon rehydration in *S. stapfianus*, leaves desiccated on the plant regained almost all of the lipid content, whereas detached dried leaves suffered a complete lipid degradation with the loss of polyunsaturated fatty acids (Quartacci *et al.*, 1997).

Vitrification

Vitrification involves application of cry protectants solution to increase cell viscosity to a critical point at which water forms a meta stable glass on expose to ultra-low temperature.

Vitrification of the cytoplasm may not be due to the effects of sugars only, but probably results from the interaction of sugars with other molecules, most likely proteins (Hoekstra 2005). The formation of an intracellular glass phase is believed to be indispensable to survival during desiccation, and cells of many desiccation-tolerant plants and animals undergo vitrification upon drying to protect organelles from damage (Buitink and Leprince 2004) [13].

Vitrification upon drying helps to protect organelles from damage. Vitrification limits the production of free radicals by reducing rate of chemical reaction and it helps to preserve protein structure. Vitrification may be an important protective mechanism for resurrection plants against oxidative damage during desiccation.

Anti-oxidant systems

Recovery of a resurrection plant correlates with its capacity to establish a number of anti-oxidant protective mechanisms during dehydration, and to maintain these systems upon rehydration (Kraner *et al.*, 2002) [18]. Desiccation results in the production of reactive oxygen species (ROS) that can damage membrane lipids and proteins.

An important protective mechanism in *S. stapfianus* is the induction of free radical-scavenging enzymes such as glutathione reductase, ascorbate peroxidase, and dehydroascorbate reductase to remove the ROS. Antioxidant activity also increases in other resurrection plants during desiccation (Sherwin and Farrant 1998) [25]. It has been shown that more damage occurs during rehydration than during desiccation because of intensified oxidative stress during the recovery phase.

In desiccation-sensitive *S. stapfianus* leaves dried detached, however, ascorbate peroxidase activity decreased during desiccation, resulting in reduced antioxidant capacity. This may be another reason for the failure of detached dried leaves of *S. stapfianus* to recover from desiccation.

Anti-oxidant enzymes such as superoxide dismutase, glutathione reductase, and ascorbate peroxidase are induced in response to various abiotic stresses in both desiccation-tolerant as well as desiccation-sensitive organisms, and are considered as general 'housekeeping' protectants. However, only in desiccation-tolerant tissues can the activities of these enzymes remain elevated during dehydration. This may be a consequence of mechanisms that protect and maintain the anti-oxidant enzymes in their native states, which results in increased activity and/or half-life of the proteins, rather than a unique desiccation tolerance mechanism. Resurrection plants can persist in the desiccated state for several years. However, they cannot remain indefinitely in this anabiotic state because, in part, oxidative damage increases with duration of

desiccation and results in the gradual loss of viability. Failure of the anti-oxidant system during long-term desiccation triggers programmed cell death, causing ageing and eventual death of the plant (Illing *et al.*, 2005) [15]. The acyl chains of the membrane polar lipids, which may contain unsaturated double bonds, are particularly sensitive to free radical attack.

Pigment Modification

Some homoiochlorophyllous resurrection plants retain all of their chlorophyll during desiccation, whereas, others poikilochlorophyllous lose their chlorophyll (Oliver *et al.*, 2000) [22]. In contrast, the photosynthetic machinery in desiccation-tolerant bryophytes appears to be constitutively protected during drying such that photosynthetic activity recovers quickly following rehydration (Oliver *et al.*, 2005) [24].

The desiccation-tolerant grass *S. stapfianus* is partially poikilochlorophyllous, and retains most of its chlorophyll content during desiccation (Quartacci *et al.*, 1997). After a cycle of dehydration to air-dryness and rehydration to full turgor, *S. stapfianus* regained all of its photosynthetic capability within 24 h. *S. stapfianus* lowered its PSII during dehydration. In general, water deficit causes a reduction in the photosynthesis rate, resulting in the decline in the photochemical efficiency of PSII and electron transport rate in desiccation-tolerant as well as desiccation-sensitive plants. The decline in PSII activity could represent a protective mechanism from toxic oxygen production in order to maintain membrane integrity and to ensure protoplast survival (Di Blasi *et al.*, 1998) [9]. However, only proteins within the thylakoid membranes of resurrection plants remain stable during desiccation and rehydration, whereas those of desiccation-sensitive plants are completely destroyed after a short-term desiccation event (Deng *et al.*, 2003).

