

# Magnesium transporter family: sequence, evolution and expression analysis in soybean (*Glycine max* L.)

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### Edited by

Dr. S Hamidreza Hashemipetroudi,  
Genetics and Agricultural Biotechnology  
Institute of Tabarestan (GABIT), Sari  
Agricultural Sciences and Natural  
Resources University (SANRU), Iran

### Date

Received: 10 January 2024

Accepted: 30 January 2024

Published: 3 February 2024

### Correspondence

Dr. Parviz Heidari  
heidarip@shahroodut.ac.ir

### Citation

Heidari, P. Saberi, B. and Seifi A. (2023). Magnesium transporter family: sequence, evolution and expression analysis in soybean (*Glycine max* L.). *J. Plant Mol. Breed* 11 (1): 62-73.  
doi:10.22058/JPMB.2024.2020070.1287.

Parviz Heidari\*, Bahar Saberi and Ariana Seifi

Faculty of Agriculture, Shahrood University of Technology, Shahrood 3619995161, Iran

**Abstract:** *Magnesium transporter (MGT)* genes play a critical role in plant growth, development, and stress responses. These genes involve Mg uptake, transport, and distribution within cells and organs. In this study, 48 MGT family members were screened from the soybean genome, and three subfamilies, including MRS2-like (18 members), CorA (3 members), and NIPA (22 members). The length of soybean MGTs ranged from 160 amino acids (aa) (GLYMA\_06G214500) to 555 aa (GLYMA\_15G125900). The results revealed that NIPA subfamily proteins have more genetic distance than MRS2-like and CorA proteins. In addition, the NIPA subfamily members showed a high variation in physicochemical properties such as theoretical isoelectric point (pI), grand average of hydropathicity (GRAVY), and instability index. All NIPAs were identified as hydrophobic proteins, while the MRS2-like and CorA members were predicted as hydrophilic. Moreover, the instability index revealed that NIPA members are more stable, while more MRS2-like and CorA proteins are predicted to be unstable. Additionally, several duplication events were recognized among MGT family members, and all duplicated genes have been created through segmental duplication. The expression profile of soybean MGT genes showed significant differences in expression levels across various s. These results confirm that MGTs' widespread distribution across organs, regulating magnesium homeostasis.

**Keywords:** ion transporter; plant genome; gene family; physicochemical properties.

## Introduction

Magnesium (Mg) is an essential cation that plays a crucial role in various physiological processes in plants, including photosynthesis, growth, and product quality (Chen et al., 2018). Mg deficiency can lead to leaf chlorosis and negatively impact plant growth and development (Lin and Nobel, 1971; Ko et al., 1999). Mg transporter (MGT) proteins facilitate the absorption, transport, and distribution of Mg in plants. MGT proteins are characterized by two conserved transmembrane domains in the C-terminal region and a Gly-Met-Asn (GMN) motif at the end of the first transmembrane domain (Lin and Nobel, 1971; Ko et al., 1999; Li et al., 2016; Chen et al., 2018; Heidari et al., 2021). The presence of the GMN motif is essential for the activity of MGT proteins (Palombo et al., 2013). Based on sequence structure, MGTs are classified into three subfamilies: CorA, MRS2-like, and NIPA (Heidari et al., 2022). While the CorA subfamily has been extensively studied, limited information is available on the functions of MGTs in the MRS2 and NIPA subfamilies. The CorA protein was firstly identified in *Salmonella typhimurium* (Silver, 1969), although its homologues have also been identified in plants, animals and yeast (Knoop et al., 2005). CorA proteins are involved in both efflux and influx of magnesium (Franken et al., 2022).

MGTs play diverse roles in plant growth and development. Some MGT proteins are involved in the distribution and accumulation of Mg within cells. For example, in *Arabidopsis thaliana*, AtMGT2 and AtMGT3 contribute to Mg accumulation in the vacuole (Lenz et al., 2013), while AtMGT10 regulates Mg homeostasis in chloroplasts (Drummond et al., 2006). It stated that AtMGT2 and AtMGT3 proteins increase Mg accumulation in the vacuole under high concentration of Mg and enable plant growth under low calcium concentration (Faraji et al., 2021).

MGT genes are expressed in different plant organs, such as the leaf, root, stem, and flower, to maintain optimal magnesium concentrations (Faraji et al., 2021). AtMGT5 and AtMGT9 are specifically involved in pollen growth and chloroplast development, respectively (Chen et al., 2009). AtMGT9 acts as a transporter that translocates Mg

from roots to shoot parts in *Arabidopsis* (Gebert et al., 2009). In root tissues, MGTs like OsMGT1 in *Oryza sativa* and AtMGT6 in *Arabidopsis* are responsible for Mg uptake from the soil (Chen et al., 2012; Mao et al., 2014). Additionally, MGTs have been found to enhance plant tolerance to environmental stresses. For instance, OsMGT1 in rice is associated with salt stress tolerance (Chen et al., 2017), while the expression of MGT genes correlates with aluminum (Al) stress tolerance. Transgenic lines expressing AtMGT1 in *Nicotiana benthamiana* exhibited reduced aluminum toxicity (Deng et al., 2006).

