



Identification and Analysis of *PGM* and *SUS* Gene Families in *Leymus Chinensis* Seed Transcriptome

Wang Bo, Gong Ting, Li Ran, Wang Qi, Yang Jie, Liu Wei, Yang Zouzhuang, Zhang Pan, Hu Guofu ✉

School of Animal Science and Technology, Northeast Agricultural University, Harbin, 150000, China

✉ Corresponding author Email: guofuh2003@163.com

Molecular Plant Breeding, 2021, Vol.12, No.7 doi: [10.5376/mpb.2021.12.0007](https://doi.org/10.5376/mpb.2021.12.0007)

Received: 29 Jan., 2020

Accepted: 05 Feb., 2020

Published: 19 Feb., 2021

Copyright © 2021 Wang et al., This article was first published in Molecular Plant Breeding in Chinese, and here was authorized to translate and publish the paper in English under the terms of Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

Preferred citation for this article:

Wang B., Gong T., Li R., Wang Q., Yang J., Liu W., Yang Z.Z., Zhang P., and Hu G.F., 2021, Identification and analysis of *PGM* and *SUS* gene families in *leymus chinensis* seed transcriptome, Molecular Plant Breeding, 12(7): 1-8 (doi: [10.5376/mpb.2021.12.0007](https://doi.org/10.5376/mpb.2021.12.0007))

Abstract *Leymus chinensis* (*Leymus chinensis* (Trin.) Tzvel.) is a good perennial forage with good palatability, high yield and high feeding value. In addition, because of its strong resistance, *Leymus chinensis* can improve the disadvantaged environment such as poor land, and it is an important species to protect grassland ecology in China. Therefore, in order to promote the germination of *leymus chinensis* seeds and explore the mechanism of Germination, this study used sterile water treatment of *leymus chinensis* seeds as control, exogenous GA3 as treatment conditions. Based on the analysis of pre-transcriptome data, it was determined that *PGM* and *SUS* genes in sucrose and starch metabolic pathways play a significant role in seed Germination. Members identification, conserved domains, and evolutionary trees were analyzed for both gene families using the bioinformatics method. The expression pattern of *PGM* and *SUS* genes were analyzed with FPKM value. The results showed that 7 members were selected from each of the the *PGM* and *SUS* families based on the data of *Leymus Chinensis* seeds transcriptome. The molecular weight of *PGM* genes ranged from 15 471.3 to 67 912.9 Da, and the isoelectric point value ranged from 4.45 to 6.31, showing weak acidity. *PGM* family in *Leymus Chinensis* seeds are hydrophilic stable proteins. The molecular weight of *SUS* genes ranged from 30 421.5 to 110 262.9 Da. The isoelectric point of *SUS* genes was neutral except *LcSUS1,5* and 7, while the other four genes were weak acidic. *LcSUS4,6* were stable hydrophilic proteins, the rest were unstable hydrophilic proteins. The *PGM* and *SUS* gene families in *Leymus chinensis* seeds play an enzyme role in promoting sucrose and starch synthesis in sucrose and starch metabolism pathways. The expression pattern analysis of *Leymus chinensis* seeds showed that the genes of *PGM* and *SUS* gene families in GA3-treated *Leymus chinensis* seeds promoted the germination of *Leymus chinensis* seeds by regulating the sucrose and starch pathways with different expression levels.

Keywords *Leymus chinensis*; *PGM* and *SUS* gene families; Bioinformatics analysis; Expression analysis

Phosphoglucosyltransferase (PGM) is a member of the phosphohexose mutase family (Egli et al., 2010; Stray-Pedersen et al., 2014; Weyler and Heinzle, 2015). Regulating and controlling the mutual conversion of glucose-1-phosphate and glucose-6-phosphate, and further promoting the synthesis of glucose is its main role and function in plants (Uematsu et al., 2012b; Chauton et al., 2013). Therefore, it plays a positive regulatory role in the sucrose and starch pathway and participates in regulating the synthesis of sucrose and starch in plants (Paparelli et al., 2013; Pal et al., 2013), thereby participating in the growth and development of plants. In plant research, the PGM family can be divided into two types with different cell localizations: plastid localization (pPGM) and cytoplasmic localization (cPGM) (Herbert et al., 1979). The main process of PGM is to produce glucose-1-phosphate from glucose-6-phosphate. Glucose-1-phosphate can be introduced from the cytoplasm in heterotrophic tissues or produced by photosynthesis in autotrophic tissues. There are also studies on plants lacking PGM gene regulation. Malinova et al. (2014) studied *Arabidopsis thaliana* lacking cPGM activity and found that its growth was significantly inhibited, and starch synthesis slowed down. Fettke et al. (2012) studied the lack of activity regulation of PGM in potato (*Solanum tuberosum* L.) and found that its external morphology showed that the overall plant was short, and the number of tubers decreased. However, studies on the sugar metabolism of *Lotus corniculatus* L. lacking pPGM regulation have found that the leaves cannot effectively accumulate starch, which results in not being stained by iodine (Vriet et al., 2010). Therefore, it is proved that the lack of PGM gene regulation greatly reduces starch synthesis in leaves and storage organs. Overexpression of PGM can effectively

increase starch synthesis. Uematsu et al. (2012a) overexpressed pPGM through tobacco (*Nicotiana tabacum* L.) leaves. Compared with wild-type plant leaves, they found that the activity of pPGM was improved in the leaves of transgenic plants, and the content of starch is also increased by 2 to 3 times (Vriet et al., 2010), which indicates that pPGM plays a role in promoting starch synthesis.