Anthocyanin: Anthocyanin synthesis increases in water stress condition. For protection against photo-oxidation and it avoid interaction between chlorophyll and solar radiation by reflecting

Morphological adaptations

Leaf folding

Water deficit induces many morphological changes in desiccation-tolerant vascular plants, the most obvious of which is leaf folding. The folding of leaves during drying is not unique to resurrection plants and also occurs in desiccation sensitive plants. Leaves of the desiccation-tolerant dicot *C. wilmsii*, which are fully expanded when watered, progressively curl inward during drying and become tightly folded so that only the abaxial surfaces of the older leaves in the outer whorl are exposed to the sun (Sherwin and Farrant 1998) [25]. Leaf folding is thought to limit oxidative stress damage from UV radiation, and is an important morphological adaptation for surviving desiccation. Indeed, *C. wilmsii* plants do not survive desiccation in sunlight if the leaves are mechanically prevented from folding (Farrant *et al.*, 2003).

The leaf blades of the desiccation-tolerant monocot *X. humilis* fold in half along the midrib upon dehydration, leaving only the abaxial surfaced exposed to the light (Sherwin and Farrant 1998) [25]. The leaves of *M. flebellifolia* are wedge-shaped with crenate-dentate leaf apices and are flabellate with five to seven folds. The unique arrangement of alternating ridges and furrows allows the leaves to fold parallel to the leaf face upon

dehydration. This probably facilitates a rapid return to the hydrated shape.

Epicuticular waxes

In the desiccation-tolerant grass *S. stapfianus*, the leaf adaxial side, which is most exposed to sun radiation, is very rich in Epicuticular waxes.

Function of Epicuticular wax: To limit irradiation and heating of leaf tissues, Closure of stomata, helps to decrease the rate of water loss, Helps in the protection of the thylakoid membranes, which are maintained in the chloroplasts, Protects from the light damage in water stress condition by reflection of solar radiation

Gene expression

Genes expressed in response to drought stress are classified into two main types:

1. Genes encode for products which have protective functions: Synthesis of compatible solutes like sucrose, proteins (LEA) involved in protection of cell organelles and maintenance of water potential
2. Genes encode for regulatory proteins such as transcription factors: Myb and home domain-leucine zipper (HD-Zip) family Regulator of the drought response pathway involved in ABA and glucose signaling responses

In *C. plantagineum* the dehydration process is characterized by the activation of many dehydration-induced genes and the accumulation of the respective gene products, which rapidly decline during the rehydration process (Bernacchia *et al.*, 1996). This is different to the moss *T. ruralis* where most changes in gene expression occur during the first hours of rehydration and so-called rehydrins are synthesized. In *T. ruralis* the changes mainly occur on the translational level by selecting different mRNAs for translation from an unchanged pool of mRNAs available for translation independent from the water status of the moss. These observations suggest that different mechanisms must be involved in desiccation tolerance in the moss and higher plants.

Based on conservation of gene contents the following functional categories of dehydration-induced genes in *C. plantagineum* can be distinguished:

1. Genes encoding protective proteins including hydrophilins and detoxifying enzymes
2. Genes encoding products with regulatory functions (proteins and RNAs)
3. Genes encoding enzymes related to carbohydrate metabolism
4. Proteins involved in transport of water and other molecules

Nearly all of the drought-induced transcription factors isolated thus far from resurrection plants have come from *C. plantagineum* and they belong to either the Myb or the homeodomain-leucine zipper (HD-Zip) family. Two Myb-related genes, *cpm10* and *cpm7*, show differential expression and regulation in response to desiccation in *C. plantagineum*. Two HD-Zip genes, CPHB-1 and CPHB-2, are induced by dehydration in leaves and roots of *C. plantagineum*.

Bio molecule synthesis and their role

Compatible solutes

Compatible solute accumulation in the cell increases cellular osmolarity, this process is called as osmoregulation. Upon dehydration, many plants accumulate nontoxic or

'compatible' solutes such as proline, mannitol, and glycine betaine (Chen and Murata 2002) ^[4]. The net result of compatible solute accumulation is an increase in cellular osmolarity which, leads to an influx of water into, or at least a reduced efflux from, cells (Hare *et al.*, 1998) ^[13]. Compatible solutes have been proposed to protect cells during drying through the stabilization of cytoplasmic constituents, ion sequestration, and increased water retention.

Sugar contents

Water deficit results in a reduction of photosynthesis and starch content in leaf tissues. There is a rapid conversion of starch into sugars, the most common of which are sucrose and trehalose (Crowe *et al.*, 1998) ^[6].

