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Article

Use of bioinformatics characterization of molybdenum transport genes in *Ipomoea trifida* and *Ipomoea triloba*

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Abstract: Molybdenum (Mo) is considered and described as an essential element for living organisms' development. Until now, no studies have been performed on genes involved in the Mo transporter in ancestral *Ipomoea* species. This study aimed to identify potential *Mo* genes in *Ipomoea trifida* and *I. triloba* genomes using bioinformatics tools. We identified four *Mo* transporter genes, two in *I. trifida* and two in *I. triloba*. Based on the RNA-seq datasets, we observed that *Mo* genes are expressed (*in silico*) and present different mechanisms between the tissues analyzed. The information generated in this study fills missing gaps in the literature on the *Mo* gene in an important agronomic crop.

Keywords: gene expression; *in silico*; molybdate; motif signature; phylogeny

1. Introduction

Sweet potato [*Ipomoea batatas* (L.) Lam.] ($2n = 6x = 90$) is highlighted as one of the most significant vegetables in Brazil. Its agronomic, social, and economic importance is mainly attributed to its rusticity, climate adaptation, and high production capacity [1,2]. The oldest known domesticated sweet potato (approximately 2500 BC) in the world is believed to have been discovered by experts at an excavation in the Casma Valley in Peru [3]. Botanically, the *Ipomoea* belongs to the Convolvulaceae family, which comprises approximately 1660–1880 species, with 59 genera and 12 tribes [4]. Popularly known as sweet potato, [*I. batatas* (L.) Lam.] represents a highly relevant food crop widely cultivated worldwide [5]. In addition to playing a crucial role in food, sweet potatoes also stand out as a valuable alternative source of bioenergy, serving as a raw material for fuel production [6]. Austin [7] suggested that the ancestor of the sweet potato [*I. batatas* (L.) Lam.] originated from natural hybridization between *I. trifida* (diploid—$2n = 2x = 30$) and *I. triloba* (diploid—$2n = 2x = 30$).

Mineral nutrition of plants through mineral fertilization is important for the development and growth of plants [8]. Nitrogen (N) has several elements that are extremely important involved in the efficiency of assimilation and transport [9,10]. Some studies have been performed to better understand the transport of some these elements in plants [11–15]. Among the various elements available to plants, molybdenum (Mo) is one of the essential microelements and also a crucial metallic component of the cofactor Mo (Moco) biosynthesis [16,17]. It is only in recent years that the biosynthesis of Moco in bacteria has been described [18]. It is believed that in the form of Moco in plants, it can perform the function of a catalyst during the

assimilation of N, vital for purine metabolism, synthesis of some phytohormones (abscisic acid, auxin), and also in sulfite detoxification [17,19]. Briefly, there are two types of cofactors related to Mo: i) a pterin-based molybdenum cofactor (Moco); ii) an iron-molybdenum cofactor based on the iron-sulfur cluster, called (FeMoco) [20]. In plants, five molybdoenzymes are described: nitrate reductase (NR), aldehyde oxidase (AO), xanthine dehydrogenase (XDH), sulfite oxidase (SO), and mitochondrial amidoxime reducing (mARC) [17,21–23]. Without this element, plant growth and development are compromised, as they are unable to process N effectively [21]. In plants, the micronutrient Mo presents a rapid translocation and requires small quantities [21,24]. Proper management of nutritional aspects, especially the micronutrient molybdenum, can provide significant gains in crop production [8].