Sucrose is a key metabolite in the metabolic pathway of sucrose and starch. Sucrose cannot be used directly by the plant itself, and only when it is broken down into other soluble sugars can it participate in various physiological metabolic activities of the plant. Sucrose Synthase (SUS) is a restriction enzyme that acts in the process of plant sugar metabolism (Chen et al., 2019). At present, there are many studies on the SUS gene family in plants. In recent years, researchers have not limited to identifying this family in model plants but have also focused on pepper (*Capsicum annuum* L.) (Wei et al., 2019) and pear (*Pyrus* spp) (Lv et al., 2018), seedless honey pomelo (Honey pomelo) (Deng et al., 2018) and other plants. In the study of soybean (*Glycine max* (Linn.) Merr.), it was found that members of the SUS gene family have tissue expression specificity. When the research on soybean plants containing sucrose synthase mutants showed that the enzyme activity of SUS gene is associated with nitrogen fixation by rhizobia in direct proportion to ability, lower SUS gene enzymatic activity will cause some tissue degradation (Chao et al., 2018). Due to the reversible hydrolysis of sucrose by SUS, Maria et al. (2019) studied tomato (*Lycopersicon esculentum* Mill.) and found that the reversible hydrolysis of sucrose mediated by SUS1 is not only useful for maintaining the balance between sucrose and its monomers in fruits, but also for other the balance in the tomato organs is crucial. Danyu et al. (2019) studied the SUS gene family in the phloem of *Arabidopsis thaliana* and found that SUSy2 was present in the endosperm and embryo of developing seeds, while other genes were found in different parts. Therefore, it was inferred that the SUS gene family was involved in the process of sucrose metabolism in phloem. The PGM and SUS genes not only regulate the metabolism and accumulation of sucrose and starch, but also catalyze the synthesis and decomposition of sucrose and starch and have a variety of functions in the metabolic pathway of sucrose starch.

Leymus chinensis has the characteristics of strong rhizome penetration, so it can improve the disadvantaged land, so as to protect the ecological environment of Chinese grassland (Liu and Qi, 2004). Systematic identification and analysis of PGM and SUS gene families in *Leymus chinensis* can help to explore the germination mechanism of seeds. Therefore, the basic biological properties of PGM and SUS gene families in seeds of *Leymus chinensis* were analyzed in this study. This study through gibberellic acid (GA3) processing of *Leymus chinensis* seeds as experimental material for the transcriptome sequencing, based on the transcriptome sequencing data of PGM in *Leymus chinensis* and SUS gene families, verification and domain of conservative structure is analyzed and the construction of the evolutionary tree and the analysis of the expression, etc., in order to for further research on *Leymus chinensis* PGM and SUS gene families provide theoretical support for the function and high efficient breeding *Leymus chinensis*.

1 Results and Analysis

1.1 Identification of PGM and SUS Gene Families in Seeds of *Leymus chinensis*

A total of 10 PGM sequences were obtained through local BLAST retrieval of transcriptome database. After retrieval and analysis of CDD online database, 7 effective PGM protein sequences were finally obtained (Table 1). It can be seen from the table that the number of amino acids encoded by the 7 LcPGM genes is 153-60, and the theoretical molecular weight of the encoding protein is 15 471.3~67 912.9Da. The value of the isoelectric point of the 7 LcPGM genes is found to be between 4.45~6.31 through the analysis of the isoelectric point, and the average value is about 5.67, indicating that it mainly plays a role in the environment of weak acid cells. The prediction of the instability coefficient showed that the values were all less than 40, so it could be presumed to be a stable protein. The average hydrophilic coefficients were all less than 0, indicating that the proteins of these seven genes were hydrophilic proteins. The results showed that the seven LcPGM proteins were different in predicting the length of amino acid sequence and the physicochemical properties of the proteins, suggesting that LcPGM proteins had different biological properties.

