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Expansin Gene Family in Legumes: Structural Diversity and Expression Dynamics

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Abstract Expansins are plant-specific proteins that play crucial roles in cell wall loosening and are essential for various developmental processes and stress responses. This study comprehensively analyzes the expansin gene family in legumes, focusing on its structural diversity, evolutionary patterns, expression dynamics, and functional relevance. We classify expansins into α-expansin, β-expansin, and expansin-like A and B subfamilies and discuss their gene duplication events, chromosomal localization, and conserved domain structures in major legume species. Phylogenetic relationships and Ka/Ks ratio analyses provide new insights into their evolutionary trajectories and selective pressures. Furthermore, we investigate tissue-specific and developmental stage-specific expression patterns, highlighting the roles of expansins in root growth, nodulation, and pod formation. Expression profiles under various abiotic and biotic stress conditions reveal their involvement in stress adaptation mediated by hormone signaling pathways. Functional studies involving gene overexpression, gene knockout, and omics-based analyses highlight their contributions to cell expansion, stress tolerance, and the regulation of root system architecture. A case study focusing on soybean illustrates how differential expression and transgenic validation of expansin genes influence drought resistance and nodulation. This study lays the foundation for understanding the functions of expansin genes in legumes and provides prospects for their application in molecular breeding, genome editing, and improving stress tolerance in legume crops.

Keywords Expansin proteins; Legumes; Gene expression dynamics; Evolutionary analysis; Stress response

1 Introduction

In the growth regulation of plant cell walls, a type of substance called blotin has long been regarded as a key player. They do not break the components of the cell wall through hydrolysis, but rather help the cell wall extend in a specific way under acidic conditions by breaking non-covalent bonds. This type of protein is not just one or two, but A superfamily consisting of four subclasses: α -butenin (EXPA), β -butenin (EXPB), butenin-like A (EXLA), and butenin-like B (EXLB). Among them, EXPA and EXPB are the most active, especially in the aspect of loosening the cell wall. They are not only involved in seed germination or pollen tube growth, but also in leaf morphology, root bud elongation, flower and fruit development, and even the process of plant shedding. But the role of expansion protein is not limited to growth. When plants are subjected to abiotic stresses such as drought, saline-alkali conditions or abnormal temperatures, they are also "showing up". Furthermore, when symbiosis with microorganisms (such as mycorrhizae and rhizobia), these proteins also play a role in communication and adaptation (Cosgrove, 2015; Mohanty et al., 2017).

Especially in leguminous plants, the expression of the expansin gene is of particular concern. They are involved in many important links related to adaptation and development, such as the adjustment of cell walls, which directly affects the structure of root systems and the formation of root nodules-and root nodules are closely related to nitrogen fixation. The expression of these genes is usually tissue-specific and can flexibly adjust according to external conditions such as drought, salt content changes, and even nutritional status. Take soybeans and alfalfa as examples. The expression of their tumescent protein genes in different tissues varies significantly, and they are also upregulated when subjected to osmotic pressure or salt stress. This indicates that they do not play a passive role in stress responses. During the symbiotic process with rhizobia, they also regulate the related mechanisms of root infection and root nodule development, and this regulation is often influenced by hormone levels and environmental signals (Giordano and Hirsch, 2004; Li et al., 2014).

This study focuses on the diversity and expression changes of the expansin gene family in leguminous plants. We will systematically sort out their classification methods, evolutionary features and structural compositions, and analyze them in combination with their expression patterns during plant growth, development and under adverse conditions. Of course, leguminous elements such as root development, nodulation, and adaptation to drought or salt stress will be the focus of our attention. With the rapid development of genomics and transcriptomics, our understanding of the regulatory mechanisms and functions of these genes is gradually deepening, which provides new directions and research foundations for the molecular improvement of leguminous crops in the future.

2 Structural Diversity of the Expansin Gene Family in Legumes

2.1 Classification of expansins: α-expansins, β-expansins, expansin-like A, and expansin-like B

The blotin family in leguminous plants is not A collection of a single type. In fact, it is divided into four categories according to phylogenetic relationships: α-expansin (EXPA), β -expansin (EXPB), expansin-like A (EXLA), and expansin-like B (EXLB) (Figure 1). Among them, the α and β types have the strongest presence and the most research. Functionally, they mainly involve the relaxation of cell walls and the process of plant development. In contrast, Sample A and Sample B are much quieter. Currently, our understanding of them mainly remains at the level of gene sequences, and there is a lack of experimental evidence to prove whether they truly possess cell wall activity. Take soybeans as an example, this point is quite obvious. Researchers have identified 75 expansin genes and classified them into four subfamilies, with EXPA taking the majority, followed by EXLB, then EXPB and EXLA (Wang et al., 2024a). This distribution also indirectly confirms the focus of research and function of each sub-family.

