Insight into Silicon Transporters in Major Cereal Crops of Poaceae: A Bioinformatics Approach

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Abstract— Cereals are used as a major source of energy among food sources and are grown in abundance throughout the world. Silicon has been demonstrated as an essential element as it helps in increasing the growth and yield of numerous plants and also by boosts their endurance against stresses caused by biotic and abiotic factors. Among cereal crops, Wheat, Rice, Maize, Sorghum and Barley are the species showing high levels of silicon accumulation but their levels of accumulation vary. This variation is attributed to the differences in the uptake capacity of silicon as silicic acid by silicon transporter among and within the species. The silicon transporter proteins of 5 different crops were analyzed. Protein-protein interaction analysis was performed to explore all possible functional proteins involved in the interaction network. The analysis revealed that proteins possessed important families and domains such as Aquaporin like domain, Major intrinsic protein (MIP) and Citrate transporter-like domain. The structure of silicon transporter proteins has been anticipated and proposed models were assessed for their precision and dependability based on qualitative and quantitative criteria. These findings would be helpful for better understanding of silicon uptake mechanism in cereal plants.

Keywords— Computational, silicon transporter protein, cereal crop, biotic stress, abiotic stress

I. INTRODUCTION

Silicon transporters are proteins that help to move silicon from the roots to the shoots of plants. In cereal crops of the Poaceae family, which includes major crops such as rice, wheat, maize, and barley, silicon transporters have been identified and studied. One of the most well-known silicon transporters in cereal crops is Lsi1, which was first discovered in rice. Lsi1 is responsible for the uptake of silicon from the soil and its transport to the shoot of the rice plant. Similar silicon transporters have also been identified in other cereal crops, such as HvLsi1 in barley and ZmLsi1 in maize. In addition to these transporters, other genes and proteins involved in silicon uptake and transport have been identified in cereal crops. For example, in rice, Lsi2 and Lsi6 are involved in the transport of silicon from the root to the xylem, while Lsi3 and Lsi4 are involved in the distribution of silicon within the shoot. Research has shown that the expression of these silicon transporter genes can be regulated by a variety of factors, such as soil silicon availability, plant age, and environmental stresses. Understanding the role of silicon transporters in cereal crops is important for improving crop yield and resistance to biotic and abiotic stresses. Bioinformatics techniques are often used to study the function and expression of genes and proteins, including silicon transporters, in major cereal crops of Poaceae. Here are some examples of bioinformatics approaches that can be used:

- Sequence analysis: Bioinformatics tools can be used to analyze the DNA and protein sequences of silicon transporters in different cereal crops. This can help to identify conserved regions and domains, predict protein structure and function, and compare the sequences across different species.
- Transcriptomics: RNA sequencing (RNA-seq) can be used to analyze the expression of silicon transporter genes in different tissues and under different conditions. This can help to identify the genes that are most important for silicon uptake and transport in different cereal crops.
- Proteomics: Mass spectrometry-based proteomics can be used to identify and quantify the silicon transporters and other proteins involved in silicon uptake and transport in different cereal crops. This can provide insights into the protein-protein interactions and post-translational modifications that regulate silicon transport.
- Phylogenetics: Phylogenetic analysis can be used to study the evolutionary relationships between different silicon transporter genes and proteins in different cereal crops. This can help to identify conserved and divergent features that are important for the function and regulation of these transporters.

Overall, bioinformatics approaches can provide important insights into the function and regulation of silicon transporters in major cereal crops of Poaceae, which can be used to improve crop yield and resilience to environmental stresses. To

perform a protein-protein interaction analysis, researchers typically use a combination of experimental and computational approaches. Experimental methods include techniques such as co-immunoprecipitation, yeast two-hybrid, and affinity purification followed by mass spectrometry. These methods can identify direct physical interactions between proteins in vivo or in vitro. Computational methods, on the other hand, use bioinformatics tools to predict protein-protein interactions based on protein sequence and structural information. For example, network-based methods such as graph theory and clustering algorithms can be used to analyze large-scale protein interaction data and identify functional modules and pathways. Once the protein-protein interaction network has been established, it can be further analyzed to explore the functional roles of the proteins involved. For example, Gene Ontology (GO) enrichment analysis can be used to identify the biological processes, molecular functions, and cellular components that are overrepresented in the network. This can provide insights into the biological pathways and cellular processes that are regulated by the proteins in the network. Overall, protein-protein interaction analysis is a powerful approach for exploring the functional relationships between proteins in a biological system, and can provide valuable insights into the molecular mechanisms that underlie cellular processes.