Same as the method of obtaining LcPGM gene family, the 7 SUS gene protein sequences were finally obtained from the local *Leymus chinensis* seed transcriptome database (Table 2). The number of 7 genes encoding amino acids is 268~991, and the theoretical molecular weight of the encoding amino acids is the size is between 30 421.5 and 110 262.9 Da. Through isoelectric point analysis, it is found that LcSUS1, 5, and 7 play a role in a neutral environment as a whole, while the remaining 4 genes are weakly acidic. According to the prediction of the instability coefficient, LcSUS4 and 6 were all less than 40, which were presumed to be stable proteins, while the rest were all more than 40, which were presumed to be unstable proteins. Studies on the hydrophilic coefficient showed that the values were all less than 0, so all the 7 genes were hydrophilic proteins. It can be concluded that the seven genes are different in basic physical and chemical properties, indicating that they also play different roles in biological characteristics.

Table 1 Identification of basic physical and chemical properties of *LcPGM* gene family members

Gene	Transcriptome code	Protein length (aa)	Molecular weight (Da)	Isoelectric point	Instability index	Aliphatic index	Grand average of hydropathicity
<i>LcPGM1</i>	TRINITY_DN12586	606	67912.9	6.31	36.62	85.38	-0.333
<i>LcPGM2</i>	TRINITY_DN20225	336	36995.7	5.62	26.64	79.82	-0.192
<i>LcPGM3</i>	TRINITY_DN28535	598	67374.8	5.24	38.52	86.62	-0.328
<i>LcPGM4</i>	TRINITY_DN33918	583	62823.7	6.70	33.22	93.91	-0.165
<i>LcPGM5</i>	TRINITY_DN35067	153	15471.3	4.45	29.72	91.37	-0.246
<i>LcPGM6</i>	TRINITY_DN36197	565	61766.1	5.94	26.49	77.31	-0.317
<i>LcPGM7</i>	TRINITY_DN42222	602	64876.9	5.42	28.36	82.46	-0.145

Table 2 Identification of basic physical and chemical properties of *LcSUS* gene family members

Gene	Transcriptome code	Protein length (aa)	Molecular weight (Da)	Isoelectric point	Instability index	Aliphatic index	Grand average of hydropathicity
<i>LcSUS1</i>	TRINITY_DN09823	419	46390.2	6.87	44.81	79.47	-0.474
<i>LcSUS2</i>	TRINITY_DN27621	507	58237.1	6.56	40.53	85.17	-0.304
<i>LcSUS3</i>	TRINITY_DN48483	799	89074.9	5.89	43.61	86.78	-0.429
<i>LcSUS4</i>	TRINITY_DN49067	268	30421.5	4.79	25.75	100.04	-0.144
<i>LcSUS5</i>	TRINITY_DN50791	991	110262.9	6.82	45.72	85.02	-0.404
<i>LcSUS6</i>	TRINITY_DN50996	559	63702.0	5.28	36.01	93.85	-0.231
<i>LcSUS7</i>	TRINITY_DN52189	499	56418.9	7.28	42.81	85.63	-0.446

1.2 Analysis of conserved motif of LcPGM and LcSUS proteins

Analysis of the conserved Motif in the LcPGM and LcSUS protein by online software (Figure 1) shows that both LcPGM and LcSUS protein contain 10 different conserved Motifs, and the Motifs contained in different gene family members are also different. Among them, in the LcPGM gene, Motif 3 appears in all other genes except LcPGM 2, while LcPGM6 and 7 contain the same Motif structure and a large number of Motif, but the positions are different. Similarly, LcPGM1 and 4 contained the least number of Motif, only one, and the same action sites were different. In the LcSUS gene, Motif1 was found in all 7 genes, and Motif7 was also found in all 6 genes except LcSUS1. LcSUS5 contained 9 different domains, which was the gene with the largest number of domains, while LcSUS4 only had 3 domains with different lengths. Therefore, it can be inferred that different genes in the same gene family contain different domains and play significantly different biological functions in cells, and the different motifs contained in different LcPGM and LcSUS indicate that PGM and SUS family members may have different biochemical characteristics and biological functions.

1.3 Phylogenetic tree analysis of PGM and SUS gene families

In the PGM family, the whole evolutionary tree is divided into five subtribes, including Group1 subtribe contains LcPGM7, and wheat (*Triticum aestivum* L.) of PGM gene has high homology, and contains a LcPGM4 in Group4, also found a LcPGM5 in Group5, while the rest is not found in the three subtribes, suggests that, though not in the same subtribe, but there is still a low homology (Figure 2). In the SUS family, 12 subgroups were identified, and

the SUS gene of *Leymus chinensis* seeds was divided into different subgroups. Group1 contained LcSUS2, which had high homology with wheat TaSUS6, 12, and 20. LcSUS4 and 6 were classified into subgroup Group3 and had high homology with maize (*Zea mays* Linn. Sp.), rice (*Oryza sativa* L.) and wheat, while LcSUS4 had direct homology with ZmSUS6. Subgroup Group10, 11, and 12 contained LcSUS5, 3, 1, and 7, respectively, which had different degrees of homology with rape (*Brassica napus* L.), maize, rice, *Arabidopsis thaliana*, and wheat, among which LcSUS1 had direct homology with TaSUS5. Therefore, it can be concluded that the homologous PGM and SUS genes are similar in function, and the biological role of this gene family in the germination and metabolism of *Leymus chinensis* seeds can be inferred based on the biological function information of the identified model species.