MGT gene family has been identified and characterized in *O. sativa* (Mohamadi et al., 2023), *A. thaliana* (Schock et al., 2000), *Poncirus trifoliata* (Liu et al., 2019), *Zea mays* (Li et al., 2016), *Cucumis sativus* (Heidari et al., 2022), *Saccharum spontaneum* (Wang et al., 2019), and *Triticum turgidum* and *Camelina sativa* (Faraji et al., 2021), *Vitis vinifera* (Ge et al., 2022), *Gossypium hirsutum*, and *Theobroma cacao* (Heidari et al., 2021), and *Solanum lycopersicum* (Regon et al., 2019). Due to the importance of MGTs in regulating the growth and development of plants, the MGT gene family has not been identified and characterized in soybean (*Glycine max* L.). In the present study, MGT family members were analyzed based on sequence structure, evolution and expression in soybean.

## Materials and Methods

### Identification of MGT family members

The putative MGT proteins from the dicot model plant, *A. thaliana*, were used as a query in BLASTp tool of the Ensembl Plants database (<https://plants.ensembl.org/index.html>) against the soybean genome. All introduced proteins were checked to have the Mg transporter domain based on the output of the pfam tool in Ensembl Plants database. Finally, the peptide, CDS, and genomic sequence of confirmed genes were downloaded from the Ensembl Plants database.

### Sequence analysis of MGTs

The ProtParam tool (Gasteiger et al., 2005) was applied to predict the physiochemical properties of MGTs, including the grand average hydropathicity (GRAVY), instability index, theoretical isoelectric point (pI), and molecular weight (kDa).

### Upstream analysis of MGT genes

To screen the putative cis-regulatory element related to response to stress, hormones and light, the upstream region, a 1500 bp fragment before start codon, of each MGT gene was analyzed using an online server, PlantCARE (Lescot et al., 2002). Finally, the identified elements were classified based on their function.

### Phylogeny analysis

MGTs from soybean with along their orthologs in *Arabidopsis* and rice were aligned using an online multiple alignment tool, the Clustal Omega (Sievers and Higgins, 2014). Then, the phylogeny tree was constructed by Neighbor-Joining (NJ) method. Finally, tree was reconstructed using the iTOL tool (Letunic and Bork, 2021).

### Chromosome location and duplication events in MGTs

The location of each MGT was pictured on soybean genome using the TBtools software v1.132 (Chen et al., 2020). To screen duplicated genes, the similarity of more than 70% in the coding sequence of MGT pairs was considered as a selection criterion. Then, the Ka (non-synonymous) and Ks (synonymous) indexes were calculated using TBtools between the duplicated MGT pairs.

### Expression profile of MGTs

The expression profile of soybean MGTs in various soybean organs were extracted from the SoyBase database (<https://soybase.org/soyseq/>) based on the available RNA-seq information. The collected raw data were normalized and illustrated in the heatmaps.

## Results

### Physicochemical properties of MGTs

In this study, 48 MGT family members were screened from soybean genome (Table S1). The length of MGTs ranged from 160 aa

(GLYMA\_06G214500) to 555 aa (GLYMA\_15G125900) in soybean, 241 aa to 540 aa in *Arabidopsis*, and 165 aa to 572 aa in rice (Table 1). The prediction of physicochemical characteristics of MGT proteins disclosed that isoelectric points (pI) of all soybean MGT proteins varied from 4.65 (GLYMA\_10G126500) to 9.91 (GLYMA\_06G053100), and ranged from 4.78 to 9.48 in *Arabidopsis*, and 4.61 to 11.43 in rice. Interestingly, instability index revealed that MGT proteins in the studied dicots, soybean and *Arabidopsis*, are more stable than the monocot model, rice (Table 1). In addition, the GRAVY (grand average of hydropathicity) index showed that MGTs are both hydrophobic and hydrophilic. Overall, these results suggested that MGT family members are diverse in term of physicochemical properties.

### Phylogeny analysis

Phylogenetic analysis determined relationships between 43 soybean MGTs and orthologs in *A. thaliana* and *O. sativa*. MGT family members were separated into three subfamilies: NIPA, MRS2-like and CorA (Figure 1).

