

Plant Glutamate Receptor Like Genes (GLRs): Molecular Insights Physiological Functions and Agricultural Perspectives

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ABSTRACT

Over the last few years, Plant Glutamate Receptor-like (GLR) genes have been identified as the plant equivalents of animal glutamate receptors in plants. Here, we summarize their identification, construct, activity, and methodology in the current report. GLRs in plants are involved in root morphogenesis, pollen-tube guidance, embryo development, and stress responses. They are ligand-gated ion channel family that participates in signal transduction. These challenges are; the identification of native ligands, as well as the interaction signaling given potential functional overlap and for crop deployments. Different research approaches can demonstrate how GLRs contribute to plant adaptation and survival. This emergent domain holds the promise of enhancing plant resilience and sustainability.

Keywords: Glutamate Receptor like Genes (GLRs); Ion channels; Plant development; Stress Responses; Crop Improvement

Introduction

Glutamate Receptors in Animals

Glutamate receptors that exist within the tissues of the brain and nervous system of animals are the central mediators of excitatory neurotransmission and signaling of normal functions (Traynelis, et al. [1]). These receptors are classified into two main categories: iGluRs and mGluRs. iGluRs pertain to the ionotropic glutamate receptors while mGluRs to the metabotropic glutamate receptors (Bowie [2]). iGluRs are ion channels that are ligand-gated. The binding of glutamate activates channels to allow ions to flow in, mostly of cations, during depolarization, leading to the conductance of electrical signals along the neuron (Dingledine, et al. [3]). Compared to mGluRs, which are G-protein receptors that affect intracellular signal transmission, mGluRs act similarly but through a different mechanism (Niswender [4]). Glutamate receptor's role in animals has been long-known to

play several critical functional roles like synaptic plasticity, learning & memory, as have been further clarified by research as factors affecting neural disorders too (Contractor, et al. [5]).

Glutamate Receptor Like Genes (GLRs) in Plants

In reality, proteins similar to glutamate receptors (GLRs) have been found in plants, since the transmitting glutamate system is not present in the plant nervous system (Lam, et al. [6]). Causing of union between human and animal iGluRs, as a result, may demonstrate that the molecular similarities as well as specific functions provided to both substances are rooted in their evolutionary development (Lacombel, et al. [7]). Nevertheless, the know-how of plant GLRs in specific roles and mechanisms is still very limited, which has attracted much attention from scientists who anticipate the benefit that it may bring to the understanding of plant physiology and adaptation (Forde [8]).

Importance and Potential Roles of Plant GLRs

The discovery of such receptors in plants has unequivocally attracted the attention of scientists because they promptly want to understand their role in quite many stages of plant development, growth, and stress response (Chiu, et al. [9]). These receptors could be involved in such important functions as ion homeostasis regulation, signaling pathways, and the maintenance of physiological processes without which no plant can survive, reproduce, or achieve the best results (Davenport [10]). Determining the functioning of plant GLRs may represent a decisive step to getting to know the structural processes at the base of plant biology and the paradigms governing plants. So, this information would contribute to introducing new strategies for the development of breeding crops able to withstand stress conditions and using plant growth and yield optimization (Tapken [11]).

Discovery and Identification of Plant GLRs

Initial Findings and Characterization of GLRs in *Arabidopsis Thaliana*

The first GLRs from the plants were reported in the model organism *Arabidopsis thaliana* through genome-wide sequence analysis and used for homolog search (Lacombe, et al. [7]). Experts identified that the *Arabidopsis* genome was composed of many genes that bear a high degree of similarity to those that code for amino acid glutamate receptors in animals. It was evident from this that a distinct group of putative glutamate receptors was present in plants as well (Lam, et al. [6]). The findings motivated further profiling of structure, expression patterns, and machinery they may use to compass the plant GLRs which resulted in their great understanding.

Homology to Animal Ionotropic Glutamate Receptors

Mapping of such sequences and comparison of structural homologies with plant GLRs showed that these genes contain the ligand-binding domain plus the topology of the same domains that are found in animal iGluRs (Chiu, et al. [8]). Despite the little sequence identity between the plant GLRs and other animal receptors, the shared structure and domains indicated that the plant GLRs have an atypical function as ligand-gated ion channels like the other GLRs (Tapken [11]). Yet, distinguishing differences were ascertained as well. Therefore, we can conclude that plant GLRs evolved the way it was modified to perform the unique functions that plants need (Forde [8]).

Phylogenetic Analysis and Classification of Plant GLR Families

Through detailed phylogenetic research, plant GLRs have been divided into separate families relying upon their evolution relationship and sequence similarity (Chiu, et al. [8]). In *Arabidopsis*, three major families have been identified: They consist of GLR1, GLR2, and GLR3 which unlike GLR2 consist of one or more members (Roy, et al.