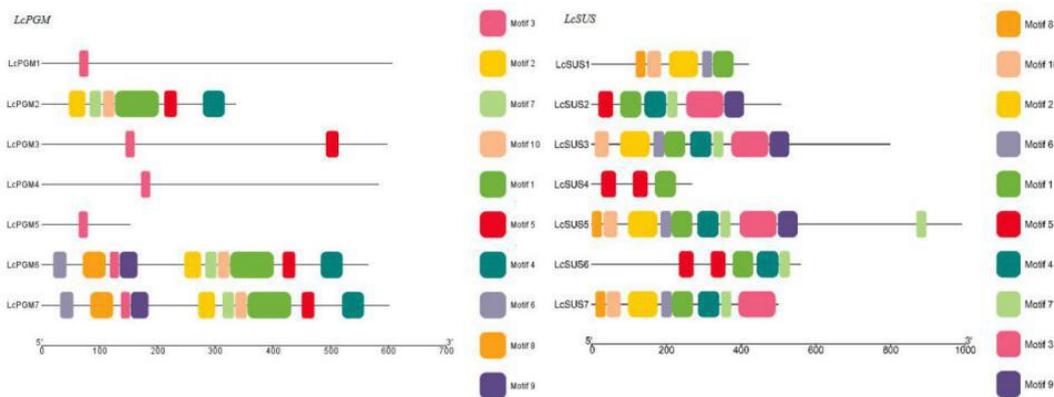


Figure 1 Conserved motifs of *LcPGM* and *LcSUS* proteins

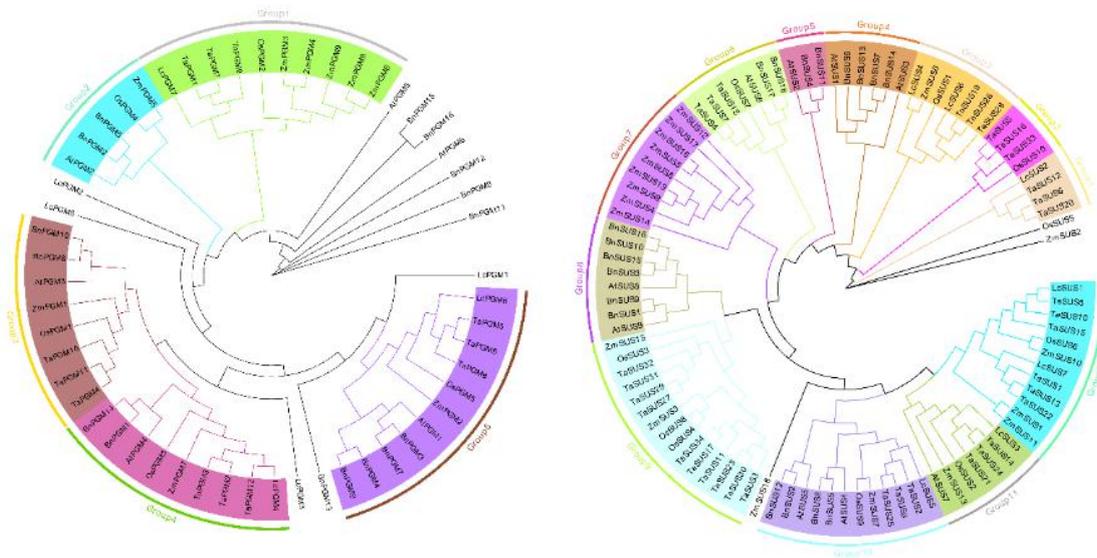


Figure 2 *PGM* and *SUS* gene family evolutionary development tree

1.4 Expression pattern analysis of PGM and SUS family genes in *Leymus chinensis* seeds

In order to analyze the gene expression patterns of *Leymus chinensis* seeds treated with exogenous GA3, we used the transcriptome data of *Leymus chinensis* to make a heat map (Figure 3). LcPGM1 and 3 genes were highly expressed in *Leymus chinensis* seeds treated with GA3, so they significantly positively regulated the metabolic pathways of sucrose and starch during seed germination. The expression levels of LcPGM5,6, and 7 genes also positively regulated the synthesis of sucrose and starch to varying degrees, while LcPGM2 and 4 played a negative role in GA3 treatment, and the down-regulation of LcPGM4 expression was the most obvious. In the process of regulating sucrose generated, GA3 treatment under the condition of *Leymus chinensis* seeds LcSUS5 with the highest expression of the quantity, thus plays a major role in the process of synthesis of sucrose, and LcSUS1, 3,4 and 7 express the amount raised in the control group, in treatment group, the presentation, including

LcSUS3 in the control group plays a major role in regulating sucrose synthesis. In general, PGM and SUS genes played different positive and negative regulatory roles in sucrose and starch metabolism pathways to promote seed germination in the GA₃ treatment group.