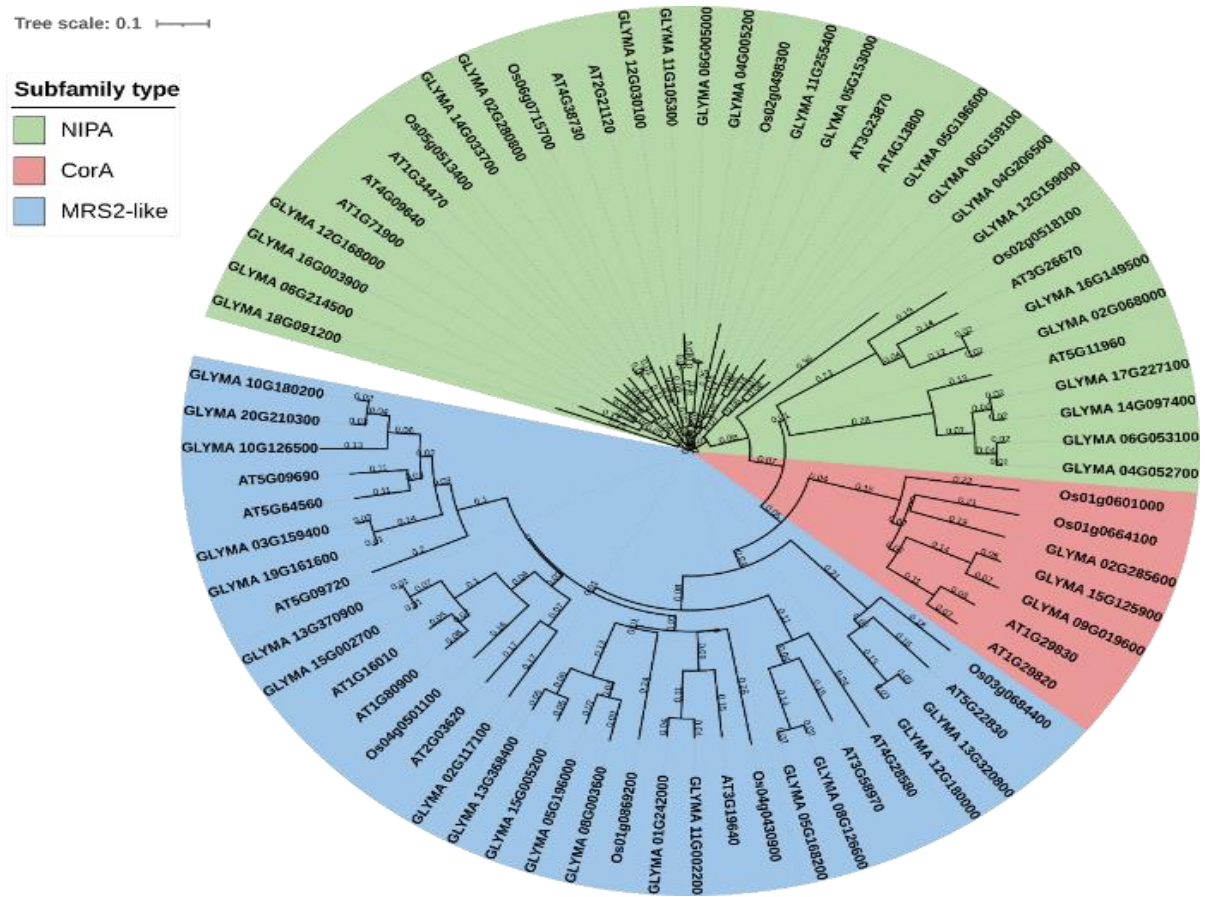
Accordingly, 22 NIPs, 18 MRS2-like proteins and 3 CorA proteins were identified in soybean. The results revealed that NIPA subfamily proteins showed more distance than MRS2-like and CorA proteins, indicating that NIPAs have had an evolutionary divergence and that CorAs and MRS2-like proteins probably had the same ancestral group.

### Structure and physicochemical comparison between the subfamilies of MGTs

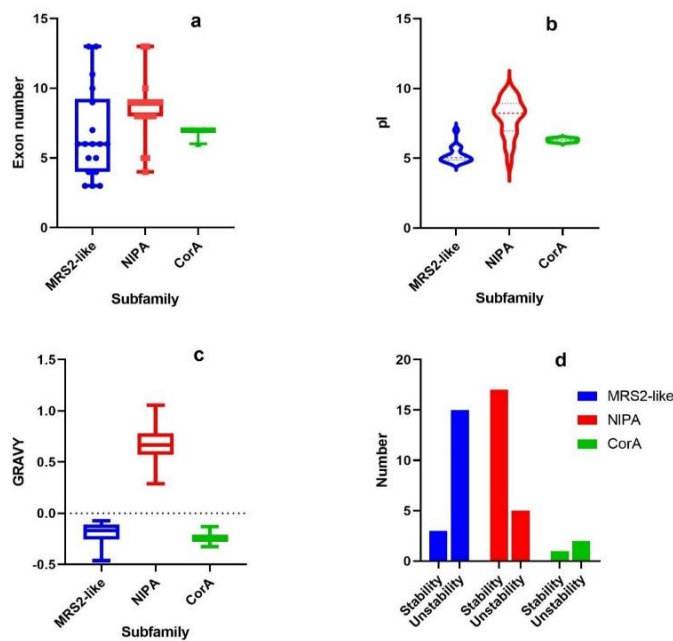
MGT subfamilies in soybean, including NIPA, CorA, and MRS2-like, were compared based on exon number, pI, GRAVY, and stability (Figure 2). The results showed significant differences between the members of these subfamilies.