2.2 Gene duplication, divergence, and chromosomal distribution across legume genomes

Why is the expansin gene family so large in leguminous plants? One major reason is gene replication. Especially tandem replication and fragment replication, these two mechanisms provide "channels" for the increase of family members. Such replication events are particularly frequent in soybeans and their wild relatives, playing a promoting role in the expansin gene families. But these genes are not evenly distributed on the chromosomes. Some chromosomes, due to the concentrated burst of tandem replication, have formed distinct gene clusters, and this concentration also brings potential functional or regulatory connections. Meanwhile, the evolution of different genes is not static-they are influenced by natural selection. Some have experienced positive selection pressure, resulting in the gradual formation of differentiated functional characteristics in some subfamilies (Zhu et al., 2014).

2.3 Conserved motifs and structural domains: insights from sequence alignment and phylogenetics

Sequence analysis of the expansin family reveals a delicate balance: on the one hand, conservation, and on the other hand, differentiation. Structurally, most inflated proteins contain two key domains: DPBB_1 (a double psi β barrel domain) and CBM63 (a carbohydrate-binding module). These structures are not randomly combined but highly conservative, especially within the same subfamily. Take soybeans as an example. EXPA members often have a set of eight conserved motifs arranged in a similar order, while other subfamilies, such as EXPB, EXLA and EXLB, although they also have their own motif combinations, the patterns are significantly different. Some motifs even only appear in specific subfamilies. This "belonging only to oneself" marker not only indicates the evolutionary differentiation among them, but may also predict the functional specialization tendency (Feng et al., 2022). In other words, although they all belong to the same superfamily, the differences between different subclasses are real, reflecting their respective "personalities" and the divergence in the process of evolution.

3 Evolutionary Insights into Expansin Genes in Legumes

3.1 Phylogenetic relationships of expansin genes among legume species and other angiosperms

The story of expansins actually dates back to an even earlier stage of green algae-their rudimentary forms had already emerged. As plants gradually "come ashore" and move towards terrestrial ecosystems, these genes have not been idle either, and have begun to continuously differentiate and evolve. EXPA was the first to appear among the four subfamilies, followed by EXPB, EXLA and EXLB. However, there are also many differences among various plants. Although in legumes and other angiosperms, most of the bulking protein genes belonging to the same subfamily can cluster into one category, showing a certain degree of conservation, the boundaries between subfamilies remain quite distinct. That is to say, they look like a family on the outside, but in fact, they have been working separately for a long time. Comparative studies have shown that the number and distribution of genes in various species are not exactly the same, but the core subfamily structure remains constant, indicating that conservation and diversity are two coexisting aspects in the process of plant evolution (Li et al., 2002; Sun et al., 2021).