[12]). Thus, dynamic patterns of expression have been found in the plant GLR families, which localize differently and possibly convey a variety of functions, reflecting functional diversification. A crossover between plant genomes uncovers the presence of GLR homologs in other plant species as well, thereby we can assume that these genes are present in all plant species (Vincill, et al. [13]).

Structural Features and Domains of Plant GLRs

Membrane Topology and Subunit Composition

It is theoretically expected that plant GLRs were arranged into tetramer forms which are similar to animal iGluRs where the extracellular N-terminal domain, the ligand binding domain (LBD), the transmembrane domain, and the intracellular C-terminal domain were assigned for each subunit (Tapken, et al. [11]). The transmembrane region is comprised of three membrane-spanning segments and an extra loop segment which forms probably the ion channel pore (Simon, et al. [14]). The plant GLR complexes may vary in subunit composition and stoichiometry, which, in turn, likely determine how the receptors act, affect their shaping and perform their effects (Tapken, et al. [15]).

Ligand Binding Domains and Selectivity

The similar structural elements in the plant GLR place and animal iGluR place strongly suggest that the plant GLR may be functioning as a glutamate receptor (Tapken [11]). Despite this, the lines of plant GLRs are not biochemically identical to the corresponding ones of their animal relatives. The LBDs have residues and motifs that do not occur in the animal GLUs and may act differently regarding ligand affinity and species (Pandey, et al. [16]). Researchers have presented the theory that GLRs of plants (glutamate receptors) probably interact with more than one kind of ligand, which can be amino acids, small molecules, or perhaps even plant-derived compounds (Michard, et al. [17]). Identifying the native ligands and the binding mechanism is a fundamental process in discovering the impact of the plant GLRs on functions.

Ion Channel Properties and Gating Mechanisms

Owing to the results of electrophysiological studies the ion channel properties and slates identifying the gating mechanisms of plant GLRs can be investigated (Tapken, et al. [15]). Many plant GLR members have been shown to work as functional ion channels while being expressed in heterologous systems; these channels can be permeable to different types of ions such as sodium, potassium, calcium, etc., and have various gating kinetics. Their exact gating processes and ion selectivity patterns might be quite distinguishable from the animal iGluRs and they may uphold a physiologically distinct role (Kong, et al. [18]). Thus, obtaining the characteristics of plant GLRs ion channels as well as their regulation will be beneficial by use which would provide insight into their role in cellular signaling as well as ion homeostasis.

Expression Patterns and Localization of Plant GLRs

Tissue Specific Expression Profiles

However, a thorough study of plant GLRs and their mRNA expression profiles has demonstrated that most of them demonstrate complex tissue and developmental specificity, further evidencing their divergent functional applications. An example is the root tissue where certain soluble glucose systems are expressed compared to reproductive or leaf tissues (Chiu, et al. [19]). Such as different organs and the growth stages, which allow the researchers to conclude their functions deeply by looking at the expression patterns of specific GLRs.

Subcellular Localization Studies

Besides their differentiated expression in cell tissues, Conveniently, obligate in these subcellular compartments, like plasma membrane, endoplasmic reticulum, and other organelles of plant GLRs have been detected (Carraretto, et al. [20]). It is thought that the plant GLR localization within the cells plays a critical role in their efficient functionality and might facilitate the diversity in their many physiological actions. The subcellular distribution of plant GLRs in different cell types and development phases have been used along with fluorescent protein tagging, and immunolocalization as means of studying the same (Wudick, et al. [21]).

Developmental Regulation and Environmental Factors

It appears that GLR expression and location in plants are brought about by plant growth and under vexation cues as revealed by the practice (Price, et al. [22]). Several lab results reported GLR expressions to change during seed germination, root development, and reproductive stages of development; the obvious implication being the mechanism's involvement in these key developmental processes. Moreover, higher-order stress factors like drought, salinity, and temperature fluctuations have also been identified to reveal the function of particular plant GLR, indicating their other functions in stress tolerance mechanisms (Chiu, et al. [23]).

Proposed Functions of Plant GLRs

Roles in plant development and growth

Root Development and Architecture: An array of evidence implies that plant GLRs carry out the functions primarily related to controlling root growth and forming patterns of roots (Michard, et al. [17]). The molecular mechanism of the gene's function postures mutant research close to the heart of botany, as disruptions in specific GLR genes lead to variations in root development, branching, and gravitropism alike. Additionally, a kind of GLRs has been identified in the tip of the root and the meristematic region of the root with the highest expression, which implies its function of coordinating cell division and elongation processes which are the key steps during seedling and plant establishment (Kwaaitaal, et al. [24]).