**Table 1.** Comparison of the physicochemical characteristics of MGTs in soybean with monocot and dicot model plants. Full details are provided in the Supplementary Table 1.

Plant	Length (aa)	MW (KDa)	pI	GRAVY	Instability
Soybean	160-555	17.85-62.27	4.65-9.91	-0.464-1.057	49% stable
<i>Arabidopsis</i>	241-540	26.56-61.05	4.78-9.48	-0.369-0.869	53% stable
Rice	165-572	17.67-62.91	4.61-11.43	-0.451-0.789	27% stable



**Figure 1.** Evolutionary analysis of MGT family members.

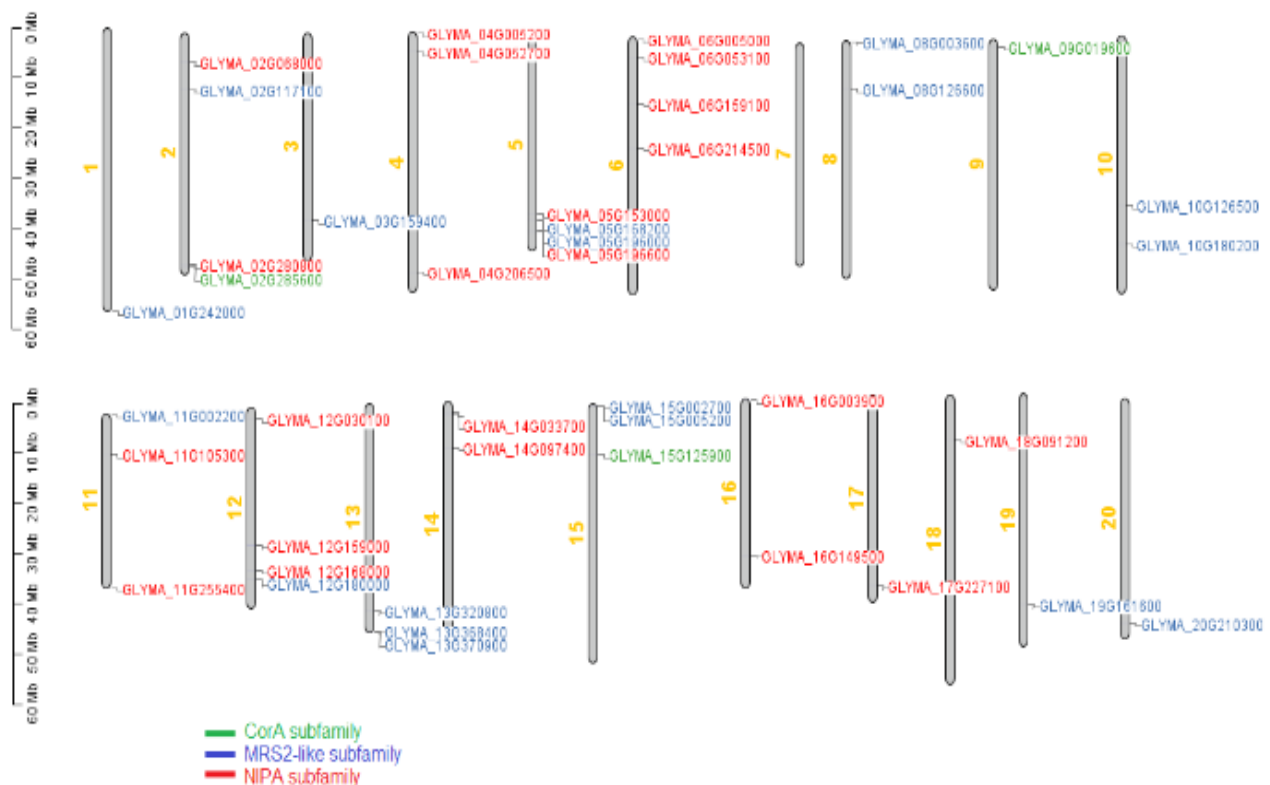


**Figure 2.** Comparison between the subfamilies of MGTs in terms of exon number (a), pI (b), GRAVY (c), and instability index (d).

