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# Functional Diversity of Early Responsive to Dehydration (ERD) Genes in Soybean

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## 1. Introduction

In many regions of the world, agriculture is the primary consumer of water. As the world population increases, and arid regions become more abundant, water will become an increasingly scarce resource [1]. In 2011, the world's soybean crops produced 263.7 million tons from an area of 103,5 million hectares [2]. This global production required an input of 0,2 to 0,25 inch of water per acre per day during peak demand, which represents a major problem for the producer countries [3]. In Brazil, the second largest soybean producer in the world, there was a 7% reduction in soybean production in 2011/2012 compared to the previous season. This yield loss can be attributed to drought in the soybean-growing regions of the country, which in turn resulted in increased use of irrigation water in an attempt to minimize yield losses [4].

Understanding the molecular consequences of drought on soybean plants can accelerate breeding programs aimed at increasing productivity and decreasing the negative impacts of climate change on this important crop. Several classical physiology reviews from recent decades consolidated knowledge of the relationship between leaf structure and function during drought stress [5,6], the morphology of the root during stress tolerance [5,6] and other aspects of the effects of drought on plant morphology. Understanding the physiological responses of plants undergoing drought stress is essential to understanding their ability to survive the water shortage.

In recent years, due to advancements in plant molecular biology methodologies, molecular aspects of drought tolerance have received special attention from researchers [7]. To date, hundreds of genes that are induced by drought stress have been identified and a range of genetic, biochemical and molecular assays (gene expression profiles, transgenic plants, and various functional assays), are being used to elucidate the roles of these genes in response to

drought. However, the complexity of the plant response to drought stress makes it difficult to identify genes that are responsible for drought tolerance [7]. In physiological terms, drought stress is characterized by reduction in plant water content, decrease in water potential, loss of leaf turgor, stomata closure and reduction in cell growth [8]. Conditions of severe and prolonged drought result in cessation of photosynthesis, metabolic disorder, and finally plant death [8].

Many abiotic stresses such as high salt levels and low temperature have similar physiological consequences to drought, and therefore similar signaling pathways are induced [7]. The similarity of the cold and drought stress response is illustrated by the observation that plants subjected to drought stress display an increase in frost tolerance [9]. An increase in osmotic pressure is common to these abiotic stresses [10]. The increased osmolarity induces transcription of genes encoding proteins involved in synthesis of osmo-protective compounds, lipid desaturases and transcription factors [11]. Several of these genes have been frequent targets of genetic engineering in breeding programs aimed at producing cultivars with increased tolerance to these adverse conditions [11]. These genes are also induced by other environmental factors such as high salinity and chemical signals such as abscisic acid (ABA), the main phytohormone related to abiotic stress responses in plants.

ABA serves as an endogenous messenger in response to biotic and abiotic stress in plants. Drought results in production of high levels of ABA, accompanied by a major shift in global gene expression in plant cells and, consequently, an adaptive physiological response to the stress [12]. In addition to stress, ABA also controls other important and finely regulated processes such as growth and development, structure and regulation of stomatal function and seed dormancy [13]. During regulation of plant development, ABA also acts in intricate cross-communication with other important phytohormones, such as gibberellic acid, ethylene, auxin and brassinosteroids [13].

How and what environmental stimuli are perceived and result in changes in physiological levels of ABA is still a difficult issue. Drought stress provides an immediate hydraulic signal to the plant, which activates ABA biosynthesis over a great distance [14]. High humidity activates cytochrome P450 enzymes that catalyze ABA synthesis minutes after perception of the stress [15]. Recent studies have shown the importance of the transport driven by absorption and export of ABA. Upon perception of the stress signal, ABA synthesis is primarily induced in vascular tissues, and ABA is exported from the site of biosynthesis to other cells. The absorption is stimulated by ATP-dependent ABC-family transporters. This mechanism allows rapid distribution of ABA to the surrounding tissues [16,17].

Although expression of many genes is induced by ABA-dependent responses to drought, cold and salinity stresses, upregulated genes can be sub-grouped according to the stress they were found to respond to and also by the timing of induction post stress. Genes included in the RD group (responsive to dehydration) include the drought-induced gene RD26, which encodes a NAC (NAM/ATAF/CUC plant protein domains)-family transcription factor [18], ERD (early responsive to dehydration), which includes a gene that encodes a Clp protease [19]. The COR (cold regulated), LTI (low-temperature induced) groups of genes include LOS2, which encodes a bifunctional enolase [20]. The KIN (cold inducible) group of

genes includes SCOF-1, which encodes a protein with a zinc finger domain [21]. The KIN group also contains groups of genes, which also respond to osmotic stress [22-23, 7]. The products of many of these genes are most likely the main components of the first line of plant defense against potential structural damage, or they may be components of signaling pathways such as transcription factors or protein kinases. An example is induction of the gene COR15a; the Arabidopsis homolog ERD1 prevents the injury to the chloroplast membrane [24]. Another gene, GmERD15, from the ERD15 gene family in soybean, acts as a transcription factor, which regulates gene transcription related to programmed cell death [25].