Pollen Tube Guidance and Fertilization: Thus, this plays a significant role when pollen tube elongation and guidance are involved which is essential for fertilization of plant species. Certain GLR proteins are highly expressed in pollen and ovules later although their disturbance leads to disorderly pollen tube growth and infertile fertilization (Kang, et al. [25]). A bidirectional communication system occurs through the pollen tubes, which are guided by the release of signal molecules or ions that help them crawl toward ovules (Vincill, et al. [13]).

Seed Germination and Seedling Establishment: The distribution and operation of particular gen types of plant GLRs seem to be most relevant to seed germination and young sprouting plants. In research mutant lines lacking in particular GLRs showed delayed or unusual germination patterns, as well as altered growth and plant establishing processes of seedlings. It is documented that GLRs may be highly responsible for studying the transition from blossom to the control of a vegetative seedling by monitoring the signaling pathways or ion homeostasis, especially at this developmental stage (Price, et al. [22]).

Responses to Biotic and Abiotic Stresses

Plant Pathogen Interactions: New data is being uncovered that plant renin is a companion of the immune system to can fight different pathogens among bacteria, fungi, and viruses (Wudick, [21]). The transcriptional regulation of specific GLRs occurs via pathogen infection and mutations of these genes may result in distinct phenotypes associated with pathogen susceptibility or resistance (Vatsa, et al. [26]). We hypothesize that the role of GLRs is related to the processes of signaling or ion transport that could induce plant immune reactions, e.g. accumulation of antimicrobial compounds or the activation of defense genes (Forde [27]).

Drought, Salinity, and ther Abiotic Stress Responses: In addition, it has been suggested by plant G-coupled Receptors to be implicated in the reactions to a multitude of abiotic stressors including drought and high temperature in particular, but many others as well (Chiu, et al. [9]). Expression of a particular GLR is tuned carefully when they experience stressful conditions, and their disturbance leads to stress intolerance or sensitivity traits. Scientists propose (Michard, et al. [17]) that different classes of GLRs may be involved with signal transduction under stress conditions, maintenance of the ion balance, or control of the physiological processes that are necessary or responsible for stress-adapting mechanisms (Carraretto, et al. [20]).

Potential Involvement in Signaling Pathways and Ion Homeostasis: Just as animal ionotropic glutamate receptors are similar to ionotropic receptors found in plants, GLRs in plants are supposed to act as the ligand-gated ion channels responsible for the cell signaling and control of cellular ion homeostasis (Ortiz Ramírez, et al. [27]). These very receptors may initiate the flow of particular ions, such as

calcium, potassium, or sodium, into or out of the cell consequently, which causes subsequent downstream signal cascades or altered membrane potentials (Traynelis, et al. [1]). Such transport events of ions and signaling through the channels may be controlling different physiological processes such as cell division, growth, and stress responses. GLRs can also be involved in communication with other proteins and signaling components functioning as a part of more complex regulatory systems aiming at the interaction of environmental and developmental factors (Akula [28]). The finding of potential binding partners and the signaling pathways downstream of plant GLRs, is going to be valuable in unraveling their multiple roles in plant biology.

Experimental Approaches and Techniques

Genetic Studies (Mutants, Overexpression Lines): The role of the plant floral enzymes has been elucidated chiefly through the means of genetic approaches (Chiu, et al. [9]). From this, they then generated mutant lines where the disruption or knockout of a specific GLR gene was observed and consequently evaluated the effects on the phenotype. This helped them to link specific genes with a potential role in various biological processes (Yu, et al., 2022). In addition to mutant lines, overexpression lines were also introduced that facilitate the evaluation of the consequences of increases in the native level of GLRs' expression on plant growth, improvement, and reaction to stresses (Zhang, et al. [29]).