The number of exons in the NIPA subfamily was higher than that of the other subfamilies, although the members of the MRS2-like subfamily had significant variation based on the number of exons together (Figure 2a). In addition, the NIPA subfamily members showed a high variation for pI, and more NIPAs were predicted activating under alkaline conditions (Figure 2b). In contrast, it was predicted that the CorA and MRS2-like subfamily members are more active in acidic environments. Based on GRAVY index, all NIPA proteins were predicted to be hydrophobic, but the MRS2-like and CorA members were identified as hydrophilic (Figure 2c). Besides, the instability index disclosed that more NIPA members are stable, while more MRS2-like and CorA proteins are predicted as unstable proteins (Figure 2c). These results indicated that NIPA subfamily members have noticeable structural differences from other MGT subfamilies and have probably undergone a different evolutionary process.

### Location and duplication events in MGT family members

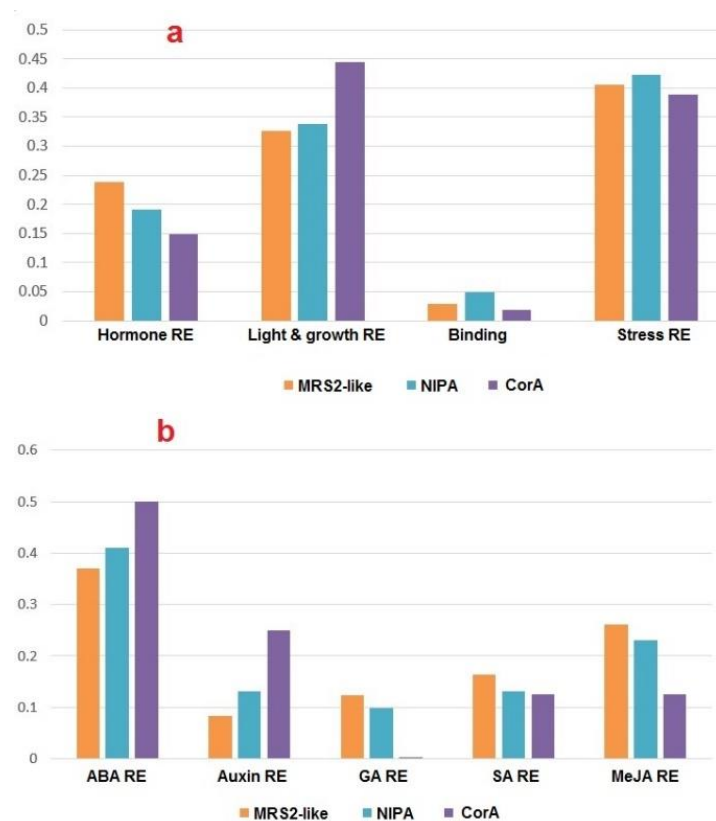
Chromosomal localization of genes can provide information related to genetic linkage, regulation and evolutionary history. In the present study, soybean MGT genes were located on 19 chromosomes, and an uneven distribution of MGT genes was observed (Figure 3). Only in soybean chromosome 7, there was no MGT gene, while four MGT genes were located in each of chromosomes 2, 5, 6, and 12. Duplication events of MGTs were predicted based on the similarity percentage between pair genes. Results revealed seven duplications between pairs of MGT genes (Table 2). Besides, all MGT genes were predicted to have been segmentally duplicated in soybean genome. Based on Ka/Ks ratio, six pairs of duplicated genes were under purifying selection, and a pair of duplicated NIPA genes (*GLYMA\_12G168000*-*GLYMA\_18G091200*) was under positive selection.



**Figure 3.** Distribution of MGTs on chromosomes of Soybean (*Glycine max*).

**Table 2.** List of duplicated *MGT* genes in soybean.

Gene 1	Gene 2	Subfamily	Ka	Ks	Ka/Ks	Duplication type
GLYMA_05G196000	GLYMA_08G003600	MRS2-MRS2	0.0817	0.1769	0.4618	Segmental
GLYMA_05G196000	GLYMA_15G005200	MRS2-MRS2	0.1197	0.2425	0.4936	Segmental
GLYMA_06G214500	GLYMA_16G003900	NIPA- NIPA	0.1253	0.1636	0.7659	Segmental
GLYMA_10G126500	GLYMA_10G180200	MRS2-MRS2	0.1089	0.2107	0.5168	Segmental
GLYMA_10G126500	GLYMA_20G210300	MRS2-MRS2	0.1010	0.1194	0.8459	Segmental
GLYMA_12G168000	GLYMA_16G003900	NIPA- NIPA	0.0102	0.0659	0.1548	Segmental
GLYMA_12G168000	GLYMA_18G091200	NIPA- NIPA	0.1654	0.1389	1.1908	Segmental

**Figure 4.** Frequency of cis-regulatory elements based on their function (a) in subfamilies of soybean *MGT*s. Frequency of cis-regulatory elements related to hormone responsiveness in subfamilies of soybean *MGT*s (b).

Overall, it seems that segmental duplication events have extended the *MGT* family members in soybean.