## 2. The Early Responsive to Dehydration (ERD) genes and their functional diversity

The ERD genes are defined as those genes that are rapidly activated during drought stress. The encoded proteins show a great structural and functional diversity and constitute the first line of defense against drought stress in plants (Table 1).

To date, a total of 16 complementary DNAs (cDNAs) for ERD genes have been isolated from 1-h-dehydrated Arabidopsis thaliana and only half of these are characterized in soybean. These genes encode proteins that include ClpA/B adenosine triphosphate (ATP)-dependent protease, heat shock protein (HSP) 70-1, S-adenosyl-methionine-dependent methyltransferases, membrane protein, proline dehydrogenase, sugar transporter, senescence-related gene, glutathione-S-transferase, group II LEA (Late Embryogenesis Abundant) protein, chloroplast and jasmonic acid biosynthesis protein, hydrophilic protein, and ubiquitin extension protein.

Gene / GenBank accession number	Function	Reference	Best hit on soybean genome / E value.	Similar genes in soybean
ERD1/D17582*	ClpA/B ATP-dependent protease	[26]	Glyma04g38050.1/ 8.9e-54	45
ERD2*/M23105	Heat shock protein (hsp70-i)	[26]	Glyma12g06910.1/ 1.7e-37	45
ERD3/NP_567575.1*	Methyltransferase PMT21	[27]	Glyma01g35220.4/ 1.7e-99	100
ERD4/NP_564354.1	Integral membrane protein	[28]	Glyma15g09820.1/ 1.8e-61	28
ERD5/D83025	Precursor of proline dehydrogenase	[29]	Glyma18g51400.1/ 2.1e-27	5
ERD6/D89051	Sugar transporter	[30]	Glyma03g40160.1/ 6.15e-2	100

Gene / GenBank accession number	Function	Reference	Best hit on soybean genome / E value.	Similar genes in soybean
ERD7/NP_179374.1	Senescence/dehydration related protein	[31]	Glyma01g36960.1/ 3.5e-43	9
ERD8/Y11827	Heat shock protein hsp81-2)	[26]	Glyma08g44590.1/0	22
ERD9/NP_172508.4*	Glutathione-S-transferase	[32]	Glyma01g04710.1/ 9.9e-22	87
ERD10/D17714*	Group II LEA protein (Iti29/Iti45)	[33]	Glyma04g01130.1/ 4e-8	3
ERD11/D17672	Glutathione-S-transferase	[32]	Glyma02g17340.1/ 1.7e-5	52
ERD12/NP_189204.1*	Allene oxide cyclase	[40]	Glyma02g11020.1/ 2.3e-36	6
ERD13/D17673	Glutathione S-transferase	[32]	Glyma08g41960.1/ 3.7e-39	63
ERD14/D17715	Group II LEA protein	[33]	No homologs identified	0
ERD15/D30719*	Hydrophilic protein	[35]	Glyma04g28560.1/ 3.5e-26	4
ERD16/J05507*	Ubiquitin extension protein	[33]	Glyma03g35540.1/ 6.6e-50	100

**Table 1.** ERD genes and their homologs in soybean. (\*) Indicates the characterized genes in soybean.

The ERD gene family has been collectively characterized as genes that are rapidly induced by dehydration [26]. ERD1 encodes a chloroplast ATP-dependent protease [26] and ERD2 encodes a, HSP70 [26], ERD3 encodes a methyltransferase in the pMT21 family [27], ERD4 encodes a membrane protein [28], ERD5 and ERD6 encode a mitochondrial dehydrogenase proline protein and a carbohydrates carrier protein, respectively [29-30]. ERD7 encodes a protein related to senescence and dehydration [31], ERD8 encodes a hsp81-family protein [26], ERD9, 11 and 13 belong to the family of glutathione S-transferase [32], ERD10 and 14 belong to the LEA protein family [33], ERD15 was first classified as a hydrophilic protein [34], which has a PAM2 interaction domain which interacts with poly-A tail binding proteins (PABP) [35].