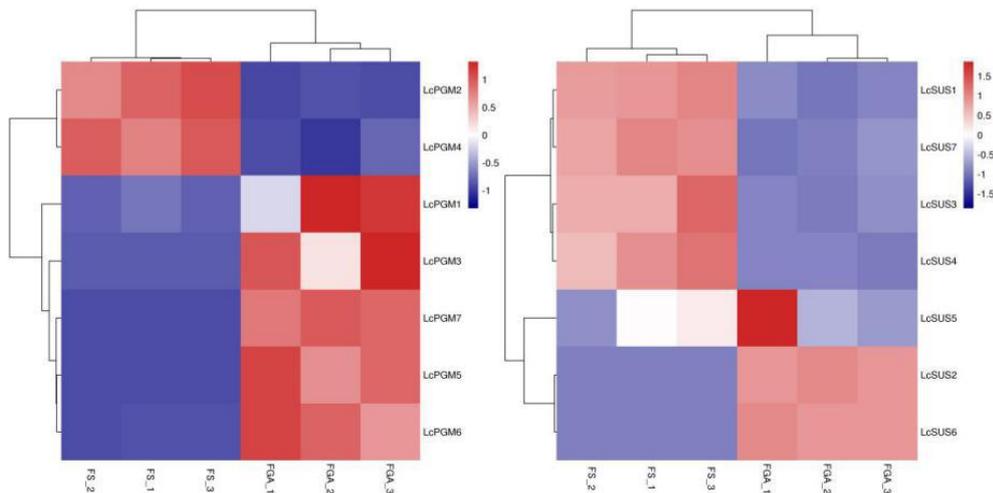


Figure 3 Heat map of *PGM* and *SUS* genes under GA₃ treatment and sterile water treatment in *Leymus chinensis* seeds

2 Discussion

Due to the current high-throughput sequencing and bioinformatics technology has become a research hotspot, so a large number of different functions and characteristics of gene families have been excavated, the gene family appraisal mainly includes the whole genome and transcriptome level appraisal, used in this study is based on the transcriptome level to identify the PGM and SUS gene families. However, there are few analyses on the PGM family at present, and most of the studies are mainly to identify this gene, for example, Tauberger et al. (2000) studied the PGM gene in potatoes. In this study, through database BLAST, it was found that there were 16 PGM genes in rape family, 12 PGM genes in wheat, and 7 PGM genes in *Leymus chinensis* transcriptome database, which mainly had high homology with wheat in the same subgroup. Li (2015) conducted a silencing experiment on PGM gene expression in *Ganoderma Lucidum* (Lyss.ex Fr.) Karst and concluded that PGM silencing would lead to blocked synthesis of sucrose and starch metabolism pathways. However, this gene was also significantly upregulated in sucrose and starch pathways in this study, so the main function of this gene family was discussed, which was consistent with the research results. The number of amino acids in this study is about 153~606, and the molecular weight is about 15~67 kDa, which is consistent with the description of Li et al. (2015). SUS gene family is involved in sucrose metabolism in higher plant key genes that promote the synthesis of sucrose in the process of the family, in the process of analyzing the SUS gene families, many species have been found to identification was carried out, such as identified in the millet nine sucrose synthase gene (king, 2017), is a small gene families, so the number of gene contained less, basic for 3 ~ 15 or so, with the number of genes identified in this study, the research on its basic physical and chemical properties, found that the molecular weight and isoelectric point range are consistent with previous research results. According to the phylogenetic relationship, PGM and SUS genes were distributed in different subfamilies, which indicated that there were some differences in evolution, and the functional diversity of the two genes could also be inferred.

PGM is a key branch enzyme in the glucose metabolism pathway, which can catalyze the reciprocal and inverse transformation between GLC-6-P and GLC-1-P, thus promoting the effective degradation and synthesis of sugar, and thus plays a crucial role in maintaining the balance of plant glucose metabolism. SUS is a soluble enzyme in sucrose metabolism, and its activity can reflect the pathway and ability of plant sucrose synthesis. Sucrose synthase exists in plants in three forms: soluble sucrose synthase, insoluble sucrose synthase and cytoskeleton bound sucrose synthase (Lingle, 1999). Sucrose synthase is also the only enzyme that enables sucrose to