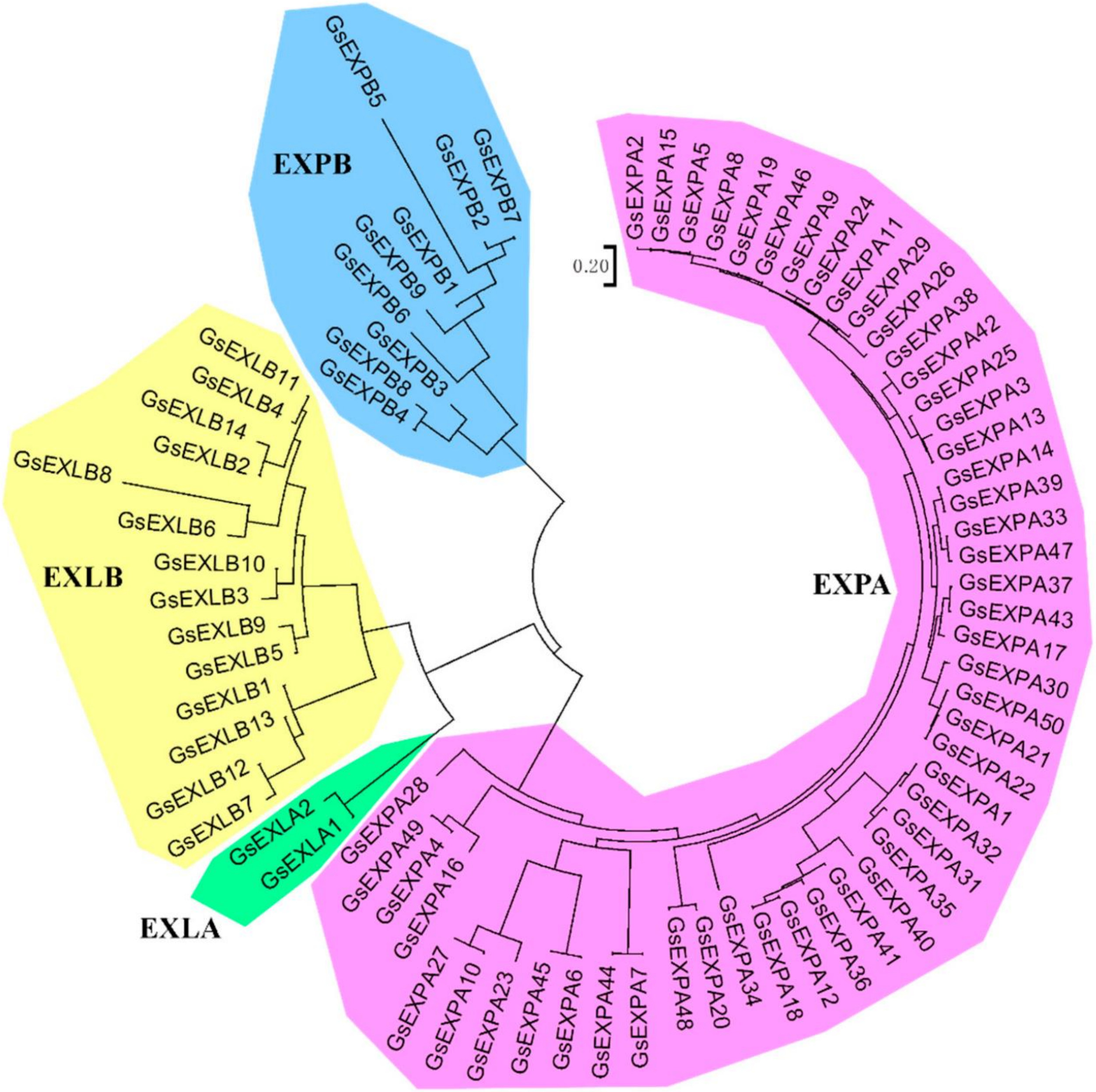

Figure 1 Amino acid phylogenetic tree of wild soybean expansin family members (Adopted from Feng et al., 2022)

3.2 Role of gene duplication events (segmental, tandem) in the evolution of the expansin family

When it comes to why the expansin gene family has become so large, it is impossible to avoid an old acquaintance-gene replication. Fragment replication and tandem replication almost constitute the main theme of the expansion of the expansin gene. This is particularly evident in the research of soybeans: nearly 70% of the expansin genes are formed through fragment replication, and tandem replication also contributes nearly 15%. Although they differ in proportion, both play a key role in "creating" diversity. Interestingly, these replications do not occur alone in one place. They often concentrate in specific regions on chromosomes and gradually form gene clusters. This local "clustering" not only enables these genes to be preserved but also provides opportunities for subsequent functional differentiation. Thus, the abilities to adapt to developmental needs and cope with environmental changes were gradually established (Li et al., 2024; Wang et al., 2024c).

3.3 Selective pressures and evolutionary rates inferred from Ka/Ks analyses

Not all genes function freely during the process of evolution. In fact, most of the genes for bloating proteins are very "regular". From the analysis of the Ka/Ks ratio, it can be seen that for both soybeans and two-grain wheat, the majority of their tumescent protein gene pairs show a Ka/Ks ratio less than 1, indicating that they have undergone purification selection and tend to retain their original functions with few modifications. But this doesn't mean there are no changes at all. Positive selection signals may appear at certain specific loci, especially in regions related to functional differences. That is to say, these places seem more willing to "take risks" and try some new changes, especially within certain specific subfamilies. The existence of such positive selection actually indirectly indicates that the expansion protein genes are not static; they are still seeking opportunities to evolve new functional possibilities (Li et al., 2023).

