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Dehydrin, a scavenger against abiotic stress in Fruit crops

Rathod PH[1], Kalariya VD[2]
[1] NM College of Agriculture, ASPEE College of Horticulture and Forestry, Navsari Agricultural University, Navsari, Gujarat, India
[2] Department of Vegetable Science, ASPEE College of Horticulture and Forestry, Navsari Agricultural University, Navsari, Gujarat, India

Abstract

Abiotic stress includes temperature, salinity, water, radiation, chemical, etc. Among which cold, salinity and drought are the major stresses, which adversely affects plants growth and productivity. Cellular response against stress includes reactive oxygen species (ROS), osmolytes and protein accumulation. Among protein accumulation, dehydrin belongs to group II of late embryogenesis abundance (LEA) protein. Dehydrins are considered all the proteins which have at least one copy of the lysine rich amino acids sequence known as K segment. K segment of dehydrins imparts structural modification when translocated to the plasma membrane and it forms α–helix which is amphipathic in nature. Genes which encode these proteins are expressed during late embryogenesis, as well as in vegetative tissues subjected to drought, low temperature and high salt conditions and enhance resistance of the transgenic lines to various adverse environments, such as cold, drought, salinity and osmotic stress.

Keywords: stress, abiotic stress, cellular response, LEA, dehydrins and fruit crops dehydrins

Introduction

Stress in terms of biology is an adverse force or a condition, which inhibits the normal functioning and growth of a biological system of plants. Stress can be broadly classified as biotic and abiotic. Biotic stress includes pathogen, insect, herbivorous, *etc*. Abiotic stress includes temperature, salinity, water, radiation, chemical, etc. Among which cold, salinity and drought are the major stresses, which adversely affects plants growth and productivity. Water availability for plant is highly affected by three environmental stresses which include salinity, low temperature (freezing) and drought (Mahajan and Tuteja, 2005) [11].

Effect of cold, drought and salinity stress on plant

Cold

- Lowers chemical reaction rate
- Reactive Oxygen Species (ROS) formation
- Loss in membrane integrity
- Damage to cell membrane and cell
- Damage to organelles by ice formation
- Loss in intracellular organelles integrity

Drought

- Removal of water from the membrane disrupts the normal bilayer structure and membrane becomes exceptionally porous
- Stress within the lipid bilayer may also result in displacement of membrane proteins
- Very severe drought conditions results in limited photosynthesis
- Accelerating senescence and abscission of the older leaves
- Production of reactive oxygen species production (H_2O_2, Superoxide, OH^- radicals)

Salinity

- High salt concentration exerts two stresses on the plant cell, an ionic stress and an osmotic stress.
- The ionic stress is mainly caused by high Na^+ and Cl^- concentrations, which leads to an influx of ions into the plant cell.
- The osmotic stress is caused by lowering of the soil water potential leading to a reduced water uptake and eventually to cellular dehydration.

Cellular response of plant

1. Reactive Oxygen Species (ROS)
   e.g. (H_2O_2), (OH^-) and ($O*_2^-$)
2. Osmolytes E.g. glycerol, mannitol/inositol, sorbitol, proline, mannitol, glycine.
3. Protein accumulation
   a. Enzymes required for biosynthesis of osmolytes
   b. LEA proteins
   c. Antifreeze proteins
   d. Chaperones (e.g. HSP)
   e. Detoxification

Late embryogenesis abundant (lea) proteins

Late Embryogenesis Abundant proteins (LEA proteins) are proteins in plants that protect other proteins from aggregation caused by dehydration. LEA proteins were initially discovered accumulating late in embryogenesis of cotton seeds. Although, abundant in seeds and pollens, LEA proteins have been found to protect against desiccation, cold, or high salinity.

Table 1: Classification of LEA protein [Dure *et al.* (1989)]

1. LEA I/ (D-19) proteins	Hydrophilic
2. LEA II /Dehydrins/(D-11) proteins	
3. LEA III /(D7/D29) proteins	
4. LEA IV /(D-113) proteins	
5. LEA V/(D- 34 D- 95) proteins	Hydrophobic
6. Atypical LEA proteins	

Dehydrins

Dehydrins are group II LEA proteins whose expression is induced by various environmental factors, which cause dehydration of the cells (drought, frost, cold and salinity). These proteins are most commonly found in higher plants, algae, yeast and cynobacteria.