A study by Arnon and Stout [25] is the first to describe the importance of this element for plants. Some important mechanisms played by the Mo element remain unknown [17]. In the case of Mo deficiency, for example, it can result in symptoms such as morphological changes in the leaves, paleness, disturbances in the formation of flowers, and wilting of the leaf edges, impairing plant growth, development, and production [24]. The deficiency attributed to Mo may also be correlated with some mutation during the Mo uptake system [21]. It is essential to highlight a lack of research on Mo transporters [24]. There are two families of specific molybdate transporters in eukaryotes, MOT1 (Molybdate Transporter type 1) and MOT2 (Molybdate Transporter type 2), respectively [25–28]. In *Medicago truncatula* and *Oryza sativa* members of the MOT1 family may present specific Mo transporters [29,30]. It is believed, for example, that the plasma membrane-associated molybdate transporter protein (MOT1) may show similarities with the sulfate transporter [28,29,31]. It is known that Mo uptake in bacteria can be mediated by different protein systems (ABC superfamily) [32]. Recently, a phylogenetic analysis performed by Wang et al. [33] demonstrated that MOT1 is evolutionarily conserved in both monocots and dicots. MOT2 was first identified in *Chlamydomonas* [28,34]. Some studies have characterized Mo transporters [16,22,26]. The present study performed a genome-wide *in silico* characterization of the likely genes involved in Mo transport in two sweet potato ancestors, *I. trifida* and *I. triloba*. Additionally, detailed information such as physicochemical properties, gene structure, analysis of promoters, transmembrane domains (TMDs), phylogenetic relationship, and evolutionary divergence is reported. In summary, this research presents information that can be used in breeding programs for this species to develop genotypes tolerant cultivated in soils with molybdate limitation.

2. Materials and methods

2.1. Identification and characterization of *Mo* genes in *I. trifida* and *I. triloba*

Mo genes identification of *I. trifida* and *I. triloba* was based on the Sweetpotato database (http://sweetpotato.uga.edu/). Candidate genes from the species *Arabidopsis thaliana* were used as bait to identify possible Mo transporters (MOT1-Q9SL95.1

and MOT2-Q0WP36.2 protein sequences/ [16]). To be sure, we compared and analyzed all Mo sequences using tools in the NCBI CDD (National Center for Biotechnology Information/ [35]) (https://www.ncbi.nlm.nih.gov/cdd) to check the presence of domains belonging to the *Mo* transporter. All sequences referring to the *Mo* genes of *I. trifida* and *I. triloba* (genomic sequences, amino acids (aa), and CDS–Coding DNA Sequence) were downloaded. Each sequence was also compared with other sequences deposited in the NCBI database, using the BLASTx and BLASTp tools to verify individual specificity. Subsequently, all physical and chemical properties of the *Mo* members were analyzed by the online tool ExPASy ProtParam (https://web.expasy.org/protparam/ [36]). In the present study, subcellular locations were predicted by the Plant-mPLoc program (http://www.csbio.sjtu.edu.cn/bioinf/plant-multi/ [37]). The genes were renamed according to their chromosomal location in the *I. trifida* and *I. triloba* genomes.

2.2. Gene structure and motif analysis

Gene structure (exons and introns) of all *Mo* genes was predicted using the Gene Structure Display Server tool (GSDS—http://gsds.cbi.pku.edu.cn/ [38]). This analysis was obtained through the genomic sequence and CDS. The MEME (Multiple Em for Motif Elicitation—http:// meme-suite.org/ [39]) platform identified conserved domains (motifs) of all Mo protein sequences.

2.3. Transmembrane and chromosomal distribution in *I. trifida* and *I. triloba*

Transmembrane helix's presence was analyzed on the TMHMM v.2.0 platform (https://services.healthtech.dtu.dk/services/TMHMM-2.0/ [40]). We also ascertained the physical locations of the *Mo* genes; this information was obtained from the Sweet Potato database, and the MG2C v2.1 tool (http://mg2c.iask.in/mg2c_v2.1/) was used to map the genes to specific chromosomes [41].

2.4. Phylogenetic tree and synteny analysis

For phylogenetic analysis, an alignment of multiple sequences was initially performed. The phylogenetic tree was constructed using the Neighbor-Joining (NJ) method in MEGA 7.0 software with 1000 bootstrap tests [42]. To compare the *Mo* genes and establish synteny relationships among *I. trifida*, *I. triloba*, *A. thaliana,* and *O. sativa*, first, we performed reciprocal BLASTp. The hit threshold values were set as *E*-value < 1e − 50, score > 200, minimum 80% coverage, and 70% identity [43]. Tbtools software [44] was used to represent the synteny events graphically.

2.5. Transcriptional profile of *Mo* genes in *I. trifida* and *I. triloba*

The tissue-specific expression profile of the *Mo* genes in *I. trifida* and *I. triloba* was investigated using the values obtained from FPKM (fragments per kilobase of exon per million fragments mapped) deposited in the sweet potato database (http://sweetpotato.uga.edu/cgi-bin/annotation_report.cgi). The plant tissues analyzed were: (callus_flower, callus_stem, flower, flower bud, leaf, root1, root2, stem (*I. trifida* genome), and (flower, flower bud, leaf, root1, root2, stem (*I. triloba*

genome). All FPKM values used were subsequently transformed into log2. The transcriptional profile obtained was expressed and presented in a figure (heatmap) with the help of the CIMMiner tool (http://discover.nci.nih.gov/cimminer).