4 Expression Dynamics during Plant Development

4.1 Tissue-specific expression patterns in roots, stems, leaves, flowers, and nodules

Different tissues "speak" in different ways during development-each tissue has its own "language", that is, a specific combination of gene expressions. In parts such as roots, stems, leaves and flowers, different genes each take the stage and perform their own functions. In model plants like *Arabidopsis thaliana*, through transcriptome and proteome studies, it has been found that each tissue has its own unique expression profile, which varies greatly from one another. Take Gen for example, studies on single-cell transcriptomes have revealed significant differences in gene expression among different cell types, and these differences are constantly adjusted as the development stage progresses. But not all parts are as clear as the roots. For instance, in above-ground organs such as leaves and flowers, the changes in expression are more closely related to tissue maturity. The later it goes, the more regular the expression becomes (Jean-Baptiste et al., 2019). There are also tissues such as flowers and seeds, which belong to reproductive structures. Their expression changes are often related to organ identity confirmation and maturation rhythm (Wellmer et al., 2006).

4.2 Temporal regulation during key developmental stages

Gene expression is not always so "free and unrestrained". At some critical junctures, such as when seeds just germinate, organs first form, or when entering the reproductive stage, the rhythm of expression becomes particularly tight and layered. During the early embryo and germination stages, many genes suddenly "come online", with changes in expression regions and times. This transcriptional recombination is actually setting the tone for cell fate and paving the way for subsequent differentiation (Palovaara et al., 2017). However, once it comes to the development period of the floral organs, the situation is quite different. Some specific gene families are only expressed when flower buds are formed or organs are initially established, and then they fall silent. And groups of co-expressed genes act like a baton, dominating the entire process from organ initiation to maturity (Ryan et al., 2015). The development process of the stem is similar, but with a slightly different rhythm. It usually goes through a series of stages from cell division to expansion and then to secondary growth, and the transcriptome expression also changes accordingly (Zhang et al., 2024).

4.3 Correlation of expansin expression with cell expansion and morphogenesis

Regarding the expansion proteins in leguminous plants, we don't have much direct data at hand yet, but some studies on model plants have already revealed quite a few clues. Cell expansion is not something that can be accomplished by a single gene working alone; it requires the collaborative efforts of an entire "team": those that regulate cell wall relaxation, maintain turgor pressure, and respond to hormone signals will all be collectively upregulated at critical stages. For instance, during the rapid growth period of leaves, the expression levels of those genes related to the cell wall are often very high, especially those responsible for wall structure adjustment

(Mergner et al., 2020). This type of expression dynamics is highly consistent with the stage of rapid cell volume growth and organ formation, and also indirectly indicates that the participation of expansion proteins in the development process is actually quite high-especially in morphological formation and structural shaping.

5 Expansin Gene Regulation under Abiotic and Biotic Stress

5.1 Expression modulation in response to drought, salinity, cold, and heat stress

In the face of various abiotic stresses, plants do not just sit and wait to die. Expansin genes show significant expression changes under such environmental stress, but these changes often vary depending on the species, tissue and type of stress. In wild soybeans, the *GsEXLB14* gene is activated under stress. Overexpression can promote root growth and enhance the plant's stress resistance at the same time (Figure 2). Not only soybeans, but similar examples can also be found in other plants. Once the expression of *NtEXPA4* in tobacco and *BrEXLB1* in Brassica plants is upregulated, proline accumulation increases and the root system becomes longer, resulting in enhanced drought and salt tolerance (Muthusamy et al., 2020). However, it is not always so direct in all cases. For instance, under cold and hot stress, the expression of blotin will also increase, but the underlying mechanism of action may be more complex. Like *TaEXPB7-B* in wheat, it is activated under the combined influence of low temperature and ABA (abscisic acid), which helps to enhance cold resistance and maintain growth (Feng et al., 2019). From these circumstances, it can be seen that the expression regulation of the expansion protein gene is intricately related to osmosis regulation, cell wall structure stability, and even antioxidant mechanisms (Kuluev et al., 2016; Chen et al., 2019).

5.2 Induction by pathogen infection and involvement in defense signaling

As soon as a plant encounters a pathogen, its defense system begins to be activated, and the expansin gene is often involved. But things are not that simple. Sometimes their roles are even a bit "contradictory". In wild peanuts, a gene called *AdEXLB8*, when introduced into tobacco, can significantly enhance resistance to pathogenic bacteria and nematodes, and also improve drought tolerance. This is mainly achieved by activating jasmonic acid and ABA signaling pathways, thereby enhancing antioxidant defense capabilities (Brasileiro et al., 2021). However, this positive effect is not static. For instance, in tobacco, although *NtEXPA4* can make plants more drought-resistant and salt-tolerant, it appears more "vulnerable" when facing powdery mildew or bacterial infection-infection becomes easier (AbuQamar et al., 2013; Chen et al., 2018). This indicates that there may be some kind of "tug-of-war" between immunity and growth for expansins, and it is not always the best of both worlds.