- The distinctive feature of all dehydrins (DHNs) is a conserved, lysine-rich 15-amino acid domain, EKKGIMDKIKEKLPG, named the K-segment
- Molecular weight ranges from 9 to 200 kDa
- They are water soluble and thermo stable (up to 100°C)

Dehydrin found in cell cytoplasm and nucleus (Houde *et al.*, 1995) [4], near to plasma membrane (Danyluk *et al.*, 1994) [4], also found in cell organelles, such as mitochondria (Borovskii *et al.*, 2000) [2] and vacuoles (Heyen *et al.*, 2002) [8].

Structure of dehydrin

Dehydrins are considered all the proteins which have at least one copy of the lysine-rich amino acid sequence known as K-segment (Close, 1996) [3]. Dehydrins are structurally characterized by three conserved sequences; Y, S and K-segments.

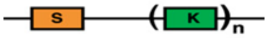
The amino acids separating the conserved segments are

1. **K – Segment (EKKGIMDKIKEKLPG)**
   - The K segment is the only segment present in all dehydrins
   - The K-segment was proposed to form a class A amphiphatic α-helix
   - It is usually present near the C-terminus
2. **S – Segment (SSSSSSSS)**
   - Rich in polar amino acids
   - Y segment has V/TDEYGNP amino acid sequence
   - Present at N- terminus
3. **Y – Segment (DEYGNP)**
   - Five to seven serine residues form the S-segment
   - Serine rich domain
4. **Φ – Segment**
   - Less conservative rich in glycine amino acid residues

Structural classification of dehydrins

There are mainly 5 types of dehydrins *viz.*, YnSKn, Kn, SKn, KnS and Y2Kn (Close, 1996) [3].

1. **Y_nSK_n dehydrins**
   - This is the most abundant class of dehydrins
   - These are basic or neutral proteins
   - They are induced by drought (but not by cold temperatures)



2. **SK_n dehydrins**
   - They are acidic dehydrins
   - Induced by low temperatures
   - For example, at 4°C accumulation of WCOR410 dehydrin

3. **K_{en} dehydrins**
   - These cidic or neutral proteins
   - Induced by cold temperatures, dehydration

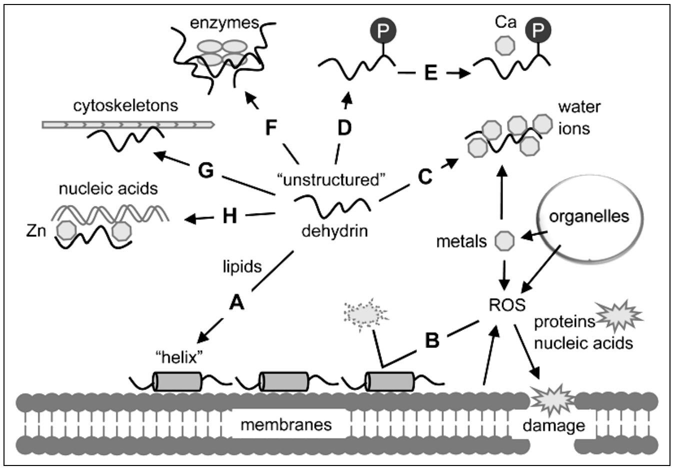
4. **K_nS dehydrins**
   - Induced by dehydration and cold temperatures

5. **Y_nK_n dehydrins**
   - Acidic ehydrins

Multiple Functions of Dehydrins

Dehydrins actually show multifunctionality, whereas all the dehydrins do not necessarily have all of the functions (Figure 1). It is necessary to identify which functions are common in many dehydrins and which are restricted to specific dehydrins. At present, binding to acidic phospholipids, binding to ions and cryoprotection are common functions of dehydrins.

Generally, dehydrins are believed to interact non-specifically to partner molecules. In fact, dehydrins bind to various molecules such as water, ions, phospholipids, proteins and nucleic acids. However, in most cases, the direct binding between dehydrins and target molecules was assessed without any mediating factors, except the binding between CuCOR15 and nucleic acids, which was dependent on zinc. If appropriate co-factors are thus supplied to the assay system, more kinds of interactions can be detected. Finding such co-factor-mediated interactions could be the breakthrough needed to find unidentified functions of dehydrins.