3. Results and discussion

3.1. Genome-wide characterization and gene structure analysis of *Mo* genes in *I. trifida* and *I. triloba*

In silico studies increasingly provide a starting point for new gene discovery. Plants can grow and develop in environments with highly heterogeneous soils and variable nutrition [45]. Mo is an essential element for almost all living organisms, especially for the growth and development of plants (reviewed by [17]). In the interim, two genes involved in the Mo transporter were identified in each of the *I. trifida* and *I. triloba* genomes (detailed in **Table 1**). The genes identified in this study corroborate some of the species studied by Vatansever et al. [16]. However, except for the species *Panicum virgatum*, five Mo transporters have been described [26]. It was observed that Mo varied little between the species studied based on their physicochemical properties. In *I. trifida*, ItfMo varied between 459 (ItfMo2) and 470 (ItfMo1) aa, and their pI (isoelectric point value) ranged between 9.09 (ItfMo1) and 9.44 (ItfMo2). Molecular weight (kDa) ranged from 48.16 (ItfMo2) to 50.48 (ItfMo1). In *I. triloba*, ItbMo varied between 461 (ItbMo2) and 470 (ItbMo1) aa, and their pI ranged between 9.10 (ItbMo1) and 9.32 (ItbMo2). The molecular weight ranged from 50.53 (ItbMo1) to 48.51 (ItbMo2) kDa (see **Table 1**).

Table 1. The Mo transporter information of sweet potato, *I. trifida*, and *I. triloba*.

	Gene	Sequence ID	Chromosomal localization	aa	kDa	pI	GRAVY	Subcellular localization
Ipomoea trifida	*ItfMo*1	itf02g26610.t1	Chr02:24585347-24583503	470 aa	50.48	9.09	0.601	Chloroplast/Peroxisome
	*ItfMo*2	itf15g22130.t1	Chr15:21177796-21179736	459 aa	48.16	9.44	0.604	Cell membrane/Chloroplast/Golgi apparatus/Mitochondrion/Peroxisome/Vacuole
Ipomoea triloba	*ItbMo*1	itb02g25620.t1	Chr02:26382609-26384583	470 aa	50.53	9.10	0.601	Peroxisome
	*ItfMo*2	itb15g23220.t1	Chr15: 25969438-25971774	461 aa	48.51	9.32	0.570	Chloroplast/Golgi apparatus

The grand average of hydropathy (GRAVY) value in both genomes indicates that the proteins are hydrophobic. Furthermore, we predicted protein subcellular localization, suggesting that these proteins present a certain plasticity and function in the *Ipomoea* studied, as shown in **Table 1**. The subcellular localizations of Mo transporters may be questionable. Two studies demonstrated, for example, that AtMOT1;2 and OsMOT1;2 are localized in the tonoplast [46,47]. In *A. thaliana*, for example, the protein MOT2 is involved in Mo transporter activity in vacuoles [19]. In a previous study, *in silico* analysis revealed that the AtMOT1;1 transporter can perform mitochondrial localization signaling in the N-terminal region [48]. In our understanding, evolutionarily, when faced with the organization of introns of a given gene, we can consider it strong evidence that there has been a gene family

diversification, respectively [49,50]. However, gene structures (exons/introns) were generated using the GSDS bioinformatics program to better understand the evolution of *Mo* genes in *Ipomoea*. We used information from the Sweetpotato platform (genomic sequences and CDS) (**Figure 1**).

