
REVIEW

The Plant Dehydrins: Structure and Putative Functions

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Received January 15, 2003

Abstract—This review deals with recent data on the structure and biochemical properties of dehydrins, proteins that are normally synthesized in maturing seeds during their desiccation, and also in vegetative tissues of plants treated with abscisic acid or exposed to environmental stress factors that result in cellular dehydration. The dehydrins are considered as stress proteins involved in formation of plant protective reactions against dehydration. The generally accepted classification of dehydrins is based on their structural features, such as the presence of conserved sequences, designated as Y-, S-, and K-segments. The K-segment representing a highly conserved 15 amino acid motif (EKKGIMDKIKEKLPG) forming amphiphilic α -helix has been found in all dehydrins. The pathways of regulation of dehydrin gene expression, putative functions of dehydrins, and molecular mechanisms of their actions are discussed.

Key words: dehydrins, desiccation, stress factors, abscisic acid

The evolution of plants has resulted in the elaboration of protective mechanisms responsible for adaptation to constantly changing environmental conditions of growth. Stress-induced changes in expression of certain genes represent the genetic basis for the development of the protective reactions. It is well known that intensity of growth and development of plants depends on their water supply. However, dehydration is a normal process during seed maturation, which is realized by programmed expression of specific genes and the phytohormone abscisic acid (ABA) plays a key role in the regulation of this process. Several genes specifically expressed in this ontogenetic period have been recognized. They include genes encoding so-called LEA (Late Embryogenesis Abundant) proteins. LEA proteins have been found in ABA treated vegetating plants and also under the stress conditions that result in cellular dehydration such as drought, salinity, and low temperatures. That is why LEA proteins can be considered as stress proteins. Dehydrins represent one of the groups of the LEA protein family, which are involved in reactions of plants to drought, salinity, and dehydration. In the present review we have summarized current knowledge on structure, properties, and functional importance of dehydrins.

A previously unknown protein population found in embryos at late stages of embryogenesis was originally

described by Dure et al. [1-3]. These proteins were called LEA (late embryogenesis abundant) proteins. Usually these proteins are not seen in premature embryos and young seedlings. It is interesting that appearance of the LEA proteins in embryonal tissue depends on content of endogenous ABA, whose level is usually increased during seed formation and especially before their maturation. That is why LEA proteins have been called ABA-inducible proteins. For example, in mature cotton-plant seeds 18 LEA mRNA have been identified, and 13 of these were induced by ABA treatment in premature embryos [3]. Later the existence of LEA proteins was also found in other plant species representing various taxonomic groups [4-10]. This implies wide distribution of LEA proteins in the plant kingdom.

The fact of intensive synthesis and accumulation of LEA proteins in seeds at the late stages of their maturation, during dehydration, suggests the involvement of these proteins in protective reactions promoting maintenance of embryo structures under conditions of water deficit [11]. The existence of genes encoding LEA-proteins in the genetic programs controlling normal seed maturation is very "useful" for the vegetating plants because impairments of water balance (e.g., under drought and low temperature conditions) are always accompanied by induction of LEA proteins; (the latter is also observed during ABA treatment) [12]. This suggests involvement of LEA proteins in protection of plant cells

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against damage induced by dehydration, but particular functions of these proteins are still unknown and represent a field for various speculations [13-17].

STRUCTURE AND PROPERTIES OF DEHYDRINS

LEA proteins of group II [10, 17], also known as the D-11 family of LEA proteins [11], are the most studied among drought-induced water-soluble proteins. These proteins have been called "dehydrins" [18]. Dehydrins have been isolated and purified from maize seeds [19, 20], vigna seeds [21], from barley and maize seedlings [18], and from bark tissue of peach [22]. Arabidopsis dehydrins RAB18, LTI29, LTI30, and COR47 [23] and wheat dehydrin WCOR410 [24] have been isolated from recombinant *E. coli* cells. Isolation and purification of native dehydrins allowed the investigation of their biochemical properties *in vitro*. These proteins are characterized by a wide range of molecular masses from 9 to 200 kD [10, 25]. Dehydrins are thermostable and maintain their integrity in aqueous solutions at up to 100°C. Generally, dehydrins are enriched with glycine and lysine residues, but they lack cysteine and tryptophan [22]. Analysis of the amino acid composition of a 35 kD dehydrin isolated from seedlings of cowpea (*Vigna unguiculata*) revealed that (apart from absence of cysteine and tryptophan), it is characterized by a high content of glycine, threonine, asparagine, glutamine, serine, and aspartic and glutamic acids; this explains the highly hydrophilic nature of this protein [21]. In arabidopsis LTI30 dehydrin with molecular mass of 21 kD, glycine, histidine, lysine, and threonine represent 56% of the total amino acids, whereas cysteine, tryptophan, arginine, and valine were not found [23].

