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# Role of GRAS Transcription Factor in Plant Growth, Development and Various Stresses: A Review

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## ABSTRACT

The GRAS transcription factor family is a plant-specific regulatory proteins that play fundamental roles in various biological processes. The acronym “GRAS” stands for “Gibberellic Acid Insensitive, Repressor of GA1-3 and Scarecrow,” representing three of its founding members. Additionally, GRAS members are instrumental in orchestrating symbiotic interactions, stress responses and other vital physiological functions. The N-terminal of GRAS protein is very diverse, but the C-terminal GRAS domain is conserved. The GRAS proteins’ C-terminal conserved domain directly influences how they work. For instance, in the Arabidopsis plant, alterations to the phenotype of the slender rice 1 (SLR1) and Repressor of GA (RGA) proteins result from mutations in this domain. More than 30 plant species have been found to have GRAS proteins, which have been classified into 17 subfamilies so far. This review focused on the structural characteristics of GRAS proteins, their growth and diversity in plants, GRAS-interacting protein complexes and their function in biological processes. Moreover, GRAS proteins also mediate responses to phytohormones, such as gibberellins and strigolactones and regulate phytochrome signaling, which is crucial for light perception and plant growth. It also discussed the significance of GRAS proteins throughout various biological processes in plants. Additionally, we outlined recent studies that used CRISPR-Cas9 technology to modify GRAS genes in a plant for various features. Additionally, there have been discussions of using GRAS genes in agricultural enhancement efforts.


**Key words:** Abiotic stress, DELLA, Development, GRAS protein, Growth.

Gibberellic acid (GA), a pivotal plant hormone, involved diverse growth and development processes. Its initial discovery in rice seedlings dates back to 1926. The acronym GRAS, derived from GIBBERELLIC-ACID INSENSITIVE (GAI), REPRESSOR of GAI (RGA) and SCARECROW (SCR), identifies proteins within the GRAS domain that play pivotal roles in GA signaling pathways (Hirsch *et al*., 2009). These proteins evolved from bacterial Rossmann fold methyltransferases through lateral gene transfer, further diversifying in terrestrial plants (Zhang *et al*., 2012). GRAS transcription factors (TFs) govern a spectrum of functions including plant development, phytochrome A signal transduction, root radial patterning, gibberellin signaling, shoot meristem maintenance and axillary meristem initiation (Guo *et al*., 2017).

Most GRAS proteins span 350 to 900 amino acids, characterized by hydrophobicity, mono-exonic structure and common motifs at their carboxyl (C-) and amino (N-) ends (Fig 1). These motifs intricately relate to GRAS protein activities. C-end motifs encompass LHR II, PFYRE, VHIID SAW and LHR I associated with protein interactions in bZIP TFs (Cenci *et al*., 2017). Meanwhile, the C-termini contain conserved residues with uncertain roles. The N-terminal region, excluding the DELLA subfamily, displays remarkable diversity and significantly contributes to gene activities (Guo *et al*., 2017). Notably, mutations in these patterns, as seen in Arabidopsis SLR1 and RGA proteins, trigger pleiotropic phenotypic changes (Tian *et al*., 2004; Itoh *et al*., 2002). The presence of two or three domains in rice’s OsGRAS39 and OsGRAS54 respectively suggests annotations stemming from tandem duplication events (Zhang *et al*., 2012). Considering their pivotal role, GRAS TFs hold promise for crop breeding by influencing diverse crop facets. This review succinctly captures their advancements and versatile functions in enhancing growth, productivity and resilience against biotic and abiotic challenges. Furthermore, it underscores the roles of GRAS genes in mycorrhizal and nodular connections, arbuscular mycorrhizal interactions and signal transduction.

