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Plant annexins: Structural diversity, evolution, and multifunctional roles in development and stress tolerance

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Abstract

Annexins are an evolutionarily conserved multigene family of Ca^{2+}-dependent, phospholipid-binding proteins distributed across prokaryotes, fungi, plants, and animals. Structurally, all annexins share a conserved calcium-binding core domain along with variable amino-terminal regions that play crucial roles in post-translational modifications and protein-protein interactions. In plants, annexins have emerged as multifunctional proteins involved in growth, development, and adaptive responses to environmental challenges. Increasing experimental evidence indicates that plant annexins participate actively in abiotic stress tolerance by modulating calcium signaling, maintaining cellular redox homeostasis, and protecting membrane integrity. Several annexin members exhibit peroxidase activity and contribute to reactive oxygen species detoxification, thereby alleviating oxidative damage under stress conditions. Moreover, annexins have been shown to enhance tolerance to drought and salinity through osmotic adjustment and regulation of stress-responsive pathways. This review summarizes current knowledge on the structural and functional attributes of plant annexins and highlights their pivotal roles in mediating plant responses to abiotic stresses.

Keywords: Annexinsm calcium signaling, plant stress tolerance, oxidative stress, osmotic stress, reactive oxygen species, abiotic stress, gene family, transgenic plants

Introduction

Annexins are an evolutionarily conserved multigene family of Ca^{2+}-dependent, phospholipid-binding proteins (Tong *et al.*, 2025) [46] found in prokaryotes, fungi, plants and animals (Mortimer *et al.*, 2008; Huh *et al.*, 2010) [36, 23]. Significant homology between eukaryotic annexins and alpha-giardin proteins of unicellular protozoan *Giardia lamblia* evidence annexins existence back ~1-1.5 billion years ago (Morgan and Fernandez, 1995) [35]. The annexins superfamily has been classified into annexins in vertebrates (A family), in invertebrates (B family), in fungi and few unicellular eukaryote groups (C family), in plants (D family), and in protists (E family). Additional gene subfamilies have been emerged as a result of extensive and independent lineage-specific gene (or) genome duplication which is evident through their molecular phylogeny, gene structure and chromosomal distribution (Warmus *et al.*, 2026, Moss and Morgan, 2004) [48, 37]. Annexins are abundant in plants representing 0.1% of their total cell protein and resemble animal annexins in size and activities. Partial peptide sequences of annexin proteins precipitated in the presence of Ca^{2+} and phosphatidylserine in tomato, corn and lily showed homology to sequences found in animal annexins (Davies, 2014) [10].

Structural features

Structurally, all annexins have a common core domain made up of four identical domains/repeats of ~ 70 amino acids long. Each domain/repeat is made up of five short α helices which are wound into a right-handed super-helix and contains a characteristic type II motif (conserved endonexin sequence of GxGT-(38 residues)-D/E) for binding calcium ions (Shail and Prasad, 2022) [42]. These α helices are joined together by short loops, which are essential for Ca^{2+}-annexin interactions (Laohavisit and Davis, 2011) [31]. Annexins also contain a variable long amino-terminal region with sites for post translation modifications and interaction with other proteins (Yan *et al.*, 2026 Moss and Morgan, 2004) [51, 37].

Annexin resembles a flattened disc like structure on which Ca^{2+} binding motifs are located towards convex surface and amino and carboxyl termini towards concave surface. In plant annexins, characteristic type II motif for binding calcium ions present in the first and fourth repeats only (Moss and Morgan, 2004; Jami *et al.*, 2012) [37, 24]. Recent biochemical analysis and three-dimensional crystal structure studies shown that plant annexins exhibit Ca^{2+} dependent phospholipid membrane binding via domain I and IV (Hofmann *et al.*, 2000, 2003; Hu *et al.*, 2008) [20, 19, 22]. Plant annexins also contain short amino-terminal region (~10 amino acids) which have the sites for post-translational modifications and protein-protein interactions. This amino-terminal tail is thought to be the regulatory domain which may confer specific functions upon each annexin member (Liemann and Huber, 1997) [34]. Lack of long amino-terminal region and predicted calcium binding sites in their second and third domains made up plant annexins a monophyletic cluster in contrast to annexins of vertebrates (Moss and Morgan, 2004; Jami *et al.*, 2012) [37, 24]. Presence of motifs responsible for calcium channel and actin binding activity as well as peroxidase and ATPase/GTPase activity in plant annexins has been confirmed through sequence analysis (Mortimer *et al.*, 2008) [36].