The existence of conservative sequences denominated as K-, S-, and Y-segments [10] are structural features of dehydrins (and the presence of a K-segment is obligate for all dehydrins). The K-segment is a highly conservative Lys-rich motif that consists of 15 amino acid residues (EKKGIMDKIKEKLP). However, some single amino acid substitutions and structural modifications may occur within the segment. For example, sequencing of cloned cDNA fragments and analysis of corresponding amino acid sequences revealed that the K-segment from *Pseudotsuga menziesii* dehydrins consists of the following amino acids (Q/E)K(P/A)G(M/L)LDKIK(A/Q)(K/M)(I/L)PG [15, 26].

Computer-aided analysis of amino acid sequences of K-segments demonstrated the possibility of formation of amphipathic α -helix [14]. Circular dichroism (CD) data also support formation of secondary α -helical structure by the K-segments. For example, the CD spectrum of vigna dehydrin suggests that in the presence of 10% SDS up to 15% of amino acids are involved in formation of secondary α -helical structure [21]. Similar results have

been obtained for maize dehydrin G50 [19]. Interestingly, this protein lacking any hydrophobic sites may be involved in hydrophobic interactions. This suggests that the potential ability for hydrophobic interactions may be attributed to formation by K-segment of secondary structure as amphipathic α -helix, which combines hydrophilic and hydrophobic features [19]. In dehydrins the number of K-segment repeats may vary from 1 to 12 [10, 15, 23]. Thus, in spite of initial designation of dehydrins as dehydration-induced proteins, only K-segment proteins are now referred to this group.

Many dehydrins contain an S-segment that consists of serine residues; this site may be phosphorylated. The latter was demonstrated for maize RAB17 and tomato TAS14 dehydrins [20, 27, 28]. Phosphorylation of S-segment is suggested to promote dehydrin interaction with specific signal peptides followed by their translocation into the nucleus [10, 15, 29]. The N-terminal region of many dehydrins contains another conservative sequence, the Y-segment. This sequence, (V/T)DEYGNP, shares significant homology with the nucleotide-binding site of plant and bacterial chaperones; however, binding of dehydrin Y-segments with nucleotides remains to be well documented [10, 15].

Besides these three conservative segments, dehydrins also contain less conservative regions enriched with glycine and polar amino acid residues (especially threonine). These regions were named ϕ -segments [15, 21]. For example, the N-terminal region of maize RAB17 dehydrin contains paired ϕ -segments positioned between K-segments [15]. In some dehydrins ϕ -segments are localized as single copies between K-segments; they are enriched with proline and alanine residues (e.g., *Arabidopsis thaliana* COR47 protein [15]). Thus, the structure and size of dehydrin molecules, which can vary from 82 to 575 amino acid residues, is determined by combination and number of K-, S-, Y-, and ϕ -segments [10, 15].

CLASSIFICATION OF DEHYDRINS

The classification of dehydrins proposed by T. J. Close [10] is based on the presence of highly conservative segments. According to their combination, dehydrins have been subdivided into five classes: Y_nSK_2 , K_n , K_nS , SK_n , and Y_2K_n .

Y_nSK_2 dehydrins. This is the most abundant class of dehydrins that contain from one to three Y-segments, one S-segment, and two K-segments. These are basic or neutral proteins. They are induced by drought or ABA (but not by cold temperatures). For example, barley dehydrins DHN1, DHN2, DHN3, DHN4, DHN6, and DHN9 share the common structure YSK_2 . In seedlings they are accumulated in response to ABA treatment and dehydration, but their content remains unchanged during

hypothermia [30]. The barley dehydrin DHN12 also belongs to this class. Its gene is specifically expressed during the embryonal stage of development (i.e., it is not expressed in vegetative tissues even under stress conditions [31]).