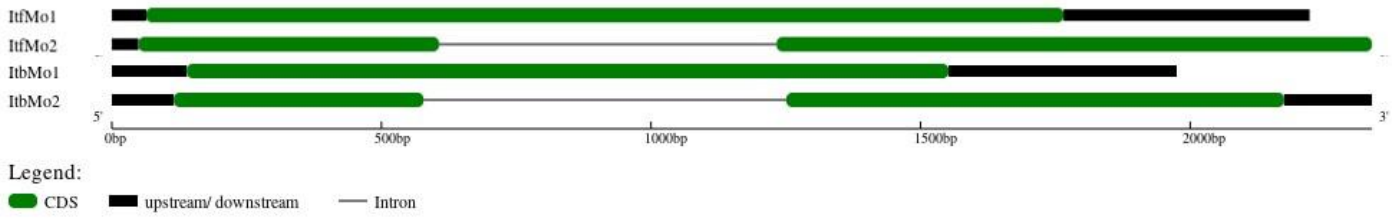

Figure 1. Structure illustration of *Mo* genes. Green boxes indicate the exons, gray lines indicate introns, and black boxes indicate the untranslated region.

3.2. Transmembrane domain profile, conserved domains, and chromosomal location analysis of *Mo* genes in *I. trifida* and *I. triloba*

We can observe that some genes (isoform 1 in both species) have one exon, and the counterparts (isoform two in both species) have two exons (**Figure 1**). Again, this information corroborates the study by Vatansever et al. [16]. This information indicates that the Mo transporter may have been conserved in higher plants. The aa sequences of Mo transporters from *I. trifida* and *I. triloba* were analyzed by the TMHMM v.2.0 program to verify the presence of Mo transmembrane domains (TMDs) (**Figure 2**). Both species' transmembrane proteins varied from 10 to 11, with five hydrophobic regions indicated in **Figure 2**.

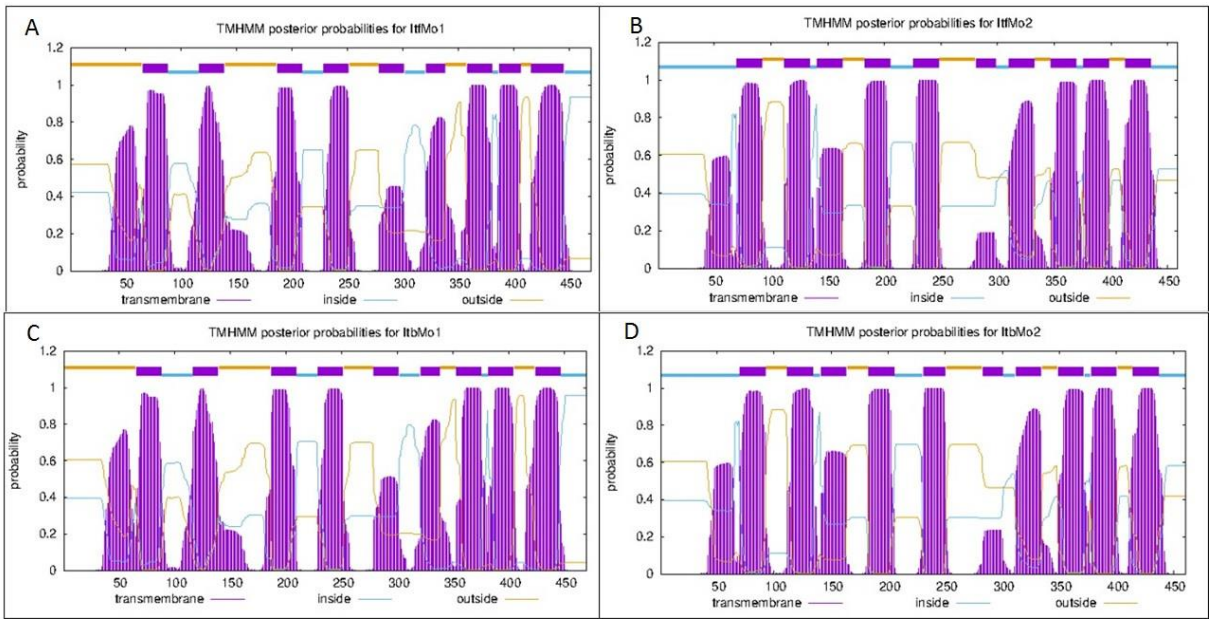

Figure 2. Putative positions of transmembrane proteins of Mo transporters in *I. trifida* and *I. triloba* species generated from the TMHMM program (http://ww.cbs.dtu.dk/services/TMHMM). **(A)** and **(B)**, *I. trifida*; **(C)** and **(D)**, *I. triloba*.