II. Literature Survey

The cereal crops are annual crops and are a part of Poaceae family including the principal crops such as rice, sorghum, wheat, millet, maize, rye and barley. Cereal crops are the major source of food for humansand their starch-containing grains are the part mostly eaten as food. Grains prove an excellent source of carbohydrates, fats, proteins, vitamins, minerals and oils. Crops like rice, maize and wheat are major staple crops and calorie source around the globe with sorghum and millet having a minor share [1], [2]. The advantageous effects of silicon on soil and growth of plants has been known for a long time. The members of Poaceae family use distinct methods for silicon absorption from soil in the form of silicic acid and its unloading into the xylem via aquaglyceroporins low silicon (lsi) 1 & 2 [3]. Grasses use silicon to protect themselves from biotic and abiotic stresses by assimilating it in their tissues [4]. Silicon is required to assistthe productivity of crops not just in temperate areas buttropical countries as well [5]. Silicon is the element found second most commonly in soil. Previously thought to be dispensable for growth of plants, it's now heeded by plant biology experts for its reported role inrelieving biotic and abiotic stress. Silicon makes plants more resistant to fungal and bacterial diseases such as powdery mildew, rice blastand sheath blight [6]. It also helps in reducing lodging, toxicity caused by metals and also stress caused by drought and salt. Siliconis a tissue constituent of all sorts of plants but its level of accumulation among plants varies from 0.1% - 10% of the total shoot dry weight [7]. The concentration of silica is observed to be more in monocots (10-15%) as compared to dicots (0.5% or less) [8]. Silicon is absorbed in the form of an uncharged molecule, silicic acid through the roots [9]. The absorption and dissemination of silicon depend on 3 transporters, namely Lsi1, Lsi2, and Lsi6 in crops like wheat, rice, maize, corn and barley. These are discovered from rice which is referred to as a typical silicon-accumulating plant species [7], [10], [11]. These transporters belong to a family of proteins called aquaporins (AQPs). The AQPs have a role in water transport across the membrane and they are responsible in maintaining and controlling the flow during vital processes such as cell elongation, germination of seeds, phloem loading/unloading and stomatal movement etc. Moreover, AQPs are involved in responses related to stress and reproductive growth as well[12], [13]. Here in this work, we have identified and compared silicon transporter protein in major crop belonging to Poaceae family such as rice, wheat, barley, maize and sorghum. It has already been known that the aquaporin Lsi protein play a role in silicon transportation [3], [14]. Thus, we explored Lsi protein in all selected crops. Transmembrane domain, motif and conserved domain prediction in all silicon transporters areperformed here. The transporter protein HvLsi, OsLsi and ZmLsi had 11 transmembrane domains, 5 motifs and one conserved domain. 6 transmembrane domains, one motif and family, domains and conserved site were predicted in protein SbLsi and TaLsi. In Protein-protein interactions network silicon transporter proteins showed interactions with many functionally important proteins. The 3-D structure prognostication of silicon transporter proteins revealed some excellent quality models. The analysis done in this study might help in establishing the biological roles of similar uncharacterized proteins.

III. Research Methodology

A. Data collection

The sequence of silicon transporter protein of Barley (BAH84976.1), Rice (ADH94038.1), Sorghum (AIP93582.1), Wheat (ADM47602.1) and Maize (NP001183945.1) were retrieved from the NCBI protein database.

B. Conserved motif and domain prediction

To identify conserved motifs in silicon transporters, the Multiple Expectation Maximization for Motif Elicitation (MEME) utility program was used [15]. The parameters used with following criteria: motif site distribution (0 or 1 site per

sequence); the maximum number of motifs (5); minimum width of the motif (6); and maximum width of motif (50). Domain prediction in identified silicon transporters was done by InterProScan [16].

C. Physicochemical analysis

The biological role of a protein is decided by its physical and chemical properties. The physicochemical properties of silicon transporter proteins such as molecular weight, theoretical Isoelectric point (pI), number of positive and negative residues, instability index, extinction coefficient, grand average hydropathy (GRAVY)and aliphatic index were analyzed with the help of Expasy's ProtParam [17].