K_n dehydrins. Dehydrins of this class contain from two to nine K-segments. These acidic or neutral proteins are induced by cold temperatures, dehydration, and ABA [10]. For example, blackberry K₅-dehydrin of molecular mass of 60-65 kD accumulates in flower buds during low temperature acclimatization [32]. Expression of barley *Dhn5B* gene encoding dehydrin K₉ is induced by low temperature treatment and to a lesser extent by drought and ABA [30, 33]. Soft wheat contains proteins of the WCS120 family (Wheat Cold Specific proteins), which are homologous to barley DHN5 dehydrin. Synthesis of proteins is specifically induced under low temperature and the level of their accumulation positively correlates with chilling tolerance of wheat and other cereals. WCS120 proteins differ from other dehydrins by the presence of a repeating glycine-rich motif: TGGTYQQGHTGTT [25].

SK_n dehydrins. Proteins of this class contain one S-segment and two or three K-segments [10]. They are acidic dehydrins, which are preferentially induced by low temperatures. For example, at 4°C the level of accumulation of WCOR410 protein (Wheat Cold Regulated Protein), which is an SK_n dehydrin, is significantly higher in winter wheat than in spring wheat plants [24]. The gene encoding barley acidic dehydrin DHN8 (a homolog of WCOR410 wheat protein) is actively expressed during low temperature treatment and to a lesser extent (than Y_nSK₂ proteins) during drought and ABA treatment [30]. Canadian fir dehydrin encoded by the *PgDhn1* gene is also an SK_n dehydrin. Increased expression of this dehydrin was observed in vegetative tissues during low temperature treatment, drought, salinity, wound stress, and treatment with jasmonate and methyl-jasmonate [34].

K_nS dehydrins. In contrast to dehydrins of other classes, the K-segment of K_nS dehydrins begins with the motif (H/Q)KEG (in others a similar site contains EKKG). This is the characteristic feature of these proteins. Expression of rice Wsi724 and medic Cas15a and 15b dehydrins that belong to this class is induced by dehydration and cold temperatures [10, 15].

Y₂K_n dehydrins. Acidic dehydrins of this class usually contain two Y-segments and one or two K-segments [10, 15]. These include vigna DHN1 dehydrin, which is associated with seed chilling tolerance during germination [35].

Some proteins cannot be assigned to a certain class of dehydrins. For example, chickweed leaves contain H26 protein, which has the SK₃S segment composition; it probably represents an intermediate form of proteins of SK_n and K_nS proteins [10]. One spinach protein has the following segment structure: YK₁₁. It shares some features of K_n-, Y₂K_n-, and K_nS-classes [10, 29].

Subdivision of dehydrins into several classes depending on their structural organization and biochemical properties was quite reasonable because of involvement of these proteins in plant response to various growing conditions. Synthesis of basic Y_nSK₂ dehydrins is induced by drought and ABA but not by low temperature treatments, whereas acidic dehydrins of K_nS, SK_n, and Y₂K_n classes are preferentially accumulated by plants in response to cold temperatures.

DISTRIBUTION OF DEHYDRINS

Dehydrins were initially found in flower plants [6, 18]. Immunological studies and screening of cDNA and genome libraries revealed the presence of dehydrins in other taxonomic groups [9, 26, 36-40]. Detection of dehydrins in various plant species can employ antibodies against synthetic polypeptide homolog of K-segment, the obligate component of dehydrins [8-10, 15, 29, 37]. In higher plants dehydrins are accumulated in seeds at later stages of embryogenesis and in vegetative tissues treated with ABA or subjected to stress factors (drought, salinity, and cold temperature). In lower plants dehydrin content is also increased under unfavorable environmental conditions. A certain correlation exists between the level of dehydrins and plant tolerance to dehydration. For example, cells of the drought-tolerant moss *Tortula ruralis* are characterized by increased constitutive expression of dehydrins [36]. In plants of the fern *Polypodium virginianum* and the moss *Exomotheca holstii*, dehydrin synthesis is induced by dehydration and ABA treatment [41, 42]. Immune analysis of the blue-green algae *Anabaena* and *Calothrix* cells revealed accumulation of 40 kD dehydrin in response to increase of salt concentration and polyethylene glycol addition to the cultivation medium [8]. Combination of constitutive and stress-induced dehydrin expression was found in the brown algae *Fucus spiralis*, *F. vesiculosus*, and *F. evanescens* [37] and the lichen *Selaginella lepidophylla* [15]. Thus, dehydrins are widely distributed in the plant kingdom. They have been found in the fungus *Pneumocystis carinii* (Accession No. NCBI CAC43457). Dehydrin homolog sequences were also found in *Escherichia coli* cells (Accession No. NCBI AAB18249), *Chlamidia trachomatis* [43], and even in *Drosophila melanogaster* cells [44].