participate in a variety of pathways, including plant tissue construction, material storage and cell metabolism (Li et al., 2013). Gene expression studies have shown that SUS family members are not only specifically expressed in plant tissues, but also related to the response of plants to stress. Wang et al. (2018) conducted salt stress treatment on rice at booting stage and found that SUS activity in rice leaves was enhanced under mild salt stress, which increased the accumulation of sucrose and starch and enhanced the stress resistance of the plant. However, with the increase of salt concentration, SUS activity decreased significantly, sucrose synthesis rate slowed down, and plant growth and development were significantly inhibited (Winter et al., 1997). These results indicate that the SUS gene family members play an important role in plant growth and development and in the process of resistance to stress. Therefore, sucrose synthase affects sucrose synthesis and decomposition, product transport, and cell and tissue construction in plants (Chen et al., 2001). In this study, the PGM and SUS gene families were significantly enriched when exogenous GA3 was added to *Leymus chinensis* seeds, suggesting that GA3 could effectively promote the glucose metabolism pathway in seeds and provide energy for seed germination. Functional annotations of these two gene families in *Leymus chinensis* seeds have been generally confirmed, which laid a foundation for further research on related gene families in *Leymus chinensis*. Meanwhile, it provides effective theoretical basis for promoting seed germination and increasing yield of *Leymus chinensis*.

3 Materials and Methods

3.1 Test materials

The seeds of *Leymus chinensis* (*Leymus chinensis* (Trin.) Tzvel.) were provided by the germplasm bank of Grassland Research Institute of Heilongjiang Academy of Agricultural Sciences. The seeds were dried at room temperature, then put into a ventilated cloth bag, and stored in a refrigerator at 4°C for later use.

3.2 Material handling

Choose *Leymus chinensis* seeds with full granules. First, soak with 5% sodium hypochlorite for 5 min, then rinse with sterile water for 3 times, and finally rinse with 75% alcohol for two times for disinfection and clean with sterile water for the next test.

Gibberellin treatment: a small amount of ethanol was added to dissolve GA3, then distilled water was added to prepare a solution with a concentration of 200 mg/L (the concentration was set as the optimal concentration obtained from the preliminary test).

After disinfection, the seeds (about 100 mg for each sample) were put into a beaker containing 50 mL 200 mg/L GA3 solution and immersed in an incubator at 25°C for 24 h. The sterile water was used as the control, and the treatment group and the control group were repeated for 3 times.

3.3 Identification of gene family members

Leymus chinensis seed transcriptome data is provided by this research group (part of the data is not published), using model plants *Arabidopsis* and rice as seed sequences, searching the transcriptome database through local blast comparison and searching directly in the transcriptome database using keywords, and use the Pfam and NCBI databases to identify the protein conserved domains, and finally obtained the PGM and SUS genes in the 7 *Leymus chinensis* seeds respectively, named according to the local transcriptome data gene ID sequence, namely LcPGM1-LcPGM7, LcSUS1-LcSUS7.

3.4 Analysis of basic physicochemical properties and conserved domains

Using software ProtParam (<http://web.expasy.org/protparam/>) prediction analysis of *Leymus chinensis* seeds PGM and SUS protein sequence of molecular weight, isoelectric point, unstable factor, fat coefficient and average water index and so on basic physical and chemical properties. Similarly, online software MEME (<http://meme-suite.org/tools/meme>) and TBTools were used to analyze the conserved motif of PGM family proteins in *Leymus chinensis* seeds.

3.5 Phylogenetic tree analysis

Clustal X 2.1 and MEGA 5.20 were used to construct and optimize all the PGM and SUS protein sequences of *Leymus chinensis*, *Arabidopsis thaliana*, rice, maize, rape and wheat. The phylogenetic tree was constructed by Neighbor joining (Neighbor joining, NJ) method.

3.6 Differential expression pattern analysis

Based on the FPKM value in the transcriptome database, the logarithmic log calculation method was used to perform hierarchical cluster analysis on the expression data of PGM and SUS family genes. Use Ttools software to draw expression heat map.

Authors' contributions

Bo Wang is the experimental designer and the executor of this study. Gong Ting, Li Ran, Wang Qi and Yang Jie completed the data analysis and the writing of the first draft of the paper. Wei Liu, Zouzhuan Yang and Pan Zhang participated in the experimental design and analysis of the experimental results; Guofu Hu was the architect and the person in charge of the project. He supervised the experimental design, data analysis, paper writing and revision. All authors read and agree on the final text.

Acknowledgement

This research was funded by the National Key Research and Development Project (2016YFC0500607).