D. Transmembrane domain prediction

Transmembrane domains were predicted using the SOSUI server [18]. SOSUI predicts if a protein has a soluble or transmembranous character. CD-Search was used to predict the Conserved Domain Database (CDD). It utilizes RPS-BLAST, a different version of PSI-BLAST, to rapidly examine a series of pre-calculated Position Specific Scoring Matrices (PSSMs) using a protein query [19].

E. Protein-protein interaction network

The protein-protein interaction network for OsLsi, HvLsi, SbLsi, ZmLsi and TaLsi were achieved via STRING (Search Tool for the Retrieval of Interacting Gene/Protein database 244 version 10.0) [20].The interactions comprise of direct (physical) and indirect (functional) connections and they are extracted from Genomic viewpoint, High-throughput Experimentation, (Conserved) Co-expression and prior knowledge.

F. Protein structure prediction and quality assessement

Three-dimensional structures of the chosen silicon transporter proteins were predicted with the help of SWISS-MODEL which relies on template-based homology [21], [22]. The input was given in the form of protein sequences of various crop plants such as rice (ADH94038.1),wheat (ADM47602.1), barley (BAH84976.1), sorghum (AIP93582.1) and maize (NP001183945.1).This server involved the BLASTP2 algorithm [23] to look for similarities of primary sequence in the ExNRL-3D database. Parallelly, the dynamic sequence alignment algorithm SIM [24] was utilized to choose templates with the highest values of sequence identity. Afterwards, primary and refined match analysis was performed using ProMod3. Acquired proteins were used in the form of templates for homology modelling of OsLsi, TaLsi, HvLsi, SbLsi, and ZmLsi proteins backbone trajectories. The prepared structures were analysed with the help of z-score and QMEAN scores. The QMEAN4 score is linear combinations of 4 statistical potential terms which estimate model reliability between 0-1. Statistical terms include Cβ interaction energy, All-atom pairwise energy, solvation energy, torsion angle energy. Quality of predicted structures was evaluated using VERIFY3D [25] and ERRAT [26] server.

IV. Experiments and Results

A. Analysis of motif composition

A detailed study of conserved motifs of silicon transporter proteins was done to know in detail about the compositional similarity and dissimilarity. MEME online program was used to analyze 5 different motifs, named 1-5 (Fig.**1A**). The motifs 1, 2, 3, 4 and 5 were found out to be composed of 50, 40, 37, 50 and 48 amino acids respectively (Fig.**1B**). The protein sequence of ZmLsi consist motif 1 (at position 431-470) with the *p*-value 6.15e-65, motif 2 (at position 431-470) with *p*-value 1.24e-50, motif 3 (at position 326-362) with the *p*-value 4.68e-41, motif 4 (at position 74-123) with the *p*-value 7.91e-62 and motif 5 (at position 162-209) with the *p*-value 1.18e-59. The protein sequence of SbLsi was found to have only motif 3 (at position 168-204) with the *p*-value 1.47e-26. The protein sequence of OsLsi had motif 1 (at position 183-232) with the *p*-value 1.38e-62, motif 2 (at position 358-397) with *p*-value 1.68e-50, motif 3 (at position 253-289) with the *p*-value 1.30e-43, motif 4 (at position 5-54) with the *p*-value 7.32e-61 and motif 5 (at position 93-140) with the *p*-value 1.13e-54. Protein sequence HvLsi was found to have motif 1 (at position 255-304) with the *p*-value 2.66e-62, motif 2 (at position 430-469) with *p*-value 1.68e-48, motif 3 (at position 325-361) with the *p*-value 3.04e-43, motif 4 (at position 74-123) with the *p*-value 1.36e-62 and motif 5 (at position 162-209) with the *p*-value 1.68e-58. The protein sequence of TaLsi had only motif 3 (at position 99-135) *p*-value 1.02e-26. The protein ZmLsi, OsLsi and HvLsi shared similar motif composition and contained all 1-5 motifs, while protein SbLsi and TaLsi shared similar motif and contained only motif 3. Proteins showed identical motif distribution patterns, indicating functional similarity among them.