5.3 Crosstalk with plant hormones (ABA, auxin, ethylene) in stress adaptability

When plants are under stress, hormone signaling pathways are almost impossible to be absent. The expression changes of the expansin gene are largely regulated by abscisic acid, auxin and ethylene. These three hormones play different roles in stress responses, but all can influence the behavior of dilator proteins. Abolic acid, which has long been regarded as the "big boss" of drought and salt resistance responses, can induce the expression of genes such as *TaEXPA2* (wheat) and *OfEXLA1* (osmanthus), thereby helping plants enhance their adaptability (Dong et al., 2023). Auxin related dilating proteins, on the other hand, are more inclined to promote root growth and cell expansion, representing a more "growth regulation" pathway. The role of ethylene is slightly complex. It is involved in regulating cell wall remodeling. For example, the upregulation of GsEXLB14 when there is insufficient water can help maintain the extended state of cells (Han et al., 2012). The three do not operate independently but interweave and collaborate to jointly determine whether the plant maintains its state, accelerates growth, or adjusts its shape under stress. This coordination ability is essentially a manifestation of plant adaptability and also indicates that the regulation of expansion proteins is far more complex than it appears on the surface.

6 Functional Characterization of Expansin Genes

6.1 Gene knockout and overexpression studies in model and crop legumes

What exactly can expansive protein do? The most direct way is to "turn them on" or "turn them off" to see the effect. Through the research on gene knockout and overexpression, many problems have begun to become clear

(Chen, 2024; Wang et al., 2024b). For instance, in wild soybeans, the overexpression of *GsEXPB1* has led to an increase in the number and length of roots, as well as a significant rise in weight. Not only that, but its tolerance to salt stress has also increased. This change is quite revealing-the connection between the activity of expansins and the improvement of root structure and stress adaptation is indeed not accidental. Similar effects have also been observed in other plants. For instance, in tobacco and Brassica plants, once some blotting protein genes (such as *NtEXPA4*, *NtEXPA11*, *BrEXLB1*) are highly expressed, they can push the root system to break through the soil downward, and also help maintain ion balance, enhancing the plant's drought and salt resistance. However, if we knock out certain genes, such as *OsEXPA10* in rice, the result changes-the elongation of root cells is significantly reduced, indicating that these genes are actually "indispensable" for normal development (Che et al., 2016).