REGULATION OF DEHYDRIN EXPRESSION

Dehydrin encoding genes are expressed in response to various stress-factors inducing moisture deficit. This implies the existence of many pathways for regulation of this process. Since stress-factors usually induce accumulation of ABA, treatment with this phytohormone also causes dehydrin gene expression in various plants [18, 30,

39, 41, 45-49]. So, dehydrins are referred to as RAB (Responsive to Absciscic acid)-proteins [6, 10, 15, 18, 46, 50, 51].

However, certain evidence exists that drought- and cold temperature-induced dehydrin genes were not expressed in plants treated with ABA [52-54]. Use of ABA-deficient sunflower mutants *nd-1* and *w-1* revealed that they accumulated transcripts of the *HaDhn1a* gene during seed embryogenesis and in seedlings subjected to water stress, and this accumulation was comparable to that found in wild type plants [55]. Thus, regulation of dehydrin gene expression occurs via ABA-dependent and ABA-independent pathways [30, 55-57].

Genes are sensitive to ABA due to the presence of certain *cis*-elements, known as ABA Responsive Elements (ABRE) in their promoters. These elements contain the ACGT sequence, denominated as the G-box; it should be noted that the presence of a single copy is not enough for ABA-dependent gene expression [30, 46, 50, 55, 58, 59]. For example, the promoter site of barley ABA-inducible *dhn1* gene contains a fragment, TACGTCCgccccagacgaGGCCGCG, which consists of a G-box and GC-motif; its removal was accompanied by loss of promoter sensitivity to ABA [60]. Promoter sensitivity to ABA also depends on the presence of the MYC-element, containing the CACCTG sequence, and the MYB-element, which contains the TAACTG-motif [46, 58]. Their presence was demonstrated during sequencing of promoter regions of barley dehydrin genes [30]. Responsiveness to ABA signals also requires ABRE coupling elements (CE) [46, 61]. It was shown that ABRE-elements interact with bZIP transcription factors [50, 59, 62]. ABA-induced gene expression probably involves MYC- and MYB-transcription factors interacting with corresponding *cis*-elements [46, 59] and also transcription factors VP/ABI3 [50, 59, 63, 64].

ABA-independent pathways of regulation of dehydrin gene expression are realized by specific sites, such as DRE (Drought-Responsive Elements) [65] also known as CRT (C-repeat)-elements [66, 67]. These elements were found in promoters of genes expressed in response to dehydration, salinity, and cold temperatures. In the barley dehydrin gene promoters the number of repeats of DRE-elements may vary from 1 to 3 [67]. CBF (CRT-Binding Factor)/DREB (DRE-Binding Factor) transcription factors interact with DRE/CRT-elements [67-70]. These factors regulate transcription activity of dehydrin genes [67, 71-73].

Promoters of wheat *wcs120* dehydrin genes induced by cold temperatures contain the CANNTG motif; these genes may have up to eight repeats of this motif [25], which is the binding site for bHLH class transcription factors. Some other factors, such as CPRF₃ (Common Plant Regulatory Factor) and GBF₃ (G-Box Binding Factor), which are related to bZIP proteins, also specifically interact with this motif [25].

MOLECULAR MECHANISMS RESPONSIBLE FOR PROTECTIVE EFFECTS OF DEHYDRINS

Although functions of dehydrins remain unknown, their induction in vegetative tissues during cell dehydration suggests their involvement in protective reactions. In fact, during water deficit transcription activity of sunflower dehydrin gene *HaDhn2* is significantly higher in drought-tolerant than in drought-sensitive lines [74]. The dependence between drought-tolerance of plants and dehydrin accumulation was also found in sorghum plants [75]. In salinity-tolerant rice lines, the level of ABA-induced dehydrin expression was significantly higher than in sensitive plants [76]. Many plants demonstrate a direct interrelationship between the level of dehydrins and cold-tolerance [16, 22, 25, 32, 52, 77-82].