ERD15 from Arabidopsis has been functionally characterized as a common regulator of the abscisic acid (ABA) response and salicylic acid (SA)-dependent defense pathway [35]. Overexpression of ERD15 reduced ABA sensitivity, as the transgenic plants had reduced drought tolerance and failed to increase their freezing tolerance in response to hormone treatment [35]. In contrast, loss of ERD15 function due to gene silencing caused hypersensitivity to ABA, and the silenced plants displayed enhanced tolerance to both drought and freezing. The antagonis-



tic effect of ERD15 activity on ABA signaling enhanced SA-dependent defense; overexpression of ERD15 was associated with increased resistance to the bacterial necrotroph *Erwinia carotovora* and enhanced induction of systemic acquired resistance reporter genes [35]. The authors also addressed the antagonistic effect of ABA on SA-mediated defense by demonstrating the enhanced expression of reporter genes for systemic acquired resistance in the plant null mutants *abi1-1* and *abi2-1*, which are defective for ABA metabolism. These results together implicate *Arabidopsis* ERD15 as a shared component of ABA- and SA-mediated responses. The ERD15 homologs from *Solanum lycopersicum* are 98% identical and belong to the same group as *Arabidopsis* ERD15, indicating a possible conservation of function [36]. Nevertheless, the tomato protein clearly localizes to the nucleus and confers freezing tolerance when ectopically expressed in transgenic tomato plants. These phenotypes are in marked contrast with the phenotypes displaying by ERD15-overexpressing *Arabidopsis* lines [35]. These contrasting results in transgene overexpression studies suggest that the *Arabidopsis* and tomato ERD15 homologs have divergent functions. Finally, a soybean homolog, GmERD15, has been described as an ER stress- and osmotic stress-induced transcription factor that activates the promoter and induces the expression of the NRP-B gene. These results indicate that GmERD15 functions as an upstream component of the NRP-mediated cell death signaling pathway, which is induced by ER and osmotic stress [37].

ERD16 encodes a ubiquitination extension protein [33]. Previous studies also showed that ERD13/AtGSTF10, a plant phi specific class GST (Glutathione S-transferase) is an interaction protein with BAK1 (BRI1 Associated receptor Kinase 1). BAK1 is a co-receptor, which forms a receptor complex with BRI1 (brassinosteroid (BR) receptor) to regulate brassinosteroid signaling in *Arabidopsis*. Overexpression of AtGSTF10 resulted in plants with increased tolerance to salt stress. In contrast, silencing AtGSTF10 by RNAi caused increased tolerance to abiotic stress and accelerated senescence of the transformants [38]. These findings suggest that modulation of ERD13/AtGSTF10 may regulate plant stress responses by regulating brassinosteroid signaling via interaction of AtGSTF10 with BAK1. ERD10 and 14 have chaperone activity, which aid in protein folding during stress [39]. ERD12 encodes a protein with homology to an allene oxide cyclase [40].

With respect to expression controlled by phytohormones, ERD genes present varied functions and responses in ABA signaling, some being sensitive to ABA during germination and development [41], and /or are involved in stress tolerance [42]. Other genes are induced in response to more than one phytohormone [35]. Early Responsive to Dehydration 15 (ERD15) was characterized as a negative regulator of ABA and is induced by ABA, SA, injury and pathogen infection [35]. ABA application increases the expression of some members of the ERD group including ERD10 and 14 [34] while causing no effect on others, such as ERD2, 8 and 16 [33].

Some contradictory data regarding the induction, as well as the function, of ERD genes are present in the literature [35-37]. Reduced expression of the ERD15 gene in response to wounding was reported [43], while an increased number of ERD15 transcripts were observed by other authors [35]. Furthermore, *Arabidopsis* plants showed increased tolerance to salt stress through the overexpression of AtSAT32, a key gene in the salinity-tolerance family *Arabidopsis*. These plants showed an increase in the number of ERD15 transcripts

relative to control plants [44]. Transgenic wheat plants over-expressing TaDi19A, a gene responsive to salinity in wheat, exhibited increased expression of ERD15 [45]. In contrast to these findings, Arabidopsis plants over-expressing ERD15 demonstrated susceptibility to drought and freezing [35]. In regard to function, a soybean ERD15 homolog was characterized as a transcription factor [25], a function not previously attributed to this protein family, as reported by Kariola and colleagues [35] and Ziaf and colleagues [36].