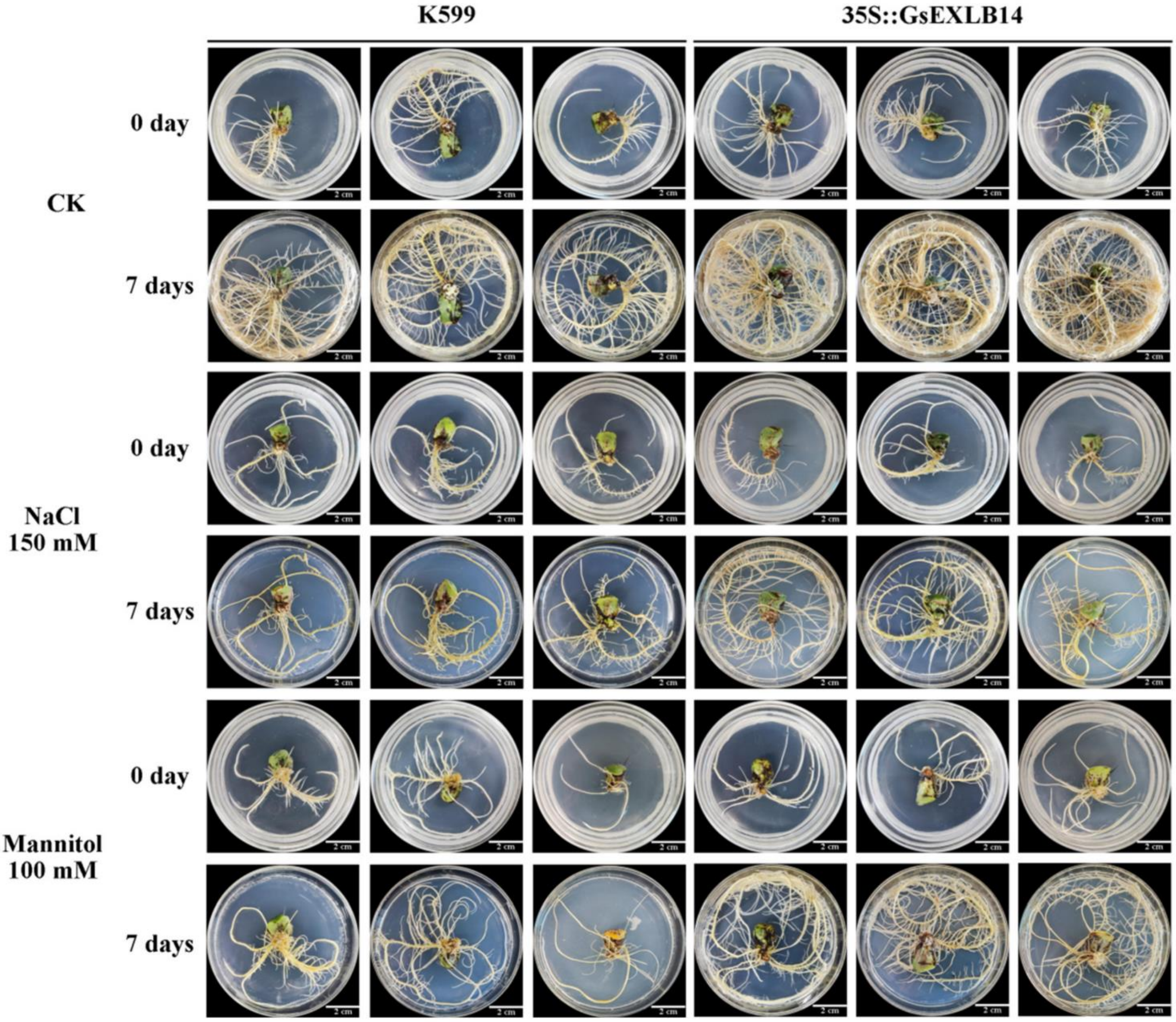

Figure 2 Phenotype of soybean hairy roots overexpressing *GsEXLB14* under normal, salt, and drought stress conditions (Bar = 2 cm) (Adopted from Wang et al., 2024a)

6.2 Functional assays linking expansins to cell wall loosening and root architecture

What exactly is expansin doing? They do not directly determine how cells grow, but they play a significant role in the "loosening" of cell walls, which is precisely the key link for cells to expand and organs to elongate. Some short-term expression experiments and pilous root transformation studies have found that the expansion protein is indeed located within the cell wall. For instance, when *GsEXPB1* of soybeans is overexpressed in hairy roots, the roots not only grow faster but also can better cope with salt stress. Not only that, experiments on other model plants such as *Arabidopsis thaliana* have also made similar findings-seeds germinate more easily, root hairs grow more, and even the overall growth of roots has improved. Behind these phenomena, almost all of them are inseparable from the "behind-the-scenes actions" of bloating proteins in cell wall modification (Dabravolski and Isayenkov, 2025). Judging from these results, whether in normal development or under adverse conditions, blotin seems to be helping cells "unbind", allowing plants to cope with the environment more calmly.

6.3 Omics approaches (transcriptomics, proteomics) identifying candidate expansins in stress and development

Not every expansion protein can be immediately identified for its function, especially during complex stress responses or developmental processes. At this point, omics technology comes into play. Like in wild soybeans, transcriptome analysis revealed that some expansins were specifically induced to be expressed under conditions such as salt, drought, and cold, and this expression often carried organ specificity. Promoter analysis further tells us that their regulation is not only dependent on environmental stimuli, but also involves developmental processes, hormone signals, and even adverse cis-regulatory elements (Chen et al., 2020). Proteomics and co-expression networks have not been idle either. Research results indicate that a batch of candidate genes for bulking proteins may be involved in processes such as cell wall remodeling, antioxidant defense, and osmotic regulation. Although these data cannot be used to draw a direct conclusion, they at least provide a very clear clue-we can understand the position of these genes in plant adaptability from a broader perspective, especially in leguminous crops that are particularly sensitive to environmental responses.