B. Analysis of domain in Silicon transporters

Inter ProScan allows us to study the proteins from a functional aspect by their categorization into different families and prediction of their domains as well as crucial sites. Silicon transporter protein, HvLsi, OsLsi and ZmLsi had citrate transporter-like domain such as CitMHS predicted from PFAM database. CitMHS is a family of putative citrate transporter that belongs to the Na+/H+antiporterNhaD-like permase superfamily (Fig.2). Transporter protein SbLsi and TaLsi had

family domain and important sites. The family (MIP family) consist Aquaporin transporter, predicted from PANTHER database, MIP, predicted from PFAM and CDD database and mintrinsicp, predicted from PRINT database.The domains (aquaporin-like) consist 1.20.1080.10 and aquaporin-like domain. The domain 1.20.1080.10 predicted from CATH superfamily that belongs to glycerol uptake facilitator protein. Conserved sites consist of MIP that predicted from prosite patterns database.

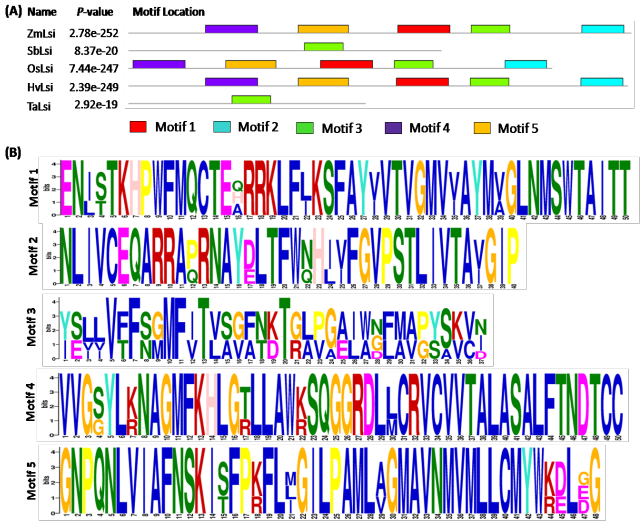

Fig. 1. Schematic diagram of conserved motifs in silicon transporter proteins. (A) Distribution of conserved motifs (boxes) in different proteins. Box size indicates the length of motifs. The motifs, numbered 1-5, were displayed in different coloured boxes. (B) Conserved amino acids of each motif.

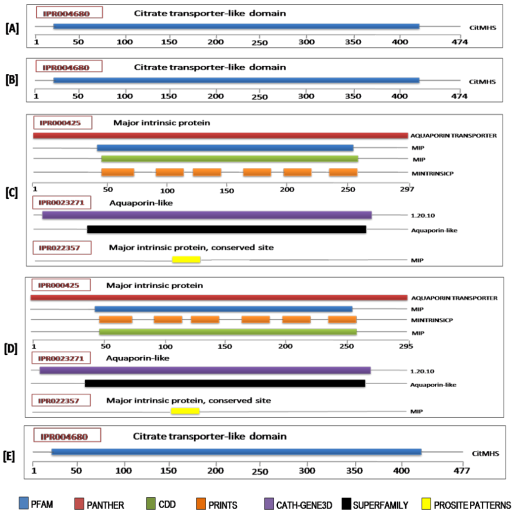

Fig. 2. Schematic diagram of family, domain and sites in silicon transporter sequences. (A)HvLsi, (B) OsLsi and (E) ZmLs, proteinshave only Domain (Citrate transporter-like) CitMHS. (C) SbLsi and (D) TaLsi have family (MIP), domain (Aquaporin-like) and sites (MIP, conserved site). Colours represent the source database.