Sucrose and trehalose contribute towards the maintenance of turgor during stress, and the prevention of protein denaturation and membrane fusions in the cell. Both sugars are capable of forming biological glasses within the dried cell. Conversion of starch, which is usually stored in plastids, into sucrose is attributed primarily to activation of sucrose phosphate synthase by reversible protein phosphorylation upon perception of osmotic stress. The activation of sucrose synthesis may also be associated with a concurrent inhibition of starch synthesis. Sucrose biosynthetic genes have been shown to be induced by both desiccation and ABA in the resurrection plant *C. plantagineum* (Kleines *et al.*, 1999) ^[17]. In fully hydrated *S. stapfianus* leaves, glucose, fructose, and galactose are present in large amounts. During dehydration, sucrose increases to high levels in air-dry leaves to become the predominant sugar (Ghasempour *et al.*, 1998) ^[12]. Other sugars such as raffinose and trehalose are also detected, and they may supplement the role of sucrose as osmotic protectants during drying. In *C. plantagineum*, the unusual eight-carbon sugar, 2-octulose, is the predominant sugar in fully-hydrated leaves. During dehydration, 2-octulose is converted to sucrose, with the reverse process being observed during rehydration (Bartels and Salamini 2001) ^[1]. Sucrose also accumulates in the roots of drying *C. plantagineum* plants, suggesting that it may play a protective role within the root systems of resurrection plants during desiccation (Norwood *et al.*, 2003) ^[21].

LEA (Late embryogenesis abundance) proteins

The ability of a plant to survive desiccation appears to depend upon the accumulation of a large set of proteins with putative protective functions. These proteins include the late embryogenesis abundant (LEA) proteins which, as their name suggests, increase markedly in abundance during the latter stages of embryo development as the seed dries. Some LEA genes are also induced in vegetative tissues in response to various abiotic stresses, including drought, cold, and salt, as well as to ABA. LEA transcripts are also abundant in *T. ruralis* during rehydration, suggesting that LEAs may also play a role in recovery from desiccation when water is reintroduced into dried tissues (Oliver *et al.*, 2004) ^[23].

LEA proteins have been classified into eighteen different groups based on sequence homology. A common feature of LEA proteins is that they are extremely hydrophilic, and are soluble at high (80 °C) temperatures. LEA proteins do not possess any apparent catalytic activity or structural domains, and most of them lack cysteine and tryptophan residues.

The functions of LEA proteins include the unwinding or repair of DNA, forming cytoskeletal filaments to counteract the physical stresses imposed by desiccation, and acting as molecular chaperones (Wise and Tunnacliffe 2004) ^[28]. It has

also been suggested that LEA proteins, possibly in combination with compatible solutes, could replace water and thus maintain the hydration shell of proteins and other molecules during desiccation (Bartels 2005) [2]. In rehydrating *T. ruralis* gametophytes, LEA proteins may function in stabilizing membranes, or in the transport of lipids for reconstitution of damaged membranes (Oliver *et al.*, 2005) [24].

Although many LEA genes have been isolated, a functional role in desiccation tolerance has been demonstrated for only few. The expression of the barley LEA gene, HVA1, increased drought tolerance in transgenic wheat plants. In rice, over-expression of HVA1 enhances tolerance to high-salt as well as drought stress.

In nature, extreme Drought resistant is found in resurrection plants which possess strong drought escape mechanisms. Resurrection plants can be exposed to severe drought for months, extending up to years, forcing them to optimize their growth for survival by using various modification in physiological, biochemical, cellular and molecular level. Improving drought resistant in crop plants is a challenge for plant breeders and crop physiologists, as it is a complex genetic trait with multiple pathways involved. Effective development of drought-resistant crop plants thus requires the pyramiding and interaction of many mechanisms, traits, and genes that are involved in resurrection plants for desiccation tolerance, and can introduce in crop plants with the aid of advance molecular technique. Success in this direction not only extends the growing area of crop plants but also achieves stable yield in drought-prone areas.