A: binding to phospholipids; B: radical scavenging; C: binding to water and ions; D: phosphorylation; E: binding to calcium; F: protection of enzymes; G: binding to cytoskeletons; H: binding to nucleic acids.

Fig 1: Functions of dehydrins with experimental evidence.

Mode of action of Dehydrins

K segment of dehydrins imparts structural modification when translocated to the plasma membrane and it forms α–helix which is amphipathic in nature (Figure 2). It combines with water molecules at hydrophilic side and lipid molecules at the other side. Thus the liquid crystalline state is maintained during cold stress and at the same time water loss due to disturbed osmotic potential can be prevented. By this means prevention of hexagonal II phase transition from liquid crystalline state can be greatly achieved (Allagulova *et al.* 2003) [1].

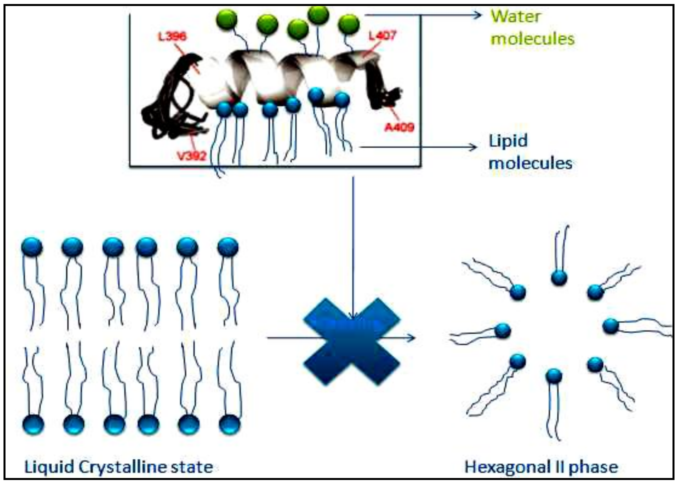


Fig 2: Interaction of K segment with water and lipid molecules

Fruit crops dehydrins

Hanana *et al.* (2014) [5] identified and isolate genes related to abiotic stress (salinity) tolerance in grapevine, a candidate gene approach led to the isolation from Cabernet Sauvignon cultivar of a full-length cDNA of dehydrin gene (Figure 3). The expression study of VvDhn was carried out within plant organs and tissues as well as under salt stresses. VvDhn was not detected in vegetative tissue, whereas it was only expressed during seed development (during late embryogenesis) at extremely high levels and was induced by salt stress.

Xu *et al.* (2014) [14] nreported that the role of EjDHNs in freezing resistance in loquat fruitlets. Two cultivars of loquat, the freezing-sensitive “Ninghaibai” (FS-NHB) and the freezing-tolerant “Jiajiao” (FT-JJ) were analyzed under induced freezing stress. Freezing stress led to obvious accumulation of reactive oxygen species, they also found seven DHNs, showing four different structure types from loquat fruitlets and used to study the characteristics of different EjDHN proteins.

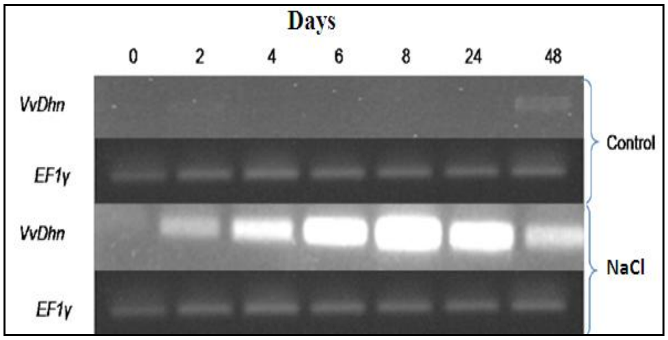


Fig 3: *VvDhn* expression under salt stress (100 mM NaCl) in grapevine.