7 Case Study: Expansin Gene Functions in Soybean (*Glycine max*)

7.1 Genome-wide identification and classification of expansin genes in soybean

If asked which crop has the "most complete" family of expansive proteins, soybeans must be on the list. So far, 75 expin genes have been identified and are distributed in four subfamilies: EXPA, EXPB, EXLA and EXLB. EXPA has the largest number of members, accounting for approximately two-thirds. In contrast, EXLA is relatively "less popular" and has the fewest quantity. These genes are not only numerous but also structurally interesting. Genes within the same subfamily are often highly similar in intron and exon structures and share some conserved motifs, which indicates that they are very likely to have evolved from a common "ancestral module". Of course, the formation of such diversity does not come out of thin air-fragment repetition and serial replication events are all driving the expansion and functional differentiation of this family.

7.2 Expression profiling under drought and nodulation stages reveals functional clusters

The presence of expansive proteins in soybeans is not even, especially in areas such as roots and root nodules, where they are often much more active. The analysis of the expression profile reveals some patterns, but also brings out a lot of complexity. Genes like *GsEXPB1* and *GsEXLB14* are "resident" genes in the roots, and they will be significantly upregulated especially when encountering drought or salt stress. GmEXPB2 and GmINS1, on the other hand, are more likely to be expressed when root nodules form or when plants are deficient in phosphorus. Their changes are even associated with the size of root nodules and the enhancement of nitrogen fixation capacity. Not all expansins are activated under adverse conditions. Some only work at specific times and in specific areas. For instance, during the tumor formation stage, some genes are activated particularly early, while others "make a grand entrance". Transcriptome data further support this point-their expression is influenced by both abiotic stress and developmental stage (Li et al., 2015; Yang et al., 2021).

7.3 Transgenic approaches demonstrate roles in root elongation and abiotic stress tolerance

The most direct way to figure out exactly what a certain expansin is "responsible for" is through transgenic experiments. Many studies nowadays are conducted in this way. Both transgenic experiments on the hairs of soybean roots and the entire plant have found that after overexpressing genes such as *GsEXPB1*, *GsEXLB14*, GmEXPB2 or GmEXPA7, the number, length and biomass of roots all increased, and the plant's tolerance to stress such as salt, drought and low phosphorus also improved accordingly. However, this matter is not one-sided. If we change our approach and deal with it by interfering with or inhibiting these genes, the results will soon become apparent: the roots won't grow and there will be problems with the formation of nodules. For instance, *GsEXPB1* not only promotes root growth but also enhances root tolerance under salt stress (Figure 3). The effect of GmEXPB2 is more comprehensive. It not only promotes root elongation but also improves root nodule formation and phosphorus absorption capacity (Zhou et al., 2014; Kong et al., 2019). In other words, these genes are not merely "auxiliary tools", but a core link in root development and stress response.