#### Promoter analysis of *MGT*s

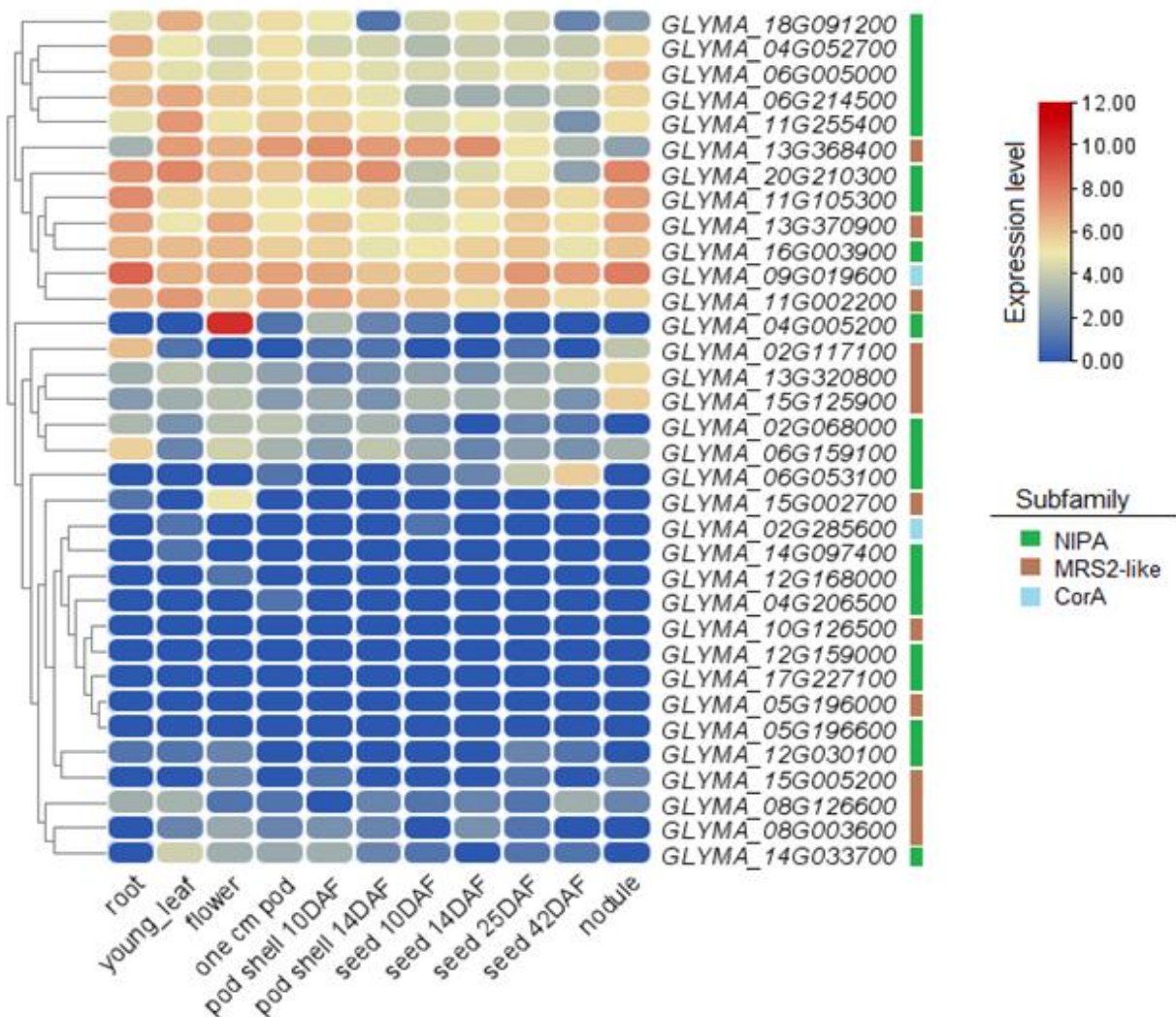
In order to better understand the regulatory system in soybean *MGT* genes, the upstream region of these genes was screened. The identified *cis*-regulatory elements were classified based on their functions in

four classes: hormone responsiveness elements (Res), light and growth Res, protein binding site, and stress Res (Figure 4a). The results disclosed that soybean *MGT* genes are involved in various processes and play roles in response to phytohormones and stress conditions as well as response to light and regulation of plant growth. *Cis*-regulatory elements-related stresses were

recognized more in the upstream site of *MGTs*. However, the distribution of *cis*-elements was different among the *MGT* subfamilies. For example, hormone-responsive elements were observed more in the promoter of *MRS2-like* genes than those of *NIPA* and *CorA* genes. In addition, *cis*-regulatory elements related to ABA responsiveness were more recognized in upstream regions of soybean *MGTs* (Figure 4b). Elements linked with GA, MeJA, and SA responsiveness were more detected in *MRS2-like* genes. These results disclosed that soybean *MGTs* are controlled by upstream signals related to hormones and stimuli.