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### Mechanism of a transcription factor regulating the stress signaling pathways

Whenever there is stress, a signaling cascade is triggered by the recognition of the stress signal by receptors on the membrane of the plant cell. Numerous plasma membrane

proteins, such as cyclic nucleotide-gated channels (CNGCs), glutamate receptor-like (GLR) channels, MscS-like proteins (MSLs), OSCA1 and COLD1 Hamilton *et al.* (2015) are all involved in (Fig 2). Through secondary messengers including Ca2+, ROS and phytohormones, these sensors subsequently relay the signal downstream (Fig 2). Similar to ROS, second messengers activate several protein kinases (PKs) and protein phosphatases (PPs), including calcium-dependent protein kinases (CDPKs), calcineurin-B-like proteins (CBLs), CIPK (CBL-interacting protein kinase) and numerous additional PKs. The mitogen-activated protein kinase (MAPK) cascade is one of these PKs (Fig 2). The information is subsequently transmitted downstream by these PKs and PPs, where it activates a number of phosphorylation/dephosphorylation cascades, including those that phosphorylate and dephosphorylate transcription factors (TFs) (D'Autreaux *et al*., 2007). Each of the aforementioned stress-responsive genes is controlled by phosphorylation- and dephosphorylation- activated transcription factors (TFs). A single transcription factor (TF) may regulate a lot of downstream target genes, unlike functional genes. Due to these qualities, they are excellent candidate genes for the genetic manipulation of complex stress tolerance traits (Nakashima *et al*., 2009). However, GRAS encoding protein DELLA acts as a positive regulator for the GA signaling pathway. DELLA and GA signaling interplay regulate MOC1 via modulating SLR1 protein levels to regulate tiller number and plant height. Moreover, DELLA proteins also regulate tiller number and hypocotyl development by interacting with chromatin remodeling complexes and brassinosteroid (BR) pathway. The DELLA interacts with chromatin remodeling complex, Pickle (PKL), which further interacts with PIF3 and BZR to regulate hypocotyl growth by inhibiting the histone methylation of genes involved in cell elongation. The SCL3 controls its functionality during ground tissue division and root elongation, where SCL3 regulates its level and is also being regulated by DELLA proteins and attenuates DELLA repressors positive regulators for the functional GA signaling pathway. The DELLA protein also makes a complex with ABSCISIC ACID INSENSITIVE 3 (ABI3) and ABI5. This complex binds to the promoter of the SOMNUS (SOM) gene, involved in the negative regulation of the seed germination process. The functional investigation of a range of TFs employing overexpression transgenic lines and knockout/knockdown mutants in model plants and other crops. In the review that follows, we concentrate on recent advancements in our knowledge of TFs and examine novel molecular mechanisms of TF activity in the presence of abiotic stress, with a focus on their role in coordinating plant responses to stress.

### Structural features of GRAS proteins

GRAS proteins span 400 to 770 amino acids, featuring variable N-termini and conserved GRAS domains at C-termini. The 390 amino acid GRAS domain holds motifs: SAW, LHRI, VHIID, LHR II, PFYRE and LHR II Hakoshima, (2018). LHRI bears NLSs, conserved across GRAS proteins Sun *et al*. (2012). Interactions, including DNA binding, involve LHRI-VHIID-LHRII motif complex. PFYRE motif holds proline, phenylalanine/tyrosine and arginine/glutamic acid residues. The SAW motif, conserved in GRAS, combines WX7G, LXW and SAW sequences. Mutations in PFYRE and SAW affect healthy development (Itoh *et al*., 2002; Heckmann *et al*., 2006). Unlike GRAS domain, variable N-termini with intrinsically disordered domains (IDDs) facilitate molecular recognition (Sun *et al*., 2012). These traits enable GRAS proteins to participate in gene-specific and protein-protein interactions. Repeated DELLA, TVHYNP and LR/KXI motifs are crucial for GA signaling and growth Murase *et al*. (2008). Similar motifs in interactions among GRAS subfamily members (Tian *et al*., 2004; Sun *et al*., 2012).