The results presented in our study were in accordance with a study performed by Vatansever et al. [16]. The literature shows that the number of TMDs for *Mo* genes showed low variation [51,52]. Bavaresco et al. [26], in their study on the characterization of Mo in *Panicoideae*, showed that TMDs ranged from six to 11 in the cultures studied. In their study, Huang et al. [17], subjected plants to abiotic stress and noted that TMDs showed adaptation in response to stress. However, the suggested hypothesis is that the number of TMDs (**Figure 2**) can influence and perform specific functions between species. To identify the diversity of *Mo* genes, putative motifs were predicted using the MEME tool (http://meme-suite.org/tools/meme). According to our results, four motifs were found in each species (**Figure 3**).

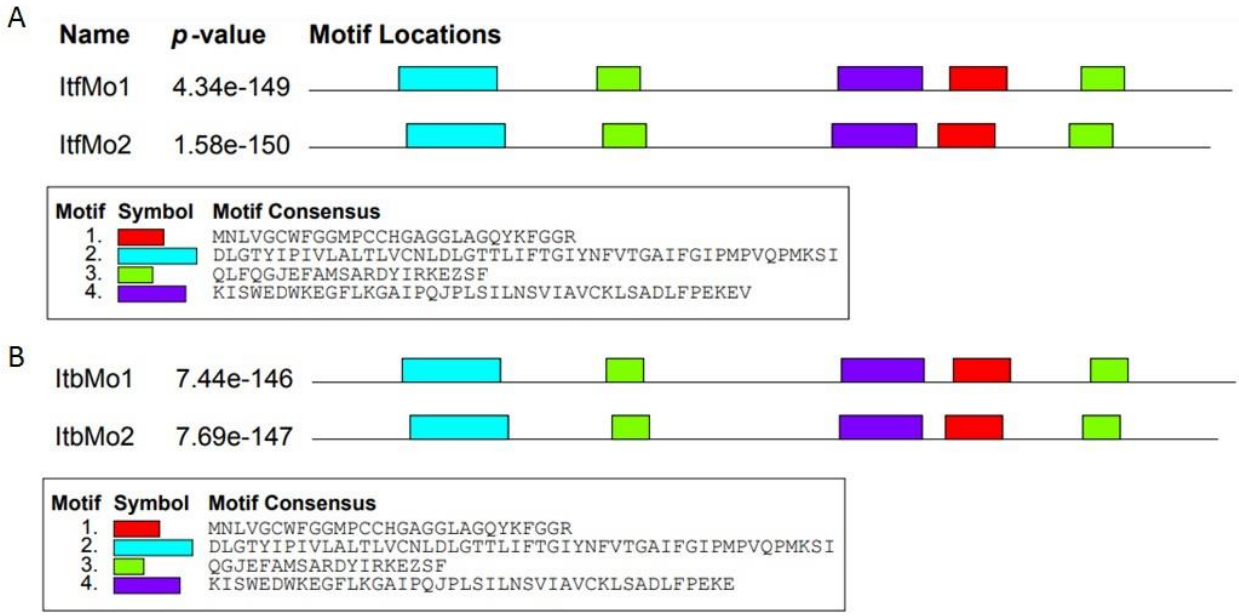

Figure 3. Motif distributions of *Mo* genes (motif presented in color), as predicted by the MEME program. **(A)** *I. trifida*, and **(B)** *I. triloba*.

However, motif three is found in both species in duplicate (**Figure 3**). Based on this information, it is possible to predict that although the sequences are present in *I. trifida* and *I. triloba*, the motifs that make up the protein structure can perform different functions between cultures. The *Mo* gene distribution on chromosomes in *I. trifida* and *I. triloba* shows the same pattern. Chromosomal location showed that *Mo* genes were randomly distributed on chromosomes Chr2 and Chr15 in the *I. trifida* and *I. triloba* genomes (**Figure 4A**,**B**).