Annexins in plants

Annexins are abundant cellular proteins found mainly in cytoplasm, cell organelles (nucleus, Golgi apparatus, chloroplast) and in the membrane system (ER, secretory vesicles, plasma membrane) and are suggested to play a role in wide variety of essential cellular processes (Yan *et al.*, 2016) [50]. Though plant annexins were first identified, thirty years ago in tomato (Boustead *et al.*, 1989) [3], only limited information of annexin gene families is available till now and so far only *Arabidopsis thaliana* and *Brassica juncea* annexin gene families have been well characterized (Clark *et al.*, 2001; Cantero *et al.*, 2006; Jami *et al.*, 2009) [6, 4, 26]. Available whole genome sequences of various plant species in the public databases provided an opportunity for detailed molecular, evolutionary and functional studies in annexin gene families. With the available whole genome sequences, eight annexin genes in *Arabidopsis* (Clark *et al.*, 2001) [6] and ten annexin genes in *Oryza* (Jami *et al.*, 2012) [24] were identified. Jami *et al.* (2012) [24] performed a genome-wide survey of annexin multigene families in 16 plant species ranging from unicellular green algae to multicellular plants, and identified 149 annexins. All the 149 deduced protein sequences further classified into nine arbitrary groups of related protein clades. Presence or absence of predicted calcium binding sites (CBS) in the core domains/repeats indicated the different calcium binding specificities of plant annexins in the nine groups. Comparative sequence analyses in 149 plant annexins through PROMALS3D for conservation of amino acid residues revealed presence of two Glycine residues, IRI-motif, DXXG-motif and histidine residue in annexin domains which are thought to be essential for ion channel activity, phosphodiesterase activity, peroxidise activityand secondary structure maintenance of annexin proteins (Jami *et al.*, 2012) [24]. The rice annexin Os05g31760 contains two RGD motifs and a Cysteine-rich and a zinc finger type (C2H2) domain that are thought to be involved in cell attachment and transcriptional regulation (Jami *et al.*, 2012) [24].

Expression and Localization

Annexin genes are expressed in most of the plant tissues and organs at different developmental stages throughout the life cycle (Mortimer *et al.*, 2008) [36]. Delmer and Potika (1997) [12] observed high level of expression of AnnGh1 and AnnGh2 proteins in all major tissue of cotton by using poly-clonal antibodies that recognizes annexin proteins. Several immunological studies showed higher expression of annexin proteins in cells actively involved in secretion or fruit ripening (Blackbourn and Battey, 1993; Clark *et al.*, 1992, 1994; Proust *et al.*, 1996) [2, 8, 39]. Enhanced tissue specific expression of annexin proteins during the process of fruit ripening was reported in strawberry (Wilkinson *et al.*, 1995) [49] and pepper (Proust *et al.*, 1996) [39]. Similarly, tissue-specific expression of several annexing gene families was observed in *Arabidopsis* (Lee *et al.*, 2004) [33], *Mimosa* (Hoshino *et al.*, 2004) [21], *Capsicum* (Hofmann *et al.*, 2000) [20], *Zea mays* (Caroll *et al.*, 1998) [5] etc. Differential expression has been noted during the cell cycle in tobacco (Proust *et al.*, 1999) [40], embryogenesis in *Medicago* (Gallardo *et al.*, 2003) [14], pollen and seed germination in *Oryza sativa* (Dai *et al.*, 2006; Yang *et al.*, 2007) [9, 52], tuber enlargement in *Manihot esculenta* (Sheffield *et al.*, 2006) [43], fiber development and elongation in *Gossypium* (Shin and Brown, 1999; Yang *et al.*, 2008) [44, 53] and lateral root development in *Medicago* (de Carvalho-Niebel *et al.*, 2002) [11].