### Expression profile of *MGTs*

Expression profile of soybean *MGT* genes was illustrated based on the RNA-seq data in different tissues (Figure 5). *MGT* genes showed significant differences in expression levels in different soybean organs. In root tissues, one *CorA* gene (*GLYMA\_09G019600*), two *MRS2-like* genes (*GLYMA\_11G002200* and *GLYMA\_13G370900*) and six *NIPA* genes (*GLYMA\_04G052700*, *GLYMA\_06G005000*, *GLYMA\_06G214500*, *GLYMA\_20G210300* and *GLYMA\_11G105300*) were more expressed, indicating that these genes are involved in the absorption of magnesium.



**Figure 5.** Expression profile of *MGT* genes in different organs of *G. max*. DAF: days after flowering.

In young leaf, four *NIPA* genes including *GLYMA\_20G210300*, *GLYMA\_06G214500*, *GLYMA\_11G255400*, and *GLYMA\_18G091200* and two *MRS2-like* genes, *GLYMA\_13G368400* and *GLYMA\_11G002200* showed high expression levels and *GLYMA\_04G005200* as a *NIPA* gene sharply expressed in flower tissues. In pod and pod shell, two *MRS2-like* genes including *GLYMA\_13G368400*, and *GLYMA\_11G002200* and a *CorA* gene (*GLYMA\_09G019600*) and a *NIPA* gene (*GLYMA\_20G210300*) were more induced. *GLYMA\_13G368400*, as a *MRS2-like* gene, and *GLYMA\_09G019600*, as a *CorA* gene, were more expressed in young seed tissues (10 to 14 days after flowering (DAF)) and old seed tissues (25-42 DAF), respectively. In addition, *GLYMA\_09G019600*, as a *CorA* gene, *GLYMA\_20G210300* and *GLYMA\_11G105300*, as *NIPA* genes, and *GLYMA\_13G370900*, as a *MRS2-like* gene were sharply expressed in nodule tissues.

## Discussion

In the current study, 48 MGT family members were identified from the soybean genome. The number of MGT family genes varies among plant species; for instance, 8 MGTs in *Poncirus trifoliata* (Liu et al., 2019), 12 MGTs in *Z. mays* (Li et al., 2016), 20 MGTs in *C. sativus* (Heidari et al., 2022), 10 MGTs in *S. spontaneum* (Wang et al., 2019), 41 MGTs in *T. turgidum* and 61 MGTs in *C. sativa* (Faraji et al., 2021), 9 MGTs in *V. vinifera* (Ge et al., 2022), and 18 MGTs in *T. cacao* (Heidari et al., 2021). The polyploidy level and duplication rate have more affected the number of members of plant gene family (Faraji et al., 2020). The identified soybean-MGTs showed diversity in terms of physicochemical properties. Differences in physicochemical properties can affect the activity conditions and performance of plant transporters (Heidari et al., 2022). According to the role and distribution of MGTs, it can be suggested that the difference in physicochemical properties affects the differentiation of their functions. Based on the phylogenetic results, three main subfamilies including NIPs, MRS2-like and CorA were recognized that NIPA subfamily proteins showed more distance than MRS2-like and CorA proteins, indicating that NIPAs have had an evolutionary divergence and that CorAs and MRS2-like proteins

probably had the same ancestral group. Previous studies have also emphasized that NIPA subfamily has significant differences compared to MRS2-like and CorA subfamilies (Heidari et al., 2021). Based on phylogeny results, it seems that the expansion and diversity occurred more in the members of MGT gene family after the derivation of monocots and dicots. In addition MGT subfamilies showed diversity in term of number of exons. The soybean-MGTs /introns affects the duration of the editing process of primary mRNAs (Hashemipetroudi et al., 2023; Puresmaeli et al., 2023). Besides, the NIPA subfamily members showed a high variation for pI, GRAVY index, and instability index, than MRS2-like and CorA members. These results indicated that NIPA subfamily members have noticeable structural differences from other MGT subfamilies and have probably undergone a different evolutionary process. Several duplication events were predicted in soybean-MGTs. It seems that segmental duplication events have extended the MGT family members in soybean. The expression profile of soybean MGT genes disclosed that MGTs are expressed in all organs. These results confirm that MGTs have been distributed in all organs for magnesium distribution and homeostasis regulation of this key element. In addition, few differences were observed in the expression level of duplicated genes, possibly due to the mutations in the genes' regulatory or coding regions (Arab et al., 2023; Hashemipetroudi et al., 2023). Based on upstream analysis, it found that soybean MGTs are involved in various processes related to phytohormones, adverse conditions and growth. Magnesium is involved in various cellular processes. The distribution of these genes in different organs shows the importance of magnesium distribution in all tissues. On the other hand, the presence of *cis*-regulatory elements related to hormones shows that the activity of this transporter is controlled by hormone-dependent signaling pathways

## Conclusion

Understanding the functions and regulation of MGT genes in plants provides valuable insights into plant growth, development, and stress responses. This study screened 48 MGT family members from the soybean genome, showing diverse



physiochemical properties, promoter structure, and expression levels. NIPA subfamily members were predicted as a different subfamily transporter of magnesium with unique characteristics. It was found that segmental duplication events have extended the MGT family members in soybean. In addition, we conclude that MGTs are induced by upstream signals linked to phytohormones and stresses to control the Mg concentration in different organs. Further research into the function of MGT genes and their role in oil production of soybean is suggested.