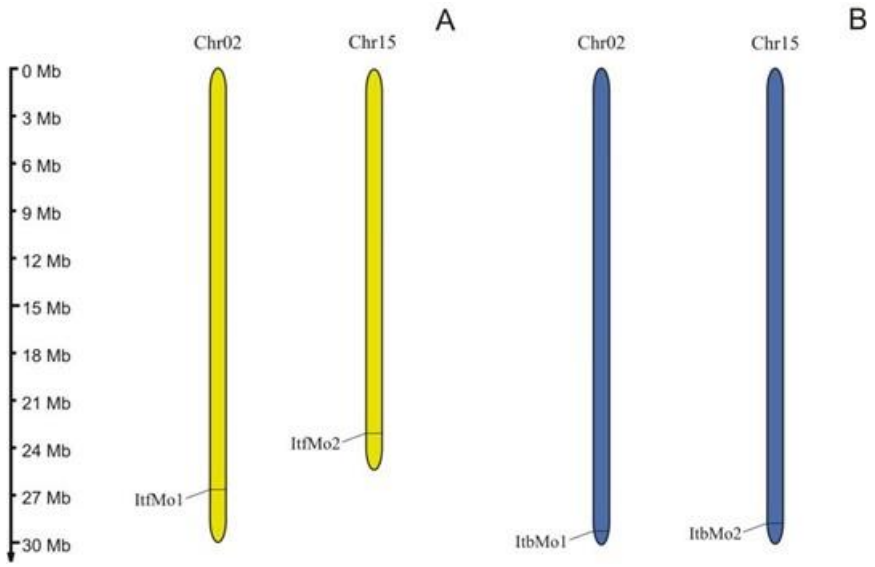

Figure 4. Chromosomal distribution and duplication events of the *Mo* genes in sweet potato. **(A)** *I. trifida*. **(B)** *I. triloba*. The number of chromosomes and their size in Mb are indicated at the top of each bar, and the vertical scale represents the size of the chromosome.

We did not find duplications of the *Mo* genes in the *I. triloba* and *I. trifida* genomes, showing that these genes can be singleton genes. In plant genomes, single genes can exhibit different behaviors regarding duplication and conservation. Some genes may not undergo duplication and remain as single genes due to functional constraints or selective pressures [53]. These genes exhibit specific expression patterns and regulatory controls that duplication can disrupt [54]. Dosage sensitivity is a crucial reason for their single-copy status, as an imbalance in gene products can be detrimental [55]. Evolutionarily, stabilizing selection and adaptive constraints keep these genes unduplicated, ensuring their vital roles are preserved [56]. The gene balance hypothesis also suggests that singletons are part of complex networks requiring balanced expression [57]. Thus, single-copy *Mo* genes can be attributed to persisting due to their essential functions, selective pressures, and the necessity to maintain the delicate balance of gene regulation and expression.

3.3. Phylogeny and collinearity analysis in *I. trifida* and *I. triloba*

The identified Mo proteins were subjected to phylogenetic analysis to predict and understand their grouping pattern and relationships (**Figure 5**).