Plant annexins in stress response

Expression of plant annexin genes is found to be regulated by various biotic and abiotic stress factors and stress inducers. Since after the first report by Kovacs *et al.* (1998) [30] in alfalfa, regulation of plant annexin genes by different stress conditions (drought, salinity, cold, heat, heavy metal and oxidative stress) and/or by different phytohormones (ABA, Jasmonic acid, ethylene, SA and auxin) has been reported in *Arabidopsis* (Lee *et al.*, 2004; Cantero *et al.*, 2006; Konopka-Postupolska *et al.*, 2009; Huh *et al.*, 2010) [33, 4, 29, 23] tobacco (Vandeputte *et al.*, 2007; Baucher *et al.*, 2011) [7, 1], *Brassica* (Jami *et al.*, 2008, 2009) [24, 25], rice (Gorantla *et al.*, 2005; Jami *et al.*, 2012) [17, 24] and turnip (Yan *et al.*, 2016) [50]. Genetic transformation approaches have shown that annexins play a significant role in protecting plants from both biotic and abiotic stresses (Lee *et al.*, 2004; Jami *et al.*, 2008; Konopka-Postupolska *et al.*, 2009; Divya *et al.*, 2010; Huh *et al.*, 2010; Zhang *et al.*, 2011; Szalonek *et al.*, 2015; Zhang *et al.*, 2015) [33, 24, 29, 13, 23, 54]. For example, ectopic expression of Indian mustard annexin gene (*AnnBj1*) in tobacco (Jami *et al.*, 2008) [24] and in cotton (Divya *et al.*, 2010) [13] provided enhanced tolerance to various abiotic stresses such as salinity, dehydration, oxidative stress and heavy metal stress during seedling growth and development. Transgenic potato plants ectopically expressing *StAnn1* have shown more efficient protection of reaction centers of photosystem II (PSII) and higher accumulation of chlorophyll *b* and xanthophylls than WT plants under drought conditions (Szalonek *et al.*, 2015) [45]. Over expression of a cotton annexin gene, *GhAnn1*, contributed to increased salt and drought stress tolerance in transgenic cotton plants (Zhang *et al.*, 2015) [54]. *AnnAt1*overexpressing mutants in *Arabidopsis* showed drought tolerance, while loss-of-function mutants were drought sensitive (Konopka-Postupolska *et al.*, 2009) [29]. Over expression of annexin gene, *CkAnn* in transgenic cotton caused a significant increase in drought tolerance and enhanced disease resistance to *Fusarium oxysporum* (Zhang *et al.*, 2011) [55].

Annexins in oxidative stress tolerance

Plant annexins from *M. sativa* and *A. thaliana* have been implicated in oxidative stress response. In particular it has been shown that an annexin like protein from *Arabidopsis*, is able to rescue *Escherichia coli* Δ OxyR mutants from H_2O_2stress (Gidrol *et al.*, 1996) [16]. It has also been shown that an *Arabidopsis* annexin, *AnnAt1* also possess peroxidase activity (Gorecka *et al.*, 2005) [18]. More recently annexins of maize, Indian mustard, capsicum, cotton were also shown to exhibit peroxidase activity (Mortimer *et al.*, 2008; Jami *et al.*, 2008; Laohavisit *et al.*, 2009; Zhang *et al.*, 2015) [36, 24, 32, 54]. The peroxidase activity of annexins is due to the presence of the conserved 30-amino acid sequence in the first annexin repeat, which has similarity to heme binding domain of plant peroxidases (Gorecka *et al.*, 2005; Jami *et al.*, 2008; Laohavisit *et al.*, 2009) [18, 24 32]. This peroxidase like motif contains critical conserved His^+ residue needed for haeme-binding domains that overlaps with the Ca^{+2}-binding site in the first repeat, raising the possibility that Ca^{+2} could regulate this peroxidase activity observed in annexins. The production of H_2O_2 is induced by several different biotic and abiotic stresses and helps to maintain plant responses to these stresses. So, the annexin-peroxidase connection raises the possibility that annexins could play a role in preventing the accumulation of damaging levels of this agent.

Jami *et al.* (2008) [25] found that excised mature leaves from *AnnBj1* overexpressing tobacco transgenic plants showed 1.8-2.6-fold more total peroxidase activity compared to wild type plants under oxidative stress. Studies on the over expression of *AnnBj1* in cotton showed an increase in total peroxidase activity ranging from 2.1-2.8-fold in transgenic plants and corresponding reduction of H_2O_2 contents when compared with the control plants under all stress (salinity, dehydration and oxidative stress) treatments (Divya *et al.*, 2010) [13]. This is corroborated by the significantly enhanced fluorescence detected by H_2DCFDA in the stomatal guard cells of wild type plants than the transgenic plants which showed less fluorescence due to ROS detoxification. This activity could be attributed to the constitutively expressed *AnnBj1* gene. Similarly, Konopka-Postupolska *et al.*, (2009) [29] observed significantly reduced levels of ABA induced ROS identified by the fluorescent dye, H_2DCFDA, in *AnnAt1* over expressed *Arabidopsis* lines compared to WT plants. Transgenic cotton plants over expressing annexin gene, *CkANN*, displayed significantly higher peroxidase activities compared to control plants when inoculated with *Fusarium oxysporum* (Zhang *et al.*, 2011) [55].