### Role of MicroRNA in regulation of GRAS transcription factors

MicroRNAs miRNAs, conserved non-coding RNA sequences of 21 to 24 length, regulate mRNA cleavage or translation suppression to govern plant growth and development. They control auxin signaling, organ formation and other processes. Arabidopsis AtSCL6 is targeted by miR171, impacting axillary meristem differentiation and shoot elongation (Schulze *et al*., 2010; Wang *et al*., 2010). miR171 regulates floral meristem determinacy and phase shifts in rice and barley, showing conservation across monocots and dicots (Curaba *et al*., 2013; Fan *et al*., 2015). It also regulates chlorophyll synthesis *via* SCL6, SCL22 and SCL27 in plants (Ma *et al*., 2014). In *M. truncatula* and L. *japonicus*, miR171 targets NSP2 transcripts, crucial for nodule formation and mycorrhiza association (Hofferek *et al*., 2014; Hossain *et al*., 2019). A regulatory loop controlling miR171h's cleavage of NSP2 during AM symbiosis exists (Lauressergues *et al*., 2012). In soybean, miR1710 and miR171q cleave GmSCL-6 and GmNSP2 mRNAs for nodulation (Huang *et al*., 2017). Tomatoes see SlGRAS24 and SlGRAS40 targeted by miR171, with SlGRAS8 inhibited translationally (Huang *et al*., 2017). These findings underscore miRNAs' role in controlling GRAS genes during various plant developmental stages.

## Biological functions regulated by GRAS TFs

### Development and maintenance of apical shoot and axillary meristem

In contrast to animals, plants constantly grow new organs throughout post-embryonic shoot growth, which is reliant on the shoot apical meristem (SAM). The axillary meristem and lateral shoots of tomatoes were both influenced by a GRAS gene known as Lateral suppressor (LAS). Similar to tomatoes, Arabidopsis has a conserved lateral shoot development mechanism. AtLAS (homolog of LeLs) gene in Arabidopsis contributes to axillary shoot development (Greb *et al.,* 2003). In rice, MOC1 controls tiller number, distinguishing monocot and dicot branching patterns. Petunia's GRAS gene, Hairy Meristem (HAM), supports lateral organogenesis and meristem maintenance, with

reduced meristem in ham mutants. HAM and WUSCHEL (WUS) cooperate in meristem upregulation; HAM's interaction with TERMINATOR and SHOOT MERISTEMLESS (PhSTM) prolongs Petunia's response. This pathway alerts meristem cells in developing shoot meristem tissues.

**Regulation by SCR/SHR in root radial patterning**

A transcription factor called SCARECROW (SCR), characterized by a plant-specific GRAS domain, was identified over 13 years ago. In *A. thaliana*, SCR and SHORTROOT (SHR) are responsible for regulating root development and radial patterning (Wen *et al.,* 2002). The root's architecture comprises pericycle and vasculature surrounding a central core stele, with radially arranged epidermis and ground tissue layers (cortex and endodermis). Quiescent center (QC), containing slowly dividing cells, maintains stem cell niche (Miyashima *et al*., 2009). SHR specifies QC and endodermis in adjacent ground tissue, extending from stele-originated expression (Wen *et al*., 2002). Positive feedback and SCR ensure confined SCR transcription to ground tissue. Understanding SHR movement regulation via interaction with SCR improved SCR/SHR insight. Entering endodermal layer, SHR forms nucleus-based complex with SCR, hindering progression to cortical layer (Helariutta *et al*., 2000). Complex triggers additional SCR production in nucleus, securing SHR sequestration in endodermal layer. This mechanism potentially explains singular endodermis layer encircling stele. As most plants possess one endodermis layer and rice's SCR/SHR orthologs share similar expression patterns, this proposed mechanism likely endures evolution.

**GRAS domain complex in NSP1/NSP2 formation**

Recent findings highlight legumes harboring GRAS domain proteins nodulation signaling pathway 1 (NSP1) and II (NSP2) (Itoh *et al*., 2002), integral to the nitrogen-fixing symbiosis between rhizobial bacteria and legume plants. Recognition of rhizobia-secreted Nod factor by root hair cells triggers morphological changes, initiating mutualistic connections. Nodule formation, a cortical cell division-driven process, provides a habitat for nitrogen-fixing bacteria. NSP1

