

Expansins: Cell Wall Remodeling Proteins with a Potential Function in Plant Defense

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Cell wall (CW) performs a number of important functions. This distinctive feature of plants determines cell structure, and plays major roles in intercellular communication and plant-microbe interactions, including defense responses against potential pathogens. Expansins are novel plant CW loosening proteins, are mainly involved in the pH-dependent extension of plant CWs that is called acid growth [1,2]. These plant CW remodeling proteins have important roles in plant cell growth, fruit softening, abscission, and emergence of root hairs, pollen tube invasion of the stigma and style, meristem function, pathogenicity and developmental processes. Expansins are linked with cell growth and CW changes that are induced by a number of plant hormones.

In plants, two main families of expansin genes have been discovered: α -expansins (EXPA) and β -expansins (EXPB). Other expansin-like genes, such as *expansin-like A* (EXLA) and *expansin-like related* (EXLB), have also been identified in plants. For example, in the genome of *Arabidopsis thaliana* and rice (*Oryza sativa*), 26 and 33 genes of EXPA, 6 and 18 of EXPB, 3 and 4 of EXLA, in addition to one EXLB gene, respectively, were identified. Thus the function has not been well-studied [2-5]. Recently, the *Arabidopsis expansin-like A2* (EXLA2) gene has been reported to link plant development and defense [6].

Expansin proteins are relatively conserved. A typical mature protein has a molecular weight of ~25-30 kilo Dalton, which corresponds to 250-300 amino acids. Expansin proteins are composed of two conserved domains: Domain I (120-135 aa), a glycoside hydrolase-like family 45 (GH45-like) at the amino (N) terminal; and Domain II (90-120 aa), a group-2 grass pollen allergen at the carboxyl (C) terminal [5]. An expansin signal peptide (SP) of 20-30 aa is also found at the N-terminal end, suggesting that this SP may direct the polypeptide into the endoplasmic reticulum (ER)/Golgi secretory pathway [2,7]. A number of conserved cysteines are present in domain I, yet no hydrolytic activity has been detected. In addition, all expansin-like proteins have one to three NXT/S motifs, which may be N-linked glycosylation sites [8]. Expansin-like proteins, unlike other expansins, lack the HFD motif at the conserved motif of the GH45 active site, and have a unique conserved motif (CDRC) at the N-terminus of domain I, and an extension of sequence in domain II [5,9]. This deletion in domain I and the insertion in domain II of expansin-like proteins may lead to a different mechanism of action from that of other expansins [6].

In general, expansins are CW remodeling agents with endogenous functions in CW extensibility. Expansins are expressed in the early stages of symbiosis of the arbuscular mycorrhizal fungus *Glomus intraradices* on tomato (*Solanum lycopersicum*) and in developing nitrogen-fixing nodules in legumes [10,11]. Expansins are also expressed under drought conditions. During dehydration, the resurrection plant (*Craterostigma plantagineum*) expresses α -expansin in leaves [12]. In response to cold stress, three EXLA genes are induced in *Arabidopsis* [13]. A recent study has shown that EXLA2 is also involved in the pathogenesis of necrotrophic pathogens and in the tolerance to abiotic stresses [5]. So far, no enzymatic activity has been found for expansins.

Expansins are well-known in loosening CWs via a nonenzymatic mechanism by inducing the slippage of cellulose microfibrils in the plant CW [2]. The recent study of the role of EXLA2 in plant defense has

uncovered a different mechanism of action from that of other expansins [6]. Mutations in EXLA2 enhance not only resistance to necrotrophic fungi, but also tolerance to phytoprostane A. AbuQamar and his group demonstrate that down-regulation of EXLA2 alters the expression of cyclopentenone-regulated genes in response to *B. cinerea*. There appears to be a common regulation between electrophilic oxylipins and *B. cinerea* that is associated with EXLA2. On the other hand, EXLA2 is induced by salinity and cold, and by abscisic acid (ABA) treatment. In addition, the *exla2* mutant showed hypersensitivity to increased salt and cold that is mediated by ABA. The work of EXLA2 presents convincing data that expansins contribute significantly to plant response to stress and impact signaling pathways that regulate gene expression. Future investigations into the mechanism of action of expansins open a new line of research in the field of plant responses to biotic and abiotic stresses at the biochemical, molecular and physiological levels.

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