Reference

- Bartels D, Salamini F. Desiccation tolerance in the resurrection plant *Craterostigma plantagineum*. A contribution to the study of drought tolerance at the molecular level. *Scientific Correspondence*. 2001; 49:1346-1353.
- Bartels D. Desiccation tolerance studied in the resurrection plant *craterostigma plantagineum*. *Integr. Computational Biology*. 2005; 45:696-701.
- Buitink J, Leprince O. Glass formation in plant anhydrobiotics: survival in the dry state. *Cryobiology*. 2004; 48:215-228.
- Chen THH, Muruta N. Enhancement of tolerance of abiotic stress by metabolic engineering of betaines and other compatible solutes. *Current Opinion in Plant Biology*. 2002; 5:250-257.
- Cosgrove DJ. Expansive growth of plant cell walls. *Plant Physiology and Biochemistry*. 2000; 38:109-124.
- Crowe JH, Carpenter JF, Crowe LM. The role of vitrification in anhydrobiosis. *Annual Review on Plant Physiology*. 1998; 60:73-103.
- Demirevska K, Simova-Stoilova L, Vassileva V, Feller U. Rubisco and some chaperone protein responses to water stress and rewatering at early seedling growth of drought sensitive and tolerant wheat varieties. *Plant Growth Regulators*. 2009; 58:97-106.
- Deng Y, Humbert S, Liu JX, Srivastava R, Rothstein SJ, Howell SH. Heat induces the splicing by IRE1 of a mRNA encoding a transcription factor involved in the unfolded protein response in *Arabidopsis*. In: *Proceedings of National Academic Science. U.S.A*, 2011; 108:7247-7252.
- Di Blasi S, Puliga S, Losi L, Vazzana CS. *stapfianus* and *E. curvula* cv. *Consol in vivo* photosynthesis, PSII activity and ABA content during dehydration. *Plant Growth Regulator*. 1998; 25:97-104.
- Fanata WID, Lee SY, Lee KO. The unfolded protein response in plants: A fundamental adaptive cellular response to internal and external stresses. *Journal of Proteomics*. 2013; 93:356-368.
- Farrant JM, Lehner A, Cooper K, Wiswedel S. Desiccation tolerance in the vegetative tissues of the fern *Mohria caffrorum* is seasonally regulated. *Plant Journal*. 2009; 57:65-79.
- Ghasempour HR, Graff DF, Williams RPW, Gianello RD. Contents of sugars in leaves of drying desiccation tolerant flowering plants, particularly grasses. *Plant growth Regulators*. 1998; 24:185-191.
- Hare PD, Cress WA, Van Staden J. Dissecting the roles of osmolyte accumulation during stress. *Plant Cell Environment*. 1998, 21:535-553.
- Hoekstra F, Golovina EA, Buitink J. Mechanisms of plant desiccation tolerance. *Trends in Plant Science*. 2001; 6:431-438.
- Illing N, Denby KJ, Collett H, Shen A, Farrant JM. The signature of seeds in resurrection plants: a molecular and physiological comparison of desiccation tolerance in seeds and vegetative tissues. *Integr. Computational Biology*. 2005; 45:771-787.
- Jones L, McQueen-Mason S. A role for expansins in dehydration and rehydration of the resurrection plant *Craterostigma plantagineum*. *FEBS Lett*. 2004; 559:61-65.
- Kleines M, Elster RC, Rodrigo MJ, Blervac AS, Salamini F, Bartels D. Isolation and expression analysis of two stress responsive sucrose synthase genes from the resurrection plant *Craterostigma plantagineum*. *Planta*. 1999; 209:13-24.
- Kranner I, Beckett RP, Wornik S, Zorn M, Hartwig WP. Revival of a resurrection plant correlates with its antioxidant status. *The Plant Journal*. 2002; 31(1):13-24.
- Navari-Izzo F, Ricci F, Vazzana C, Quartacci MF. Unusual composition of thalokoid membranes of the resurrection plants *Boea hygrosopica*: Changes in lipids upon dehydration and rehydration. *Plant Physiology*. 1995; 124:1427-1436.
- Neale A, Blomstedt CK, Bronson P, Guthridge K, Evans J, Gaff DF. The isolation of genes from the resurrection grass *Sporobolus stapfianus* which are induced during severe drought stress. *Plant Cell Environment*. 2000; 23:265-277.
- Norwood M, Toldi O, Richter A, Scott P. Investigation into the ability of roots of the poikilohydric plant *Craterostigma plantagineum* to survive dehydration stress. *Journal of Experimental Botany*. 2003; 54:2313-2321.
- Oliver MJ, Tuba Z, Mishler BD. The evolution of vegetative desiccation tolerance in land plants. *Plant Ecology*. 2000; 151:85-100.
- Oliver MJ, Dowd SE, Zaragoza J, Mauget SA, Payton P. R. The rehydration transcriptome of the desiccation-tolerant bryophyte *Tortula ruralis*: transcript classification and analysis. *BMC Genomics*. 2004; 5:8910.
- Oliver MJ, Velten J, Mishler BD. Desiccation tolerance in Bryophytes: A reflection of the primitive strategy for plant survival in dehydrating habitats?. *Integrated Computational Biology*. 2005; 45:788-799.
- Sherrvin HW, Farrant JM. Protection mechanisms against excess light in rge resurrecton plants *Craterostigma*

- wilmsii and *Xerophyta viscosa*. *Plant Growth Regulators*. 1998; 24:203-210.
26. Vire M, Farrant JM, Driouich A. Insights into the cellular mechanisms of desiccation tolerance among angiosperm resurrection plant species. *Plant Cell and Environment*. 2004; 27:1329-1340.
27. Vire M, Sherwin HW, Driouich A, Jaffer MA, Farrant JM. Cell wall characteristics and structure of hydrated and dry leaves of the resurrection plants *Craterostigma wilmsii*, a microscopical study. *Journal of Plant Physiology*. 1999; 155:719-726.
28. Wise MJ, Tunnacliffe A. POPP the question: what do LEA proteins do? *Trends in Plant Science*. 2004; 9:13-17.