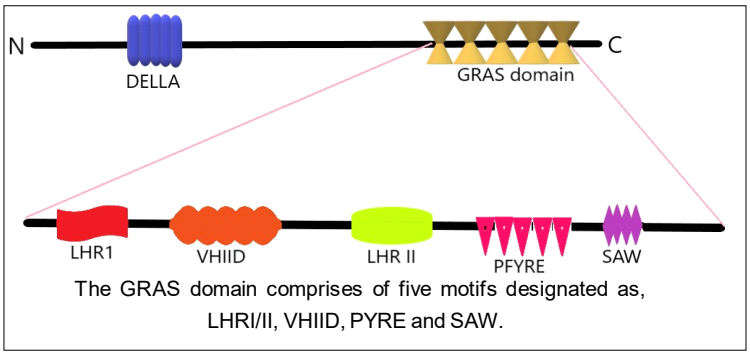


**Fig 1:** Structural features of a typical GRAS protein.

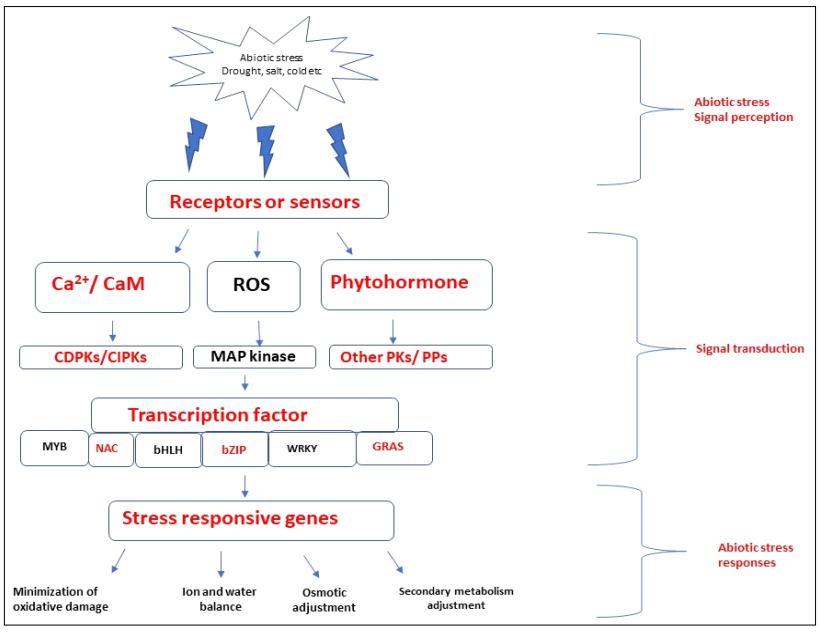


**Fig 2:** Model for transcription factors regulating abiotic stress-signalling pathways.

and NSP2, pivotal in Nod-factor signaling and nodule growth (Itoh *et al*., 2009), potentially form polymer structures. In model legume *M. truncatula*, NSP1 interacts with promoters of Nod factor-inducible early nodulin genes, crucial for nodulation Koizumi *et al*. (2012). NSP1 efficiently binds Nod factor-bound ENOD11 promoter with NSP2's assistance. Notably, a single nucleotide variation in NSP2's LHR I domain disrupts the NSP1-NSP2 interaction, vital for nodule formation. This underscores the GRAS protein-DNA complex's significance in *M. truncatula* nodulation signaling.

**Plant tillering**

The GRAS protein MONOCULM 1 (MOC1), found in the axillary buds of rice, regulates the initiation of axillary bud and, as a result, regulates tiller growth. In contrast to overexpression lines that showed significant tillering, the moc1 null mutant only had one culm and no tillering. TILLER AND DWARF 1 (TAD1) and ANAPHASE-PROMOTING COMPLEX (APC/C) are both co-activated in a cell-cycle-dependent way to control the breakdown of MOC1 (Lin *et al*., 2012). For a very long period, gibberellin (GA) is known to prevent plant tillering (Li *et al*., 2003). Additionally, it is understood that the dwarf and low-tillering (DLT) gene of rice, which produces the GRAS protein, participates in the control of plant shape *via* BR signaling. When the *DLT* gene in rice was mutated, it resulted in low tillering and dwarfism.