### 3. The ERD genes studied in soybean

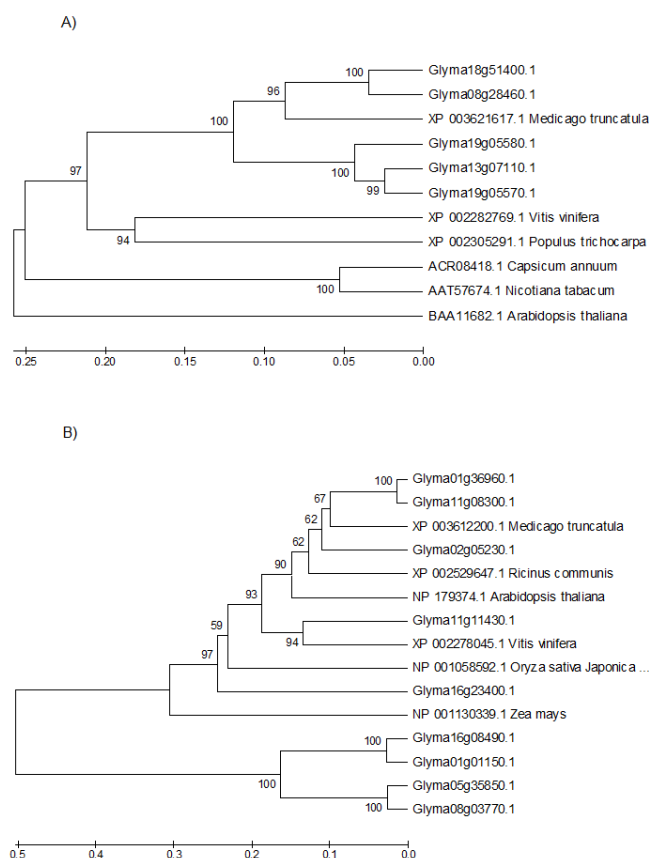
In respect to ERD genes described in soybean, the behavior of a group of eight genes (ERD1, ERD2, ERD3, ERD9, ERD10, ERD12, ERD15 gene and ERD16) was studied in response to stress. A soybean cDNA ERD1, homologous to yeast Hsp104, was isolated and characterized [46]. The soybean genes encoding homologs to yeast Hsp104 and Hsp101 have a high level of sequence identity to members of the family Clp [46]. When heterologously expressed in yeast, the soybean Hsp101 gene conferred greater thermotolerance to yeast [46]. Several genes related to Hsp70 (ERD2) have been described in soybean using proteomics studies. The first evidence of an ERD2-like protein in soybean was found during heat shock [47]. The presence of similar proteins was also found in response to osmotic and reticulum stress [48]. In respect to the orthologs of ERD3 in soybean, it was found that the GmIMT gene, which encodes a methyltransferase, acts by methylating the substrate D-ononitol. Its overexpression in Arabidopsis causes an increase in drought and salinity tolerance [49]. When a gene encoding a soybean GST, an ortholog of ERD9, was over-expressed in tobacco plants, it conferred an increase in salinity and drought tolerance [50].

Group 2 LEA (dehydrins or responsive to abscisic acid) proteins, such as ERD10 proteins, are postulated to protect macromolecules from damage by freezing, dehydration, ionic, or osmotic stress. In soybean, proteins of this group were studied for their structural and physio-chemical properties but little is discussed regarding the function of these proteins [51]. Overexpression of a member of the ERD12 family, GmAOC5, significantly increased oxidative stress resistance [52]. Within the ERD15 family, a soybean ortholog, GmERD15 has been functionally characterized as a transcription factor; in response to osmotic stress, GmERD15 acts to control transcription of a gene related to an integrative pathway in soybean [25]. Finally, orthologs of ERD16 studied in soybean genes were identified with differential expression during flood stress and hypoxia [53]. All genes studied related to different levels in response to stress, particularly drought and osmotic stress, demonstrating the conservation of function of this gene family in different plant species.

Some ERD genes not yet studied in soybean deserve special attention because of either the proven involvement of a gene with similar functions in drought response in other organisms, or due to multiple copies of the soybean homolog. ERD5 and ERD7 family members have been characterized by activity in response to drought in other organisms (discussed below). They have not been studied in soybean; however, homology to soybean genes is demonstrated by the phylogenetic tree shown in Figure 1.

ERD5 (which encodes a precursor of a proline dehydrogenase), has five orthologous genes in soybean. ERD5 has a proven role in drought response due to its role in accumulation of proline [54], a common occurrence during osmotic stress. All soybean genes are clustered in a group distinct from orthologs in other species (Figure 1), which may reflect a possible functional divergence.

ERD7 (which encodes a protein related to senescence and dehydration) has nine orthologous genes in soybean. It also has a central role in response to drought and osmotic stress and it is related with drought-induced leaf senescence in plants [55]; regulation of this process during drought tolerance has been studied in depth [55]. Phylogenetic analysis of these genes suggests the possibility of functional divergence of these genes within the same organism.



**Figure 1.** Relatedness of ERD5 (panel A) and ERD7 (panel B) proteins from different plant species. The multiple alignment was made using ClustalW, and the dendrogram was built with the MEGA5 software using the UPGMA method. The numbers at the nodes indicate the bootstrap scores. The proteins accession numbers are indicated.

## 4. Conclusion

Many studies on the roles and importance of ERD genes in soybean have become necessary due to lack of information about the importance of this group of genes during plant re-



sponse to drought. The common feature of these genes is that their expression increases rapidly in response to drought stress, suggesting that it is the first line of defense for plants against drought stress. It also suggests these genes may function to regulate expression of effector proteins and signaling pathways in response to stress.

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