C. Physicochemical properties of Silicon transporters

The physical and chemical properties of a protein are important in determining its function. Thus, to check any similarities/ dissimilarities in the functions of proteins, a computational analysis of physico-chemical properties was performed. pI is referred to as the pH at which the protein's surface contains charge but has a null net charge. Proteins having pI above pH 7.0 exhibit a positive charge and are attracted towards negative electrode while proteins having pI below pH 7.0 exhibit a negative charge and are attracted towards positive electrode. In the analyzed silicon transporter proteins, HvLsi, OsLsi and ZmLsi were found to have a pI above 7.0, thus showing they are positively charged. On the other hand, SbLsi and TaLsi were found to have a pI point below 7.0, thus showing they are negatively charged. The pI is the point where proteins show a stable and compact form, hence pI will be useful to come up with a buffer system to purify proteins based on isoelectric focusing technique. The value of extinction coefficient of hypothetical proteins homologue extends from 41035 to 63410 M^{-1} cm^{-1}at 280 nm with respect to tyrosine, tryptophan and cysteine concentrations. Silicon transporter proteins OsLsi, HvLsi, and ZmLsi were found to have a greater extinction coefficient than SbLsi and TaLsi. This high value of extinction coefficient signifies existence of amino acids tyrosine, tryptophan and cysteine in high concentrations. The calculated values of extinction coefficients allow us to perform quantitative analysis of protein to protein and protein to ligand interactions in solution. A higher instability index for ZmLsi (39.63) as compared to HvLsi (34.38) was predicted. A protein having a value of instability index less than 40 is predicted to be stable. All the predicted silicon transporters possessed an instability index value less than 40 signifying their potential stable nature. The aliphatic index (AI) of a protein which is the relative volume of a protein occupied by aliphatic side chains (Alanine, Valine, Leucine and Isoleucine) is considered as significant factor of stable nature of globular proteins. In silicon transporters, the aliphatic index for protein ZmLsi was predicted to be 116.92 which was higher than that of SbLsi (96.87). This high aliphatic index value signifies stability of these proteins over a wide temperature extent. Thus, OsLsi, HvLsi, and ZmLsi were found to have more stability than SbLsi and TaLsi. The GRAVY for a protein is referred to as the sum of hydropathy values of all its constituent amino acids, divided by the number of amino acid residues in the sequence. SbLsi was found to have a GRAVY value of 0.366 which is lower as compared to ZmLsi (0.762). This lower GRAVY value signifies less hydropathicity in the protein sequence. This low value also signifies that protein can have better

interaction with water. Hence, SbLsi and TaLsi showed better interaction with water in compared to Hvlsi, OsLsi and ZmLsi.

D. Analysis of transmembrane domain

The topology of transmembrane domains facilitates the transport of signals, channeling ions and transferring material. All the chosen proteins are transporters hence, their transmembrane domain is predicted. Transmembrane domains, extend over the phospholipid bilayer and highly communicate with the hydrocarbon tails of lipids through hydrophobic interactions. Transmembrane domains are generally 20-23 amino acids long with enriched in hydrophobic residues. The whole predicted domain has an approximate length of 23 amino acids with the hydrophobic residues being more in numbers (Fig. 3). The protein HvLsi, OsLsi and ZmLsi have more number of transmembrane helix thus they have more hydrophobic amino acids. The average of hydrophobicity of HvLsi, OsLsi and ZmLsi proteins were 0.705696, 0.710593 and 0.762054 respectively and protein SbLsi and TaLsi were 0.366330 and 0.422034 respectively). The proteins TaLsi and SbLsi revealed a structure having inverted symmetry which enables a two-way transport of silicon and also checks over-accumulation of silicic acid and following rampant auto-polymerization of silica in cytoplasm.

E. Analysis of conserved domain

In a protein, domains are evolutionarily conserved units that commonly communicate repeated structural and functional units. The specific role of a protein is dependent upon its domain combination. Considering this, conserved domains werestudied using CDD tool and potential similarities and dissimilarities in the mode of action of chosen silicon transporters were found out. These domains have been possibly used as building blocks over the course of evolution which possibly have been combined again and rearranged to modify protein [27]. The silicon transporter proteins HvLsi, OsLsi and ZmLsi had a fixed domain belonging to ArsB_NhaD_permease superfamily. The anion permeaseArsB/NhaD has been known to transport sulfate, sodium, antimonite, arsenate and organic anions across the bio-membranes in all the 3 kingdoms. Usually, anion permeases possesses 813 transmembrane helices and are ableto work individually, as a chemiosmotic transporter or as a part of ATP driven anion pump which is responsible for the formation of channel. On the other hand, silicon transporter proteinsTaLsi and SbLsi consist of MIP superfamily. Members of MIP superfamily work as channels across membranes and selectively translocate water, ions and small neutral molecules out of and among the cells. The proteins acting as channels have a common fold: the N-terminal part in cytosol which is followed by 6 transmembrane helices, which have probably emerged as a result of gene duplication. Considering the similarity shown by sequence and functions, the superfamily can be further divided into 2 main groups: glycerol uptake facilitators (GlpFs) and water selective channels called AQPs. GlpFs have been associated with microbes only while AQPs are present in all the 3 kingdoms.