**Microsporogenesis and fruit ripening**

It has been demonstrated that the GRAS protein plays a role in the transcriptional control of fruit ripening. Anthers of *Lilium longiflorum* express LISCL, a nuclear-localized microsporocytes gene, most prominently during the development of premeiotic anthers. A temporary expression experiment demonstrates its role in meiosis and how it activates the pollen mother cell (Morohashi *et al*., 2003). The axillary meristem's initiation was blocked by the Lels mutation in tomatoes. Tomato GRAS1 is also expressed differently in the breaker and mature fruits, highlighting its function in fruit development. The GRAS transcription factor SlGRAS4 has recently been shown to have a function in tomato ripening by controlling genes that produce ethylene and MADS transcription factors (Liu *et al*., 2021).

**Seed germination**

Seed germination is influenced by both the internal plant growth regulators ABA and GA as well as the external environment, which includes temperature, moisture and light. GAs regulates the beginning of germination, while ABA predominantly regulates seed dormancy. Additionally crucial in regulating seed germination is the GRAS family protein DELLA (Fig 3). The DELLA protein forms a complex with ABSCISIC ACID INSENSITIVE 3 (ABI3) and ABI5 when it binds to the promoter of SOMNUS (SOM), which takes part in the negative control of seed germination. It has been demonstrated that the DELLA/ABI3/ABI5 protein complex and the SOM promoter interact when adverse circumstances (such as heat stress or darkness) cause ABA levels to rise and GA levels to decline. It increases the transcription activity of SOM genes and prevents seed germination when external or environmental conditions are adverse.

**GRAS gene and arbuscular mycorrhizal (AM) symbiosis**

Terrestrial plants and fungi commonly engage in AM symbiosis for nutrient exchange, involving root transcriptome reprogramming and morphological changes (Pimprikar *et al*., 2018). Fungus-produced lipochito-oligosaccharides and myc-factors induce host pre-symbiotic reactions, with strigolactones from host roots as the fungus-detecting signal

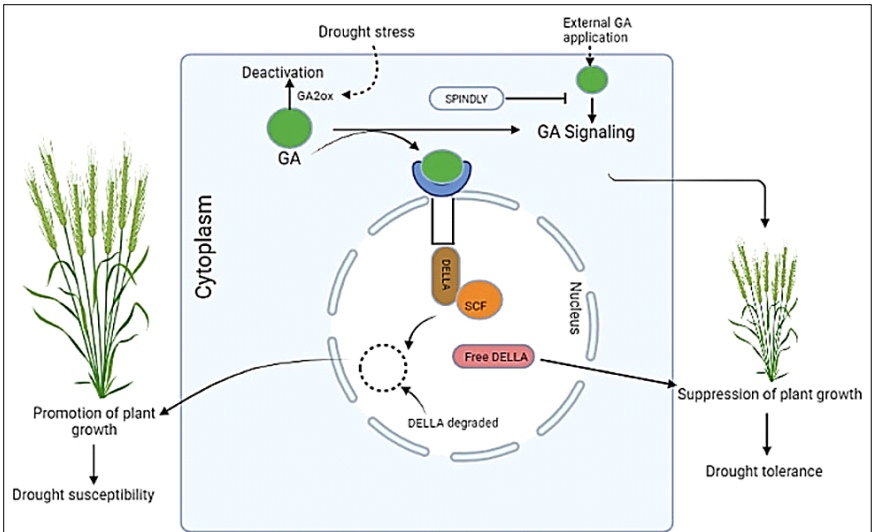


**Fig 3:** Molecular model of action of GRAS protein in plant development.

(Genra *et al*., 2013). The conserved GRAS TF plays a pivotal role in the signaling cascade, activating CCaMK to regulate CYCLOPS TF, uniquely fostering symbiotic links (Pimprikar *et al.,* 2016). Early *M. truncatula* interactions involve *GRAS* genes NSP1 and NSP2, necessary for signal transduction (Smit *et al*., 2005). Lotus transcription regulators LjNSP1 and LjNSP2 also partake in this (Heckmann *et al*., 2006). RAM1 influences AM emergence (Gobbato *et al*., 2012), while rice's DIP1 gene aids mycorrhizal development (Yu *et al*., 2014). MIG1, discovered in *M. truncatula*, associates with arbuscule-containing cells, impacting fungal interaction and root morphologies (Heck *et al.,* 2016). MtGRAS7's role in *M. truncatula* growth and Rhizobium bacterium inoculation is yet unclear (Revalska *et al*., 2019). NSP1 and NSP2 are crucial for Nod-factor signaling and nodule growth (Hirsch *et al.,* 2009). RAM1 activates arbuscule- related genes for nutrition exchange, including lipid and carbohydrate metabolism (Bravo *et al*., 2017; Jiang *et al*., 2018) and the PT4 and STR genes Rich *et al.* (2017). RAM1 and NSP2 are essential for fungus entry and cutin monomer production (Murray *et al*., 2013). NSP1 and NSP2 binding to ENOD11 promoter induces nodule growth and nitrogen fixation (Hirsch *et al*., 2009), miR171 h regulates NSP2 (Hofferek *et al*., 2014). AM symbiosis research is ongoing, aiming to uncover *GRAS* gene interactions in this relationship.