References

- Chao M.N., Huang Z.W., Wang G., Wang R.H., Zhang J.B., and Zhang Z.Y., 2018, Genome-wide identification and expression analysis of sucrose synthase family members in soybean, *Xibei Zhiwu Xuebao* (Northwest Plant Journal), 38(2): 232-241
- Chauton M.S., Winge P., Brembu T., Vadstein O., and Bones A.M., 2013, Gene regulation of carbon fixation, storage, and utilization in the diatom *Phaeodactylum tricoratum* acclimated to light/dark cycles, *Plant Physiol*, 161(2): 1034-1048
<https://doi.org/10.1104/pp.112.206177>
PMid:23209127 PMCID:PMC3561001
- Chen J.W., Chen K.S., Xu C.J., Zhang L.C., and Zhang S.L., 2001, Effects of shading on photosynthetic product distribution, carbohydrate metabolism and accumulation in developing citrus fruits, *Zhiwu Shengli Xuebao* (Plant Physiology), 27(6): 499-504
- Chen S., Chen H.L., Jin H., and Zhao Q.F., 2019, Genome-wide identification and expression analysis of sucrose synthase gene family in maize, *Xinan Nongye Xuebao* (Southwest Agricultural Journal), 32(11): 2479-2485
- Danyu Y., Eliana G.V., and Mansfield S.D., 2019, Arabidopsis sucrose synthase localization indicates a primary role in sucrose translocation in phloem, *Journal of Experimental Botany*, (6): 6
- Deng S.Y., Chen H.P., Mai Y.T., and Niu J., 2018, Gene family bioinformatics and expression analysis of sucrose synthase (SUS) and invertase (INV) in seedless pomelo, *Zhiwu Shengli Xuebao* (Plant Physiology), 54(10): 1576-1586
- Egli B., Kölling K., Köhler C., Zeeman S.C., and Streb S., 2010, Loss of cytosolic phosphoglucomutase compromises gametophyte development in Arabidopsis, *Plant physiology*, 154(4): 1659-1671
<https://doi.org/10.1104/pp.110.165027>
PMid:20959421 PMCID:PMC2996006
- Fettke J., Leifels L., Brust H., Herbst K., and Steup M., 2012, Two carbon fluxes to reserve starch in potato (*Solanum tuberosum* L.) tuber cells are closely interconnected but differently modulated by temperature, *J Exp Bot*, 63(8): 3011-3029
<https://doi.org/10.1093/jxb/ers014>
PMid:22378944 PMCID:PMC3350916
- Herbert M., Burkhard C., and Schnarrenberger C., 1979, A survey for isoenzymes of glucosephosphate isomerase, phosphoglucomutase, glucose-6-phosphate dehydrogenase and 6-Phosphogluconate dehydrogenase in C3-, C4- and crassulacean-acid-metabolism plants, and green algae, *Planta*, 145(1): 95-104
<https://doi.org/10.1007/BF00379933>
PMid:24317570
- Li H.P., Li H.M., and Pan S.M., 2013, Cloning and expression analysis of sucrose synthase gene from tropical sugarcane Badila, *Shengwu Jishu Tongbao* (Biotechnology Bulletin), (11): 58-62
- Li M.J., 2015, Functional analysis of UDP glucose phosphorylase and phosphoglucomutase in *Ganoderma lucidum*, Dissertation for Ph.D., Nanjing Agricultural University, Supervisors: Zhao M.W., pp.86-87
- Li X.Y., Li H., Lan X.G., Li Y.H., and Li Z.L., 2015, Advances in research on glucose phosphate mutase from plants, *Zhiwu Shengli Xuebao* (Plant Physiology), 51(05): 617-622
- Lingle S.E., 1999, Sugar metabolism during growth and development in sugarcane internodes, *Crop Science*, 39(2): 480-486
<https://doi.org/10.2135/cropsci1999.0011183X0039000200030x>
- Liu G.S., and Qi D.M., 2004, Advances in biology of *Leymus Chinensis*, *Caoye Xuebao* (Journal of Grassland Science), (05): 6-11