### Supplementary Materials

The Supplementary Material for this article can be found online at: [https://www.jpmb-gabit.ir/article\\_710571.html](https://www.jpmb-gabit.ir/article_710571.html).

**Supplementary Table 1.** Physicochemical characteristics of MGTs in soybean, rice and arabidopsis.

Not true?! Lines 131 & 174 refer to Table S1.

### Author Contributions

Conceptualization, P.H. and B.S.; methodology, B.S.; software, B.S. and A.S; validation, P.H.; formal analysis, B.S. and A.S; writing—original draft preparation, P.H.; writing—review and editing, P.H.; project administration, P.H. All authors have read and agreed to the published version of the manuscript.

### Funding

This research received no external funding.

### Acknowledgments

Not applicable.

### Conflicts of Interest

The authors declare no conflict of interest.

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# خانواده انتقال دهنده منیزیم: تجزیه و تحلیل توالی، تکامل و بیان در سویا (*Glycine max* L.)

پرویز حیدری\*، بهار صابری، آریانا سیفی

دانشکده کشاورزی، دانشگاه صنعتی شاهرود، شاهرود، ایران

## ویراستار علمی

دکتر سیدحمیدرضا هاشمی پطودی،

پژوهشکده ژنتیک و زیست فناوری کشاورزی طبرستان،

دانشگاه علوم کشاورزی و منابع طبیعی ساری

**چکیده:** ژن‌های انتقال دهنده منیزیم (*MGT*)، نقش مهمی در رشد، نمو و پاسخ به تنش گیاه دارند. این ژن‌ها در جذب، انتقال و توزیع منیزیم در سلول‌ها و اندام‌ها نقش دارند. در این مطالعه، ۴۸ عضو خانواده ژنی *MGT* از ژنوم سویا شناسایی شدند و به سه زیر خانواده شامل *MRS2* (با ۱۸ عضو)، *CorA* (با ۳ عضو) و *NIPA* (با ۲۲ عضو) تفکیک شدند. طول پروتئین‌های *MGTs* در سویا از ۱۶۰ (GLYMA\_06G214500) تا ۵۵۵ اسید آمینه (GLYMA\_15G125900) متغیر بود. نتایج نشان داد که پروتئین‌های زیر خانواده *NIPA* فاصله ژنتیکی بیشتری نسبت به پروتئین‌های *MRS2* و *CorA* دارند. علاوه بر این، اعضای زیر خانواده *NIPA* تنوع بالایی در خواص فیزیکی‌شیمیایی مانند *pI*، *GRAVY* و شاخص ناپایداری نشان دادند. تمام *NIPA* ها به عنوان پروتئین‌های آبگریز شناسایی شدند، در حالی که اعضای *MRS2* و *CorA* به عنوان آبدوست پیش‌بینی شدند. علاوه بر این، شاخص بی‌ثباتی نشان داد که اعضای *NIPA* پایدارتر هستند، در حالی که پروتئین‌های *MRS2* و *CorA* بیشتر به عنوان پروتئین‌های ناپایدار پیش‌بینی شدند. علاوه بر این، چندین رویداد دوبرابر شدگی بین اعضای خانواده *MGT* شناسایی شد که احتمالاً همه ژن‌های تکراری به صورت قطعه‌ای ایجاد شده‌اند. پروفایل بیانی ژن‌های *MGT* در سویا تفاوت‌های معنی‌داری را در اندام‌های مختلف نشان داد. این نتایج تایید کرد که *MGT* ها در تمام اندام‌ها برای کنترل هموستازی منیزیم توزیع شده‌اند.

**کلمات کلیدی:** انتقال دهنده‌های یونی، ژنوم گیاهی، خانواده ژنی، خواص فیزیکی‌شیمیایی.

## تاریخ

دریافت: ۲۰ دی ۱۴۰۲

پذیرش: ۱۰ بهمن ۱۴۰۲

چاپ: ۱۴ بهمن ۱۴۰۲

## نویسنده مسئول

دکتر پرویز حیدری

heidarip@shahroodut.ac.ir

## ارجاع به این مقاله

Heidari, P., Saberi, B. and Seifi A. (2023). Magnesium transporter family: sequence, evolution and expression analysis in soybean (*Glycine max* L.). *J. Plant Mol. Breed* 11 (1): 62-73. doi:10.22058/JPMB.2024.2020070.1287.