Parmentier-Line *et al.* (2002) [13] monitored two dehydrins of 65 and 30 kDa were detected with a polyclonal antibody raised against the 65 kDa dehydrin of blueberry. Using a full-length cDNA clone of blueberry dehydrin 1 as a probe, one mRNA of 0.75 kb, an appropriate size to encode the 30 kDa dehydrin, was detected on RNA blots.

Yang *et al.* (2012) [15] identified the *DHN* gene family in *V. vinifera* and the corresponding homologues were isolated from *V. yeshanensis*. The four grapevine *DHN* genes shared a low sequence identity, and exhibited clear differences in physicochemical properties and expression profiles, which indicates functional diversification within the grapevine *DHN* family. *DHN-1* appeared to be the principal stress-responsive gene in grapevine species, and was induced not only by various abiotic stresses.Conversely, *V. yeshanensis* is highly tolerant to both cold and drought. Four DHN genes were identified, all of which contained a K-segment. These genes were designated *VvDHN1*, *VvDHN2*, *VvDHN3*, and *VvDHN4*.

Table 2

Name	Type	Expression
VyDHN1	Y_2SK_2	Stress + Seed
VyDHN2	SK_2	Stress + Seed
VyDHN3	SK_3	Seed (Weak)
VyDHN4	Y_3SK_2	Seed

Hara *et al.* (2001) identified CuCOR19 mRNA or protein by Northern or Western hybridization, respectively (Figure 4). A small amount of CuCOR19 mRNA was present in leaf when it was detached and the mRNA level decreased during the control experiment.

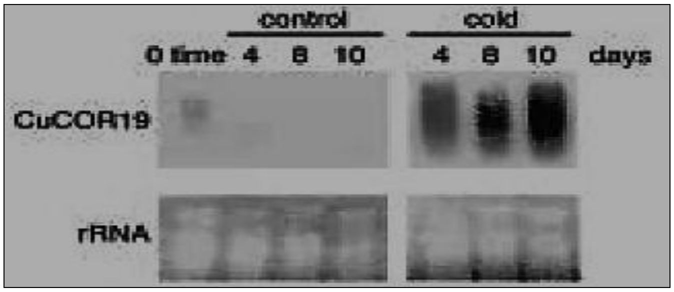


Fig 4: Effects of cold on the mRNA level of CuCOR19 in *C. unshiu* leaf.

Monica *et al.* (2009) [12] identified a DHN of the class Y2SK4 with a deduced amino acid sequence with 79–98% identity among the cultivars "Royal Gala", "Goldrush" and the M9 rootstock that showed high identity to our DHN from "Golden Delicious" (92–98%) (Table 1).

Table 3: Sequence identity of apple DHNs (Y$_2$SK$_4$) from four cultivars

	Identity (%)				
	Golden Delicious Y$_2$SK$_4$	**M*9* rootstock Y$_2$SK$_n$**	**Goldrush Y$_2$SK$_4$**	**Royal Gala SK$_4$**	**Royal Gala Y$_2$SK$_n$**
Golden Delicious Y$_2$SK$_4$		97	97	98	95
M*9* rootstock Y$_2$SK$_n$			98	79	94
Goldrush Y$_2$SK$_4$				98	
Royal Gala SK$_4$					84
Royal Gala Y$_2$SK$_n$					

Conclusion

From forgoing discussion it can be concluded that the genes which encode these proteins are expressed during late embryogenesis, as well as in vegetative tissues subjected to drought, low temperature and high salt conditions. Fascinating, over-expression of DHN genes in transgenic plants has been found to enhance resistance of the transgenic lines to various adverse environments, such as cold, drought, salinity and osmotic stress, which has raised significant interest in their putative application for crop improvement. While it is generally accepted that DHNs function to protect cells from damage caused by stress-induced dehydration, their precise mechanism remains elusive.

Future thrust

- To understand the underlying molecular mechanism of how a plant cell modulates its protein expression network to cope with the stress, an in-depth study of the organelle proteome is of great contribution toward development of stress tolerant crop varieties to meet the increasing demand of food supply worldwide
- Attempts should be made to design suitable vectors for stacking relevant genes of one pathway or complementary pathways to develop durable tolerance
- It is desirable that appropriate stress inducible promoters should drive the stress genes as well as transcription factors, which will minimize their expression under a non-stressed condition thereby reducing yield penalty

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