### GRAS versus multiple stress tolerance

Environmental stressors like salinity, drought and extreme temperatures harm plant growth, reducing yield. GRAS proteins regulate plant responses to stress. NtGRAS1 expression increases with ROS-rich stresses (Czikkel *et al*., 2007). PeSCL7, a stress-responsive GRAS-SCL protein, boosts stress tolerance by enhancing SOD and -amylase activity. Activating stress-inducible promoters, Arabidopsis SCL14 and OsGRAS23 enhance stress resistance Xu *et al*. (2015). HcSCL13, a ROS-scavenging GRAS protein (Zhang *et al*., 2020) and VaPAT1 from *Vitis amurensis* elevate salinity, drought and cold tolerance (Yuan *et al*., 2016). BrLAS overexpression in B. napus improves chlorophyll synthesis and drought resistance (Yang *et al*., 2011). SlGRAS40 overexpression in tomato enhances salt and drought tolerance (Liu *et al*., 2017). DELLA and SCL subfamilies, linked to auxins and gibberellins, play roles in stress response. DELLA mediates GA-signaling and stress tolerance (Fig 3) (Achard *et al*., 2008). SlGRAS40 overexpression affects GA and auxin levels, promoting ROS-based stress tolerance (Liu *et al*., 2017). RAD1, a GRAS-containing polymorphism in *M. truncatula*, affects symbiosis (Rey *et al*., 2017).

### Phytochrome signalling and growth regulation

GRAS proteins are vital for various developmental processes and light signaling. Key players in phytochrome A signaling include SCL21, SCL5 and PAT1 (PhyA) genes, sharing the EAISRRDL motif inducing Phy-A-related disorders Torres-Galea *et al*. (2006). SCL13 (Scarecrow-like 13), another PAT1 subfamily member, associates with the PhyB pathway. SCL13 is cytoplasmic and nuclear in Arabidopsis, influencing red light signaling and phyA responses. SCL3 antisense lines reduce red-light sensitivity and hypocotyl elongation Torres-Galea *et al*. (2006). AtPAT1 and AtSCL21 positively affect phyA signal transduction, forming a heterodimeric complex that regulates the phyA pathway, confirmed biochemically. DELLA in phytochrome signaling, notably, impacts shade avoidance. PhyB phosphorylates PIF4 TFs under low red/far red light, inactivating them; phyB controls GA20ox and GA3ox genes, breaking down DELLA and enabling PIF4 function (Colebrook *et al*., 2014).

## CONCLUSION

While our understanding of the GRAS protein family has grown, their specific characteristics and biological roles remain enigmatic. Certain *GRAS* genes, identified through functional analysis, hold promise for genetic engineering. However, research has predominantly focused on environmental responses of GRAS TFs, leaving agronomic factors influencing plant performance less explored. Unraveling transcriptional partners is vital for comprehending GRAS TFs' roles in growth and stress. Advanced methods like yeast pull-down and Co-IP are crucial for broad-scale DNA binding site identification. Given the impact of GRAS proteins alongside phytohormones like GA and Auxin on development and stress signaling, probing their connection with hormone-activated genes is vital. Refining the molecular mechanism regulated by GRAS TFs requires ongoing research. The future holds the prospect of deeper insights into plant biology, underpinning growth, development and stress adaptation.

### Conflict of interest

All authors declare that they have no conflict of interest.

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