- Lv J.H., Cheng R., Wang G.M., Wu J., Wang Y.Z., Zhang H.P., and Zhang S.L., 2018, Identification and expression analysis of sucrose synthase related enzymes SUS and SPS gene family in pear, *Yuanyi Xuebao (Chinese Journal of Horticulture)*, 45(03): 421-435
- Malinova I., Kunz H.H., Alseekh S., Herbst K., Fernie A.R., Giertych M., and Fetzke J., 2014, Reduction of the cytosolic phosphoglucomutase in *Arabidopsis* reveals impact on plant growth, seed and root development, and carbohydrate partitioning, *PLoS one*, 9(11): e112468
<https://doi.org/10.1371/journal.pone.0112468>
PMid:25401493 PMCID:PMC4234415
- Maria A.S., Anna V.S., and Elena Z.K., 2019, Differences in the sucrose synthase gene SUS1 expression pattern between *Solanum lycopersicum* and wild tomato species, *Theoretical and Experimental Plant Physiology*, 31(4): 455-462
<https://doi.org/10.1007/s40626-019-00158-6>
- Pal S.K., Liput M., Piques M., Ishihara H., Obata T., Martins M.C., Sulpice R., van Dongen J.T., Fernie A.R., Yadav U.P., Lunn J.E., Usadel B., and Stitt M., 2013, Diurnal changes of polysome loading track sucrose content in the rosette of wild-type *Arabidopsis* and the starchless PGM mutant, *Plant Physiol*, 162(3): 1246-1265
<https://doi.org/10.1104/pp.112.212258>
PMid:23674104 PMCID:PMC3707535
- Paparelli E., Parlanti S., Gonzali S., Novi G., Mariotti L., Ceccarelli N., van Dongen J.T., Kölling K., Zeeman S.C., and Perata P., 2013, Nighttime sugar starvation orchestrates gibberellin biosynthesis and plant growth in *Arabidopsis*, *Plant Cell*, 25(10): 3760-3769
<https://doi.org/10.1105/tpc.113.115519>
PMid:24096343 PMCID:PMC3877829
- Stray-Pedersen A., Backe P.H., Sorte H.S., Mørkrid L., Chokshi N.Y., Erichsen H.C., Gambin T., Elgstøen K.B., Bjørås M., Włodarski M.W., Krüger M., Jhangiani S.N., Muzny D.M., Patel A., Raymond K.M., Sasa G.S., Krance R.A., Martinez C.A., Abraham S.M., Speckmann C., Ehl S., Hall P., Forbes L.R., Merckoll E., Westvik J., Nishimura G., Rustad C.F., Abrahamsen T.G., Rønnestad A., Osnes L.T., Egeland T., Rødningen O.K., Beck C.R.; Baylor-Johns Hopkins Center for Mendelian Genomics, Boerwinkle E.A., Gibbs R.A., Lupski J.R., Orange J.S., Lausch E., and Hanson I.C., 2014, PGM3 mutations cause a congenital disorder of glycosylation with severe immunodeficiency and skeletal dysplasia, *Am J Hum Genet*, 95(1): 96-107
<https://doi.org/10.1016/j.ajhg.2014.05.007>
PMid:24931394 PMCID:PMC4085583
- Tauberger E., Fernie A.R., Emmermann M., Renz A., and Trethewey R.N., 2000, Antisense inhibition of plastidial phosphoglucomutase provides compelling evidence that potato tuber amyloplasts import carbon from the cytosol in the form of glucose-6-phosphate, *The Plant Journal*, 23(1): 43-53
<https://doi.org/10.1046/j.1365-313x.2000.00783.x>
PMid:10929100
- Uematsu K., Suzuki N., Iwamae T., Inui M., and Yukawa H., 2012a, Alteration of photosynthate partitioning by high-level expression of phosphoglucomutase in tobacco chloroplasts, *Biosci Biotechnol Biochem*, 76(7): 1315-1321
<https://doi.org/10.1271/bbb.120068>
PMid:22785487
- Uematsu K., Suzuki N., Iwamae T., Inui M., and Yukawa H., 2012b, Expression of *Arabidopsis* plastidial phosphoglucomutase in tobacco stimulates photosynthetic carbon flow into starch synthesis, *J Plant Physiol*, 169(15): 1454-1462
<https://doi.org/10.1016/j.jplph.2012.05.008>
PMid:22705254
- Vriet C., Welham T., Brachmann A., Pike M., Pike J., Perry J., Parniske M., Sato S., Tabata S., Smith A.M., and Wang T.L., 2010, A suite of *Lotus japonicus* starch mutants reveals both conserved and novel features of starch metabolism, *Plant Physiol*, 154(2): 643-655
<https://doi.org/10.1104/pp.110.161844>
PMid:20699404 PMCID:PMC2949007
- Wang X.M., Chen J.Y., Gong M.J., Huang Y.X., Mo J.J., Xie P., Ye C.H., Yang S., Zhou H.K., and Zhao X.X., 2018, Responses of SS and SPS activities to sugar accumulation at booting stage of rice under salt stress and their correlation analysis, *Jiangsu Nongye Kexue (Jiangsu Agricultural Science)*, 34(3): 481-486
- Wang Z.Y., Dong Z.P., Guo M., Liu Y.H., Ma H.L., Song J.H., Weng Q.Y., Yuan J.C., and Zhao Y., 2017, Identification and bioinformatics analysis of Sucrose synthase gene family in foxtail millet, *Jiangsu Nongye Kexue (Jiangsu Agricultural Science)*, 45(15): 30-34
- Wei H.W., Cai S.L., Chen Y.G., Gao P., and Gao Y.Y., 2019, Identification and expression of sucrose synthase gene family in *Capsicum*, *Fenzi Zhiwu Yuzhong (Molecular Plant Breeding)*, 17(14): 4537-4544
- Weyler C., and Heinzle E., 2015, Multistep synthesis of udp-glucose using tailored, permeabilized cells of *e. coli*, *Applied Biochemistry & Biotechnology*, 175(8): 1-8
<https://doi.org/10.1007/s12010-015-1540-3>
PMid:25724977
- Winter H., Huber J.L., and Huber S.C., 1997, Membrane association of sucrose synthase: changes during the graviresponse and possible control by protein phosphorylation, *FEBS Lett*, 420(2-3): 151-155
[https://doi.org/10.1016/S0014-5793\(97\)01506-8](https://doi.org/10.1016/S0014-5793(97)01506-8)