Electrophysiological Characterization: The electrophysiological approaches, e.g. patch-clamp recordings or voltage-clamp experiments, were used to investigate the ion channel architecture and gating models of plant GLRs (Teardo, et al. [30]). This technique is realized by expressing the plant GLRs in either heterologous systems such as *Xenopus* oocytes or extracts from mammalian cell lines and then measuring the ions' currents. However, unlike mammals where GLRs bind a ligand known as gonadotropin-releasing hormone (GnRH), plant GLRs do not (Michard, et al. [17]). Through such experiments, the properties regarding the plant GLRs' functional traits and the possible ways in which they influence fluxes of ions and the signaling events are often well understood. A large part of the mystery of functioning plant GLRs as channels has been removed by electrophysiological investigations. Using tools resembling the used patch-clamp electrophysiology, study, and ion conductance assays, researchers have shown that some of the members of the GLR family are also able to be functional channels when they are expressed in *Xenopus* oocytes or neuronal cell lines (Tapken, et al. [11]; Tapken [15]). One has shown that their ion permeability and gateways could be widely varied among different plant GLR sub-group members. For example, AtGLR3.4 originating from *Arabidopsis* which belongs to a group of cation channels non-selective to different types of monovalent and divalent cations, such as calcium was shown to be this kind of channel (Krzyszowicz, et al. [31]). But AtGLR3.3 is, as shown in (Qi, et al. [32]), more selective for calcium than the other cations. Besides, unlike animal ones, the opening of plant GLRs' pores works via different mech-

anisms, and available data indicates that it can be triggered by many different compounds, including amino acids, small molecules, and probably plant-derived ones (Tapken, et al. [15]). The electrophysiological investigation of plant membrane GLRs was instrumental in the identification of their possible contribution to the mediation of ion transfer and the regulation of signaling events involved in different processes including pollen tube growth, stress responses, and ion homeostasis (Choi, et al. [33]).

Imaging Techniques and Reporter Assays: Tagging with fluorescent proteins and the use of stained cells assay has gradually become the key method of the study of plants' GLRs subcellular localization, their dynamics, expression patterns, and other features (Tanz, et al. [34]). Fluorescence microscopy, FISH (Fluorescence InSitu Hybridization), and promoter-reporter constructions allow scientists to look into the spatial and temporal expression of GLRs in different plant tissues, and developmental stages (Shakoori [35]). This also reveals the role of GLR localization patterns as well as their likely translocation and traffic in the response to changes in the stimulus of a diversity of environmental cues.

Biochemical And Structural Analysis Methods: Chemical and crystal analysis methods like plant GLR purification, ligand assays, and x-ray crystallography have aided the molecular identification of plant GLRs (Alfieri, et al. [36]). The isolated GLR proteins can be utilized to amend the liaison of ligand binding sources, structural alterations, and interaction of the proteins or small molecules. In contrast, structural studies carried out using crystallography with X-ray and cryo-electron microscopy produce details related to the 3-D structure of plant GLRs from where the location of functional domains and probable binding sites of ligands can be identified (Simon, et al. [14]).

Imaging Techniques and Reporter Assays: Due to fluorescent protein labeling, promoter-reporter genetic fusion constructs, and advanced microscopy, plant GLRs are among the most studied proteins concerning their expression patterns, cellular location, and mobility in the cells (Vincill, et al. [37]). Scientists are applying fluorescent markers such as GFP or mCherry to GLR genes by gene fusion techniques. So, it has aided in viewing the spatial and temporal expression of these receptors in different plant tissues, developmental stages, and subcellular compartments (Chalfie, et al. [38]). For instance, a particular GLR family member that predominates in root tips, pollen tubes, and vascular tissues among others, was identified and therefore it follows that in these tissues, it would play a role as indicated. Moreover, modern imaging methods, such as standard confocal microscopy and fluorescence recovery after photobleaching (FRAP), have allowed researchers to observe the problem of localization and flux of emptying receptors (GLRs) triggered by various stimuli or environmental impacts (Lodde, et al. [39]). Moreover, transcriptional regulation of GLR genes was assessed using promoter-reporter fusion constructs. That approach allowed us to identify cis-regulatory elements and potential transcription factors involved in their transcription regulation. These

imaging and reporter assays have been posing team players and increasing our cognition about the spatial as well as temporal dynamics of the plant GLRs that provide the base for more accurate function studies.

Biochemical and Structural Analysis Methods: A series of biochemical and structural techniques have become helpful instruments to delve into the molecular characteristics and unravel the plant GLR mechanisms. The protein purification method that uses ligand binding assays (Tapken [11]) has been used as a reliable tool to determine the actual ligands and their ability to bind them. As an example, recent studies demonstrated a high probability of binding of GLRs derived from plants with specific amino acids, small compounds, and other plant-derived molecules, but not the compounds produced in nature remained (Michard et al. [11,17]). Structural analysis tools that include X-ray crystallography and cryo-electron microscopy (cryo-EM) have provided a reasonable framework for an in-depth structure determination of plant GLRs and allowed specifying the key functional sites and possible ligand-binding pockets (Tapken [17]). These structural studies have led to the discovery of similarities and variations between plant GLRs and their homologs in the animal kingdom, the data obtained from these findings have valuable information both for explaining animal kingdom evolutionary relationships and molecular functions diversification (Tapken, et al. [11]). Apart from techniques like isothermal titration calorimetry (ITC) and surface plasmon resonance (SPR), additional studies also used known/established methods to understand how the glutamate receptors of plants can be activated (Kang, et al. [25]).