Cold-tolerance of plants depends on the level of starch accumulation. Starch is the main source of di- and monosaccharides that protect cells against dehydration-induced damages. So, maintenance of active α -amylase is a very important factor for starch degradation. Interestingly, in wooden plants starch degradation occurs even at temperatures below 0°C [83]. Cold acclimatization of birch seedlings is accompanied by accumulation of a dehydrin of 24 kD in amyloplasts. *In vitro* experiments revealed that the presence of this protein promoted maintenance of catalytic activity of α -amylase and appropriate level of starch hydrolysis during temperature decrease [81]. This suggests that dehydrins maintain adequate local water concentration near α -amylase, which is an important precondition for enzyme-substrate complex formation and starch degradation [81]. This water-retaining capacity of dehydrins is also supported by studies of the effect of peach PCA60 dehydrin on the shape of ice crystals, decrease in temperature, and the rate of their formation [22]. So, it is reasonable to draw a certain analogy between dehydrins and arctic fish antifreeze proteins. α -Helical sites of these proteins determine their affinity to the surface of ice crystal lattice, and this prevents subsequent growth of the ice crystals [22]. Cryoprotective activity of dehydrins was also demonstrated for cold-induced spinach CAP85, wheat WCS66, and peach PCA60 dehydrins, which were able to prevent inactivation of rabbit lactate dehydrogenase induced by a freeze-thaw cycle [84, 85, 22]. Administration of cold-inducible dehydrin gene *cor15a* into arabidopsis plants increased tolerance of isolated protoplasts and chloroplasts to freezing [86, 87].

Dehydrins are involved in osmotic regulation of plant cells. For example, study of various tissues of arabidopsis revealed that in stoma closing cells RAB18 dehydrin prevents water loss in nuclei during increase of osmotic pressure in cytoplasm at opened stomas; LTI29 and ERD14 dehydrins accumulating in root tips increase water flow to dividing meristematic cells [39]. Dehydrin involvement in regulation of osmotic potential of plant

cells is possibly related to their synthesis during water stress [39].

Specific functions of dehydrins may be attributed to their particular localization in the cell. Dehydrins are localized in cytoplasm and nucleus [10, 15]. This was clearly demonstrated for wheat WCS120, maize RAB17, and tomato TAS14 dehydrins [25, 27, 28], peach PCA60 dehydrin [22], and birch 24 kD dehydrin [81]. Immunomicroscopic studies revealed that treatment of maize seeds with ABA for 15 min resulted in dehydrin accumulation in cytoplasm; during prolonged treatment they were detected in nucleus, and the maximal increase in dehydrin level in the nucleus and cytoplasm was observed after 48 h incubation with ABA [88]. In the nucleus dehydrins were associated with heterochromatin, euchromatin, nucleoplasm and nucleoli; in cytoplasm they were found mainly in cytosol, some quantity of dehydrins was also detected in organelles [88].

Nuclear localization of dehydrins in plant cells is associated with their protective role in stabilization of transcription machinery to unfavorable conditions. For example, pea embryo p16 dehydrin with molecular mass of 16 kD was isolated from the fraction of histone H3; this suggests involvement of this dehydrin in mechanisms responsible for structural integrity of chromatin during cell desiccation in the process of seed formation [89, 90]. Mechanisms underlying dehydrin translocation into the nucleus are not perfectly understood, but certain evidence exists that S-segment is involved in this process. For example, the stretch from amino acid residues 66 to 96, which contains S-segment with adjacent protein kinase CK2 recognition site and a sequence sharing similarity with NLS (Nuclear Localization Signal) viral signal peptides was identified in maize RAB17 dehydrin [91]. Since mutations of two amino acid residues in the putative NLS-fragment attenuated RAB17 dehydrin translocation into nucleus and mutations of three amino acid residues in protein kinase CK2 binding site completely blocked dehydrin phosphorylation and its transportation into the nucleus, it was concluded that maize RAB17 dehydrin translocation into the nucleus requires phosphorylation of serine residues in the S-segment; (the involvement of NLS-like sequences in this process is also possible) [91]. Dehydrins of wheat WCS120 family lack S-segment and the corresponding signal sequences and so it is proposed that the wheat dehydrins are translocated into the nucleus via protein–protein interactions [25].