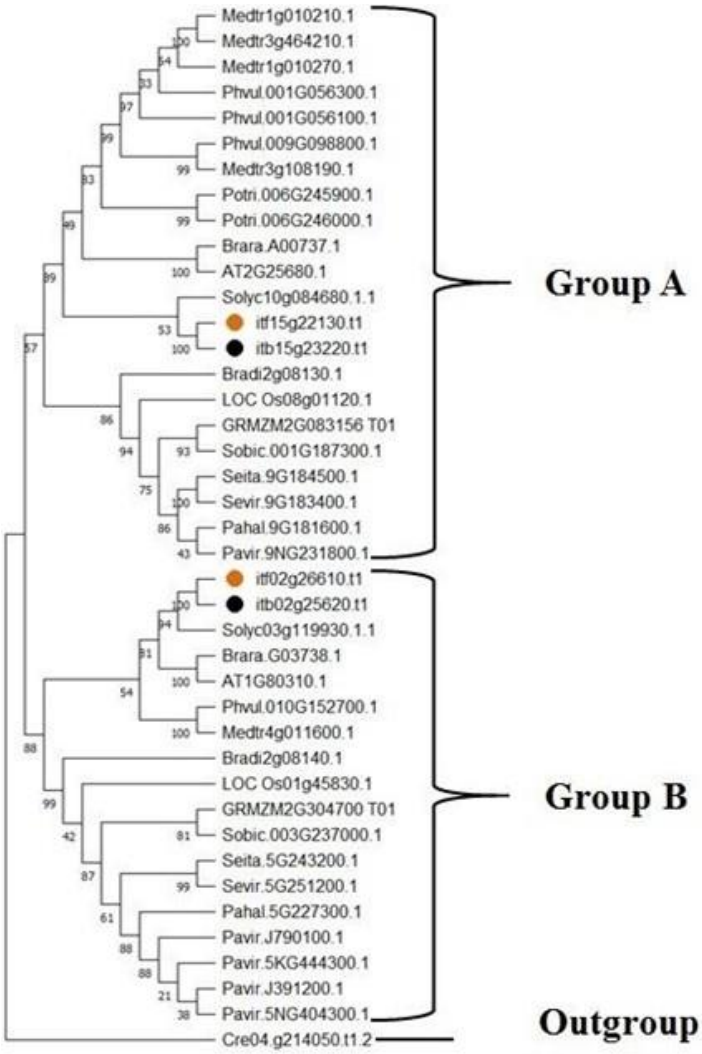

Figure 5. Phylogenetic relationships of Mo transporter in *I. trifida*, *I. triloba*, and other species. The groups were separated into clades: A, B, and outgroup.

The proteins were classified into two groups (A and B) and an external group (outgroup) representing a single member, Cre04.g214050.t1.2 (**Figure 5**). To facilitate understanding, the proteins from *I. trifida* and *I. triloba* were distinguished by the different colors in **Figure 5**. Group A is the largest group, comprising 22 members. In particular, the sequences ItfMo2 (itf15g22130.t1) and ItbMo2 (itb15g23220.t1) were grouped within group A, forming a subgroup together with the protein Solyc10g084680.1.1 (**Figure 5**). However, the sequences of the proteins ItfMo1 (itf2g26610.t1) and ItbMo1 (itb02g25620.t1) grouped with Solyc03g119930.1.1, forming a subgroup within group B, represented by 18 members (**Figure 5**). To perform the phylogenetic analysis the sequences used were: *A. thaliana* (AT1G80310.1-AT2G25680.1), *Zea mays* (GRMZM2G304700_T01-GRMZM2G083156_T01), *Sorghum bicolor* (Sobic.001G187300.1-Sobic.003G237000.1), *Setaria italica* (Seita.5G243200.1-Seita.9G184500.1), *S. viridis* (Sevir.5G251200.1-Sevir.9G183400.1), *P. hallii* (Pahal.9G181600.1-Pahal.5G227300.1), *P. virgatum* (Pavir.9NG231800.1, Pavir.J391200.1, Pavir.J790100.1, Pavir.5KG444300.1, and Pavir.5NG404300.1), *M. truncatula* (Medtr1g010210.1, Medtr1g010270.1, Medtr3g108190.1, Medtr3g464210.1, and

Medtr4g011600.1), *Brassica rapa* (Brara.A00737.1Brara.G03738.1), *P. vulgaris* L. (Phvul.001G056100.1, Phvul.001G056300.1, Phvul.009G098800.1, and Phvul.010G152700.1), *Populus trichocarpa* (Potri.006G245900.1-Potri.006G246000.1), *Solanum lycopersicum* (Solyc03g119930.1.1-Solyc10g084680.1.1), *Brachypodium distachyon* (Bradi2g08130.1-Bradi2g08140.1), *O. sativa* (LOC_Os01g45830.1-LOC_Os08g01120.1), and *Chlamydomonas reinhardtii* (Cre04.g214050.t1.2) (**Figure 5**). It is essential to highlight that the first Mo transporter described in the literature was identified in the alga *C. reinhardtii* (CrMOT1) [51]. Separations between groups (A-B) and outgroups were also observed by Bavaresco et al. [26]. Based on this information, we hypothesize that although the amino acid sequences present the characteristic domain of this family, their function within the *Ipomoea* may differ according to their specificity and gene expression. We conducted a synteny analysis using genes from *I. trifida* and *I. triloba*, as well as two model plants: a monocot (*O. sativa*) and a dicot (*A. thaliana*) (see **Figure 6**).