Challenges and Future Perspectives

Functional Redundancy and Genetic Compensation: While deciphering the roles of different plant GLRs tends to be complicated due to the presence of functional redundancies and genetic compensation between members within the same family, this intricacy is exactly why scientists seek to study these molecules (Kang, et al. [25]). In plants the structure of sewed genes is often multiple and due to this disruption of the individual gene would not lead to the phenotypic effect as other GLRs could compensate sufferer's activity. Resolving this essential mutagenesis matter involves making and assessing complete higher-ordered mutants, composed of knock-out of multiple GLR genes or employing complex gene manipulation technologies, like inducible or tissue-specific ones (Tapken, et al. [13]).

Ligand Identification and Binding Mechanisms: However, the shared structural features between the plant GLRs and the ionotropic glutamate receptors in animals should not be the only thing that is being considered because the ligands that serve as binding mechanisms for plant GLRs are yet to be discovered (Wudick, et al. [17,21]). None other but the identification of the natural ligands involved in binding to plant GLRs is of paramount importance in envisioning their physiological functions and the ensuing process in metabolic/signaling pathways (Grenzi, et al. [40]). Techniques, including ligand-binding

assays, biochemical screenings, and computational modeling, could be useful in discovering and characterizing the panel of plant-GLR ligands (Zhao, et al. [41]).

Interacting partners and Downstream Signaling Pathways:

Cellular or nuclear GLRs are expected not to be specific in themselves, but be part of a signal network together with other factors (Sanders, et al. [42]). It is of great importance to reveal among what type of proteins and further signaling pathways plant GLRs are interacting with so that it will be possible to distinguish the regulatory network and the functional roles of the plant GLRs in their broader context of plant physiology (Ahmed, et al. [43]). The methods of protein-protein interaction studies, genetic screens, and transcriptomic and proteomic analyses may eventually be useful in the elucidation of the networks interconnected with plant GLRs (Wang, et al. [44]).

Potential Applications in Agriculture and Biotechnology:

Unlocking the secrets of plant genomes implies that the applications of plant GLRs in agriculture technology as well as biotechnology are almost unlimited (Hu, et al. [29]). Switching on or blocking particular GLRs could ultimately result in crops, including those that are more tolerant to stress, vegetables that grow faster, or plants with high-quality yield. Besides, GLRs of plants might be considered the aim of creation of the new growth stimulators or herbicides, which widen the opportunities of regrouping crops for growing better with no pests (Shah, et al. [45-50]). Nevertheless, more studies are required for a comprehensive understanding of plant GLRs as well as exploring the biotechnological prospects of this class of toxins and mitigating any potential drawbacks.

Conclusion

The GLR genes Diggle is undoubtedly one of the most recent research areas that have unveiled interesting connections between plant biology and physiology. An essential feature of all plant GLRs has been revealed in the body of research where these receptors are being identified and characterized. The structure similarity of plant GLRs to the animal ionotropic glutamate receptors, their diverse expression patterns, and their localization in various tissues and development stages have also been studied. The practical function of the genealogical line encompasses different developmental aspects such as root, flower development, pollen guiding, seed germinating, stress responses, and signaling pathways. Though the great growth of research on plant GLR brings many questions and problems, no one can deny the discovery and understanding of the plant GLR is one of the most impressive research projects. Figuring out the in vivo ligands and the mechanisms of how the GLR from the plant works is a basic but essential step to capture our comprehension of their functions. Furthermore, identifying the functioning partners and flow down the pathways responsible for plant GLRs will add a more complete outlook on their mechanism of regulation and physiology. The difficulties brought about by functional redundancy and the ability to restore functions through genetic compensation will demand the

laboratory tools and intelligent approaches of the twenty-first century. In addition, investigations into the biotechnological potential of plants GLRs can provide a variety of stress-resistant crops, and better-grown plants, and revolutionize agriculture. Through challenges, study in this field progresses; interdisciplinary collaborations as well as integrating diverse experimental techniques will be compulsory for the elucidation of subtle plant GLR functions and mechanisms. Advancements in genome-wide association studies of several plants will continue to expand our knowledge of plant biology, leading to the development of revolutionary technologies in agriculture and biotechnology which will in turn improve food production and future sustainability.

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MAN collected the data and wrote the manuscript. HSH and ZN revised the manuscript.

Conflict of Interest

The authors do not have any kind of conflicts of interest.

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