It should be noted that not all dehydrins have been found in the nucleus. For example, cold-induced wheat WCOR410 dehydrin is located on the outer surface of the plasma membrane and in intercellular space (but not inside cells); it is a peripheral rather than an integral protein. In this connection, a reasonable question arises: how are WCOR410 dehydrins delivered to their correct destination [24]? Sequencing of this dehydrin revealed the presence of significant amounts of acidic and hydroxyl-

containing amino acids. This may determine the ability of the protein for interaction with membrane phospholipids and steroids [24]. Dehydrins can be associated not only with plasmalemma, but also with intracellular membrane structures (as shown for parenchymal cells of maize scutellum [88] and onion epidermal cells [15]). Membrane localization of dehydrins may suggest their involvement in stabilization of cell membrane structures; this is especially important under unfavorable (environmental) conditions [10, 15]. Maintenance of spatial organization of biological membranes involves structured water molecules [92]. The dehydration process may damage integrity of hydrate cover of macromolecules; this, in turn, may result in shortening of the distance between membrane bilayers, mixing their components and finally to irreversible changes in the structure of biomembranes [93]. Interaction between dehydrins and membrane macromolecules with damaged hydrate cover may exert a protective effect on the membrane structures [10, 15, 24].

Structural features of dehydrins suggest their involvement in hydrophobic and hydrophilic interactions. Due to the presence of K-segments forming amphiphilic α -helix, dehydrins may interact with lipid components of biomembranes and (like chaperones) with hydrophobic sites of partially denatured proteins [10, 15, 94]. Dehydrins may also interact with water-soluble low molecular weight components of cytoplasm and polar groups of proteins [10, 15]. Maize G50 dehydrin is an example of a dehydrin demonstrating hydrophobic interactions [19]. The presence of ϕ -segments may also increase hydrophilicity of dehydrin structure. Since ϕ -segments are characterized by increased proportion of polar amino acid residues, they may be involved in hydrophilic interactions between dehydrins and polar groups of macromolecules and also between dehydrins and such low molecular weight components of nucleoplasm and cytosol as sugars, amino acids, and water molecules. Due to the presence of K- and ϕ -segments, dehydrins may prevent further denaturation and aggregation of partially denatured macromolecules by forming a protecting shell; this stabilizes cell structures at all levels of their organization [10, 15].

Putative functions of dehydrins also include involvement in detoxification of salt ion excess observed during cell dehydration. It was shown that RAB18, LTI29, LTI30, and COR47 dehydrins from *Arabidopsis thaliana* can interact with Cu^{2+} and Ni^{2+} . The dehydrin LTI30 can also bind Co^{2+} and Zn^{2+} ; however, it should be noted that these dehydrins lack any specific metal-binding motifs. Metal ion binding capacity of *Arabidopsis thaliana* dehydrins may be attributed to the presence of a high number of histidine residues [22]. Wheat WCOR410 dehydrin contains up to 43% of charged amino acid residues, which may be involved in ion binding; this reduces the probability of sedimentation and crystallization of cell sap salts during dehydration [24]. These data may serve as an argument for the chelating functions of dehydrins.

Thus, dehydrins are characteristic proteins of late ontogenesis. They play an important role in seed desiccation during the maturation period and so they have been pooled into an independent group of proteins. Accumulation of dehydrins in vegetating plants in response to cold temperatures, salinity, and moisture deficit attracts much interest in relation to possible protective functions of dehydrins under conditions of cell dehydration. Dehydrin gene expression is regulated by ABA, and so these proteins are considered as components of the ABA-controlled anti-stress subprograms. Detailed study of structural organization of dehydrins revealed the existence of repeated conservative domains providing specific spatial configuration that underlines dehydrin involvement in the reactions preventing loss of water. Dehydrins are widely distributed in plants. They significantly vary in amino acid composition (from 100 to 600 amino acid residues) and by molecular mass. The amino acid composition of these proteins is characterized by high content of charged and polar residues, and this determines their biochemical properties including thermostability. This may promote their specific protective functions under conditions of cell dehydration: dehydrins may prevent coagulation of macromolecules and maintain integrity of crucial cell structures. Many researchers consider dehydrins together with other proteins accumulating in plant cells during water cells. These include some emulsifiers and chaperones stabilizing macromolecule surface in the cells. However, the precise physiological functions of dehydrins remain to be clarified.

This work was supported by the Program for Support of Leading Scientific Schools (00-15-97899, 00-15-97810, NSh - 1785.2003.4, NSh - 2217.2003.4).

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