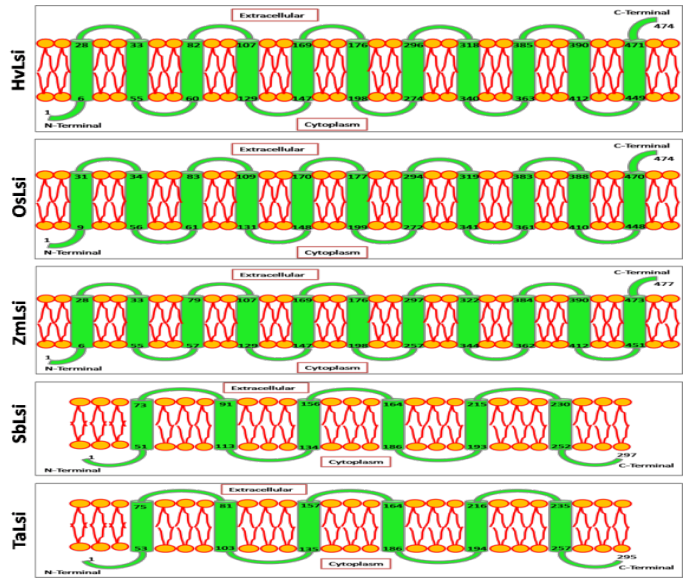

Fig. 3. Schematic illustration of the silicon transporter proteins, showing transmembrane domain structure and orientations. Transmembrane domains (green cylinders) of HvLsi, OsLsi, ZmLsi, SbLsi and TaLsi protein sequences are taken from the SOSUI topology.

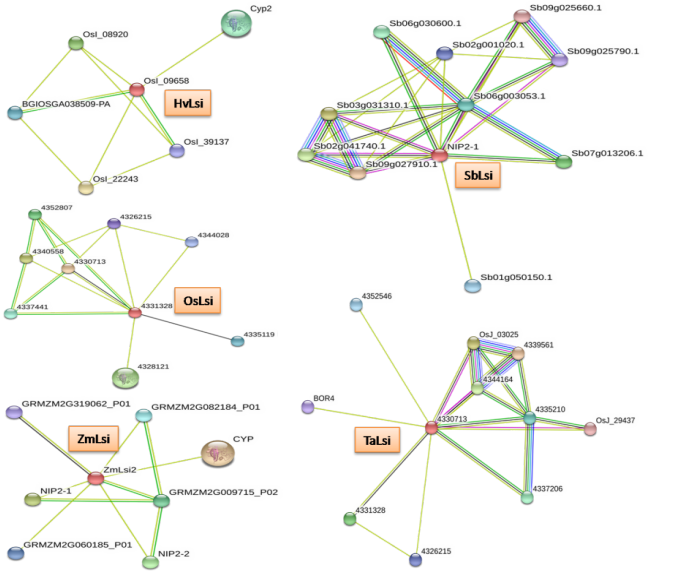

Fig. 4. Protein to protein interactions of silicon transporter as anticipated by STRING

F. Analysis of protein-protein interaction

The interactions of proteins with one another have a key role in almost all cellular functions. The mutually dependent interactions taking place between a protein and its associated proteins are responsible for a common function. Databases related toprotein-protein interactions have become an important tool for studying cellular pathways and biological networks. The result of protein-protein association network acquired through STRING server revealed diverse interacting partners for silicon transporter proteins from cereals (Fig. 4). The protein HvLsi (Osl_09658) was found to interact with Cyclophilin-Cyp2, A Peptidyl-prolyl cis-trans isomerase (PPIases) with maximum interaction score value 0.474 which accelerates protein folding. OsLsi (4331328) protein showed interaction with aquaporin proteins with maximum interaction score value 0.910. The aquaporin protein (4330713) involved in silicon transport and aquaporin protein (4340558) facilitates the transport of water and small neutral solutes across the cell membrane. OsLsi interacts with peptidyl-prolyl cis-trans isomerase (4328121) with maximum interaction score value 0.654 that accelerates protein folding. OsLsi interacts with potassium efflux antiporter protein (4352807 and 4337441) and hydrophobic protein- LTI6A (4344028) with maximum interaction score value 0.568 and 0.491 respectively. These proteins play a role in the regulation of membrane potential. OsLsi also interacts with boron transporter protein (4326215) with maximum interaction score value 0.491. All interactions showed with SbLsi (NIP2-1) are putative uncharacterized protein. TaLsi (4330713) was found to interact with glutamate synthase (4339561 and OsJ_03025) with maximum interaction score value 0.983. Glutamate synthase play role in glutamate biosynthesis. TaLsi interacts with ferredoxin-dependent glutamate synthase (4344164) with maximum interaction score value 0.973 that involved in glutamate biosynthesis. TaLsi also interacts with FGGY family of carbohydrate kinases (4337206), FAD-dependent oxidoreductase domain-containing protein (4335210), BOR4- boron transporter protein (4352546 and 4326215) and trehalose-6-phosphate synthase (OsJ_29437) with maximum interaction score value 0.882, 0.825, 0.762 and 0.592 respectively. ZmLsi showed interaction with CYP with maximum interaction score value 0.891. CYP is cyclosporine protein that involves in protein binding. ZmLsi also interact with NIP2-1 (aquaporin, NOD26-like intrinsic protein 2-1) and NIP2-2 (aquaporin, NOD26-like intrinsic protein 2-2) with maximum interaction score value 0.738 and 0.736 respectively.