Over expression of various annexin genes in tobacco and cotton transgenic plants displayed significant retention of total chlorophyll content and lower levels of TBARS with reduced lipid peroxidation and membrane damage in comparison to WT plants which displayed damaged membrane by more lipid peroxidation resulting in susceptibility to stress treatments (Jami *et al.*, 2008; Divya *et al.*, 2010; Zhang *et al.*, 2011) [24, 55,13]. These results are implying that annexins have a protective role in the stress induced membrane damage. Accumulation of ROS results in formation of MDA levels in plants due to membrane lipid peroxidation. Under salt and drought stress treatments transgenic cotton plants over expressing *GhAnn1* shown increased SOD activity with improved ROS detoxification thereby low MDA accumulation, less membrane damage, and more stable cell membrane (Zhang *et al.*, 2015) [54].

Annexins in osmotic stress tolerance

High levels of salinity and drought in plant cells leads to cellular ions imbalance and finally osmotic stress. Plants respond to osmotic stresses by osmotic adjustments through accumulation of osmoprotectants. Many studies have shown that free proline and soluble sugars are the most widely distributed multifunctional osmoprotectants to counter the stress induced by salt and drought stresses. To elucidate the role of annexins in osmotic stress tolerance, the levels of free proline and soluble sugars were estimated in wild type and transgenic plants over expressing various annexin genes under drought and salinity stress. Divya *et al.* (2010) [13] observed enhanced levels of free proline and soluble sugars (fructose, glucose and sucrose) content in *AnnBj1* over expressing cotton plants which was significantly very high compared to the WT plants under 400 mM NaCl stress. It was demonstrated that the modulation in cytosolic Ca^{2+} during salt stress can regulate the gene expression of P5CS encoding enzyme responsible for conversion of glutamate to proline in the proline biosynthesis pathway (Parre *et al.*, 2007; Divya *et al.*, 2010) [38, 13]. Semi-quantitative RT-PCR analysis recorded conspicuously higher expression levels of P5CS, which was consistent with the enhanced proline content in *AnnBj1* over expressing cotton transgenic plants under salt stress (Divya *et al.*, 2010) [13]. Previous studies have shown that over expression of proline biosynthesis genes in transgenic plants conferred salt stress tolerance (Kishor *et al.*, 1995; Reddy *et al.*, 2015) [28, 41]. Similarly, enhanced levels of free proline and soluble sugars were observed in *GhAnn1* and *CKANN* over expressing transgenic cotton plants compared to WT plants under salt and drought stress conditions respectively (Zhang *et al.*, 2011; Zhang *et al.*, 2015) [55, 54].

Accumulation of soluble carbohydrates as osmoprotectants during osmotic and salinity stresses is one of the alternate tolerance mechanisms developed by the plants and stress induced soluble carbohydrates conferring stress tolerance has been demonstrated (Kerepesi and Galiba, 2000) [27]. Sucrose accumulation can increase cytosolic calcium levels by producing Ca^{2+} influx. Enhanced cellulose deposition in fibers translocated from the enhanced sucrose pools in the leaves during elongation and secondary wall synthesis determines the fiber quality. Transgenic cotton plants over expressing Indian mustard annexin gene had significantly high proportion of better quality well developed mature fibers with higher cellulose content compared to WT plants under salt stress. This result implying the role of annexin in the cellulose biosynthesis pathway (Divya *et al.*, 2010) [13].

Taken all together, these experimental evidences indicate that annexins play a protective role in enhanced drought and salt stress tolerance.

Abbreviations

ER	Endoplasmic reticulum
ABA	Abscisic acid
SA	Salicylic acid
H_2O_2	Hydrogen peroxide
H_2DCFDA	Dichlorodihydrofluoresceindiacetate

ROS	Reactive oxygen species
TBARS	Thiobarbituric acid reactive substances
WT	Wild type
MDA	Malondialdehyde
SOD	Super oxide dismutase

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