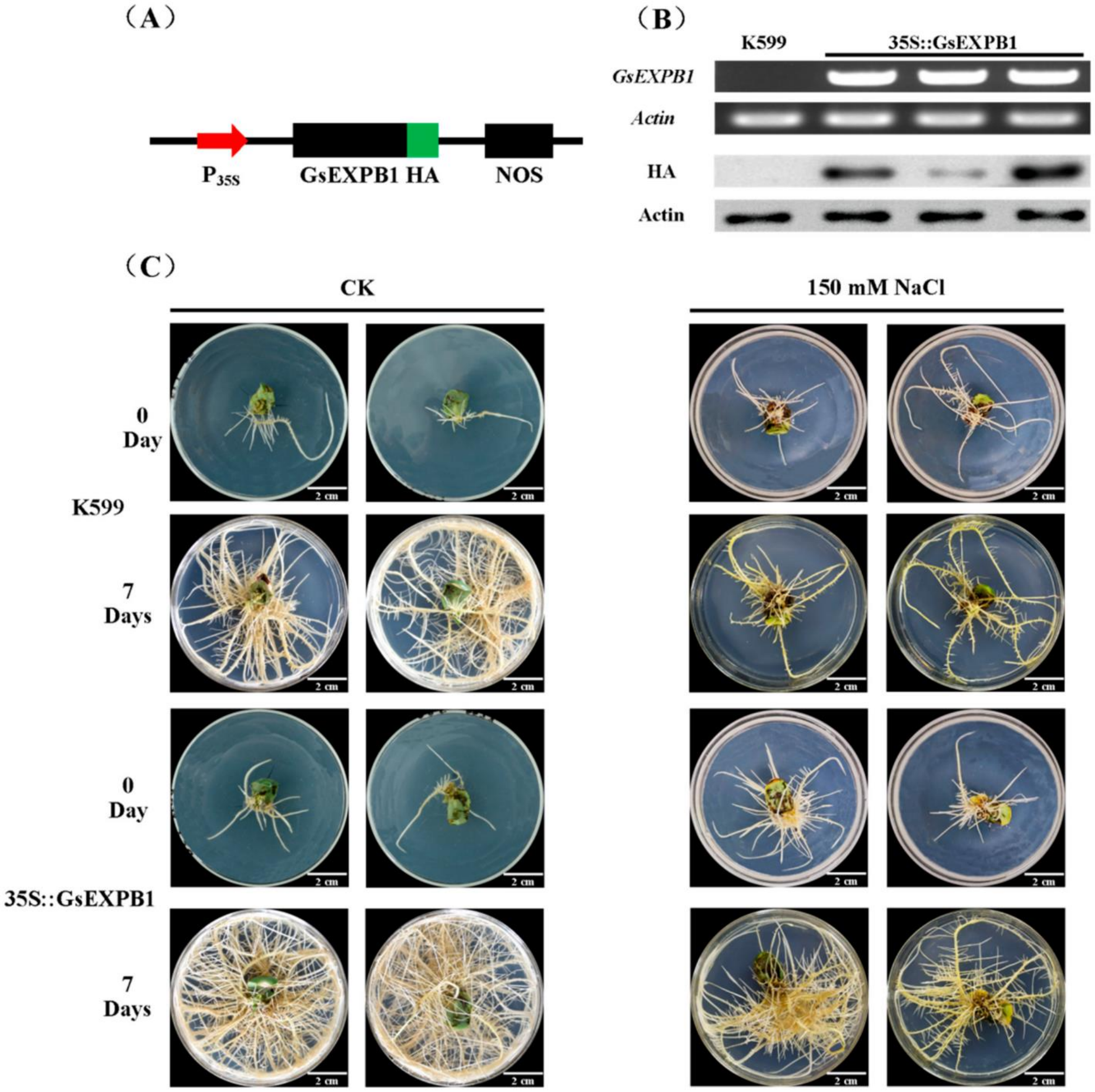

Figure 3 Overexpression of *GsEXPB1* significantly promoted cultivated soybean hairy roots growth and salt stress tolerance. (A) Construction of expression vector, P_{35S} indicates CaMV35S promoter, HA indicates HA protein tag, NOS indicates terminator. (B) Detection results of gene transcription and protein expression in transgenic hairy roots. (C) Phenotypic observation of hairy roots overexpressing *GsEXPB1* under normal growth conditions and salt stress, bar = 2 cm (Adopted from Feng et al., 2022)

8 Concluding Remarks

The expansin gene in leguminous plants is complex, but there are indeed patterns to follow. They are not a type of "uniform specification" genes, but a large family with diverse structures and functions, classified into four subgroups: EXPA, EXPB, EXLA and EXLB. Many members have similar conservative domains and repetitive motifs, which look like traces left by their "ancestors". The reason why they are increasing in number is mainly driven by fragment replication and serial replication, while the subsequent functional differentiation is gradually shaped by various selective pressures.

But the "voices" of these genes are not always synchronized. At different tissues and developmental stages, their expressions have their own rhythms, especially in the root system, root nodules, and when facing adverse conditions such as drought or salinization, they are particularly active. Genes like *GmEXPB2* have been repeatedly demonstrated in research that after overexpression, not only do roots grow faster and root nodules increase, but the stress resistance also improves significantly (and all of these are ultimately linked to yield). Of course, including these genes in the breeding program is not just empty talk. Whether using traditional marker-assisted selection or with the help of CRISPR/Cas, the "precise scissors", the application of expansion proteins is becoming more realistic. They may alter the configuration of roots, enhance nutrient absorption capacity, and even offer a feasible path in terms of reducing medication and increasing yield.

However, behind these seemingly "promising" directions, there are still many problems to be solved. For instance, how do these genes interact with each other? Do they have a deeper integration with hormone signals or stress pathways? Which ones are the core functions and which ones are merely "background signals"? In addition, many functional verifications are still at the laboratory stage, and the stability of the field environment and the applicability across varieties have not been fully tested. Future research may need to delve more into these cross-regions. It is not only about functional verification, but also delves into multiple levels such as transcription, protein, and metabolism. It is not only necessary to look at short-term phenotypes, but also to observe long-term adaptability. Only when we truly put these laboratory achievements into the fields for verification can they possibly become truly useful breeding resources, rather than just highlights in papers.

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Conflict of Interest Disclosure

The author affirms that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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