G. Protein structure prediction and model quality assessment

Computational models for the anticipated 3D structures of these silicon transporter proteins were prepared for there are no pre-existing PDB files related to these sequences. The inclusion of structural information helped in explaining the biochemical role of these proteins. Models were prepared using ProMod3 and target-template alignment was used as a base. The transporter protein HvLsi, OsLsi, SbLsi, TaLsi and ZmLsi were modelled using templates having highest Qmean score (Fig. **5**). Protein HvLsi, OsLsi and ZmLsi were modelled using template (4f35.1.A) protein Transporter, NadC family which has 3.20Å resolution. The template shows 17.41%, 17.16% and 18.09% identity, -7.19, -7.56 and -7.54 Qmean score, and sequence coverage range from 34-472 (80%), 5-470 (85%) and 11-447 (83%) amino acid residues with the HvLsi, OsLsi and ZmLsi protein sequence respectively. Protein SbLsi and TaLsi were modelled using template protein Aquaporin-4 (2d57.1.A) and Aquaporin-1 (1j4n.1.A) which has 3.20 Å and 2.20 Å respectively. The template shows 35.56% and 29.96% identity, -5.24 and -5.25 Qmean score, and sequence coverage range from 48-256 (80%) and 39-275 (80%) amino acid residues with the SbLsi and TaLsi protein sequence respectively.

The anticipated structure was verified by using the structure evaluating program, ERRAT. The overall quality factor for modelled protein HvLsi, OsLsi, SbLsi, TaLsi and ZmLsi were 84.615, 93.933, 90.274, 88.501 and 86.150 respectively, which are high quality of model is also confirmed from VERIFY 3D server as 65.83%, 69.53%, 76.56%, 65.40% and 70.47% of residues for modeled protein HvLsi, OsLsi, SbLsi, TaLsi and ZmLsi respectively. All 5 modelled proteins showed a score higher than 0.02 thus the models showed satisfactory 3D-1D scores for all the residues in the sequence.

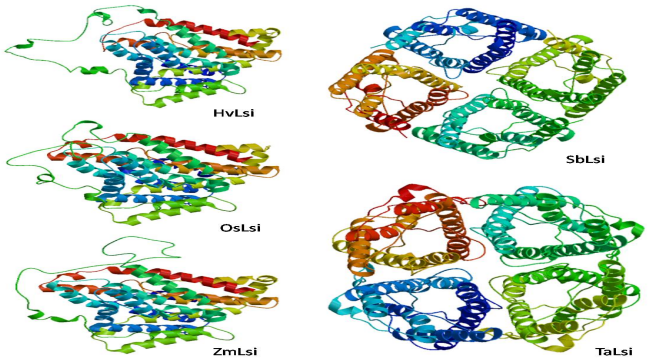

Fig. 5. Structural model of HvLsi (BAH84976.1), OsLsi (ADH94038.1), SbLsi (AIP93582.1), TaLsi (ADM47602.1), and ZmLsi (NP001183945.1) proteins

V. CONCLUSION

Various computation methods describe the structure and functions of silicon transporter based on the sequence data which may provide direct insight into sequence-based properties. In this study, we considered the silicon transporters of major crops like rice, wheat, maize barley and sorghum, specified their physical and chemical properties and found out domains and families by utilizing different bioinformatics tools and databases which are accessible publicly. The study disclosed the key functional domains and families engaged in the ion transportation through biological membranes. Presence of various domains in the silicon transporter-like aquaporin-like domains, citrate transporter-like domain, and MIP denotes stress tolerance. The present study led to various findings which might be helpful for creating new biotic and abiotic stress tolerant plant varieties.

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