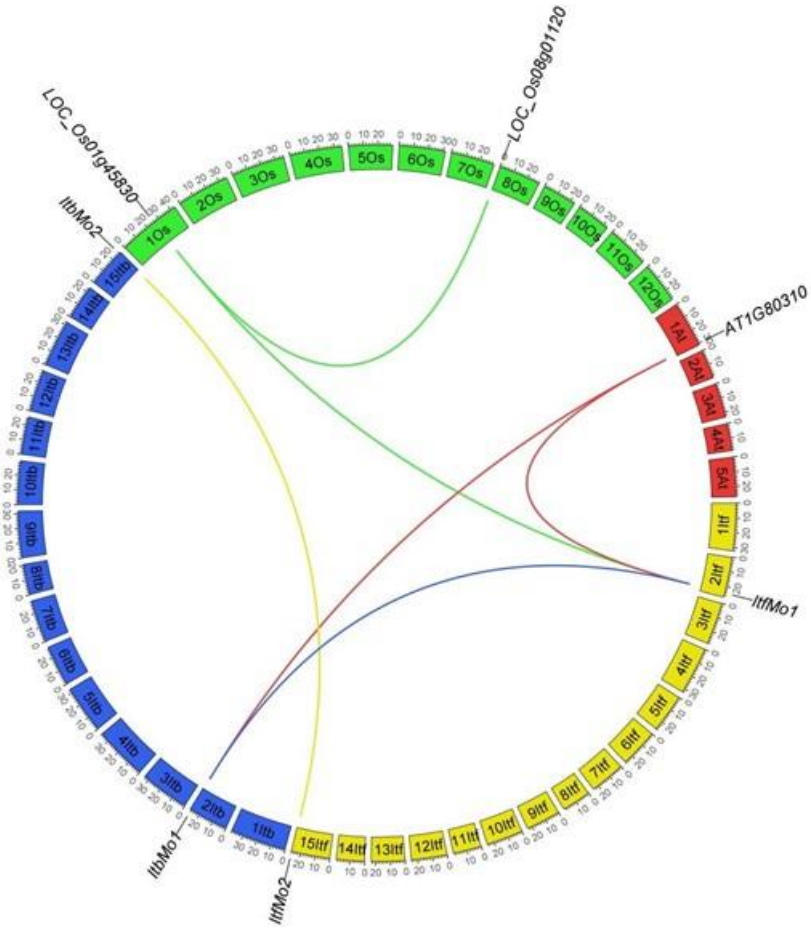

Figure 6. Representation of synteny analysis of *Mo* genes. Comparative map between *I. trifida*, *I. triloba*, *A. thaliana*, and *O. sativa*. The lines indicate the relationship between genes in that region. The suffix Itf refers to *I. trifida* chromosomes, Itb: *I. triloba* chromosomes; at: *A. thaliana* chromosomes; Os: *O. sativa* chromosomes.

Our analysis showed two syntenic relationships between *I. trifida* and *I. triloba* (*ItfMo*1-*ItbMo*1; *ItfMo*2-*ItbMo*2), indicating a recent divergence from a common ancestor with minimal genomic changes [58]. According to Wu et al. [59], an ancient *Ipomoea* lineage ancestor experienced a whole-genome triplication (WGT) approximately 46.1 million years ago (Mya). This significant event predates the ~3.6 Mya divergence of *I. nil* from the lineage containing *I. trifida* and *I. triloba*, as well as the ~2.2 Mya divergence between *I. trifida* and *I. triloba* [59]. When comparing the model plants, we found one syntenic relationship between *I. trifida* and *A. thaliana* (*ItfMo*1- *AT*1*G*80310), one between *I. triloba* and *A. thaliana* (*ItbMo1*-*AT*1*G*80310), and one between *I. trifida* and *O. sativa* (*ItfMo*1- *LOC_Os*01*g*45830), (**Figure 6**). The synteny relationship with *A. thaliana* for both *Ipomoea* species indicates the presence of essential genes conserved throughout the evolution of dicots. The synteny between *I. trifida* and *O. sativa* is particularly noteworthy, suggesting the conservation of genomic regions between monocots and dicots [60]. These genes are likely involved in primary metabolic processes, development, and responses to environmental stresses [61].

3.4. Expression patterns of *Mo* genes in *I. trifida* and *I. triloba*

In plants, the expression levels of a particular gene in a specific location or tissue can reflect its role and function. This tool allows you to trace the spatio-temporal expression profile based on data from a given transcriptome. The results of our study suggest that these genes showed higher levels of expression and may also trigger different expressions in the tissues analyzed. This study obtained RNA-seq (FPKM) values from *I. trifida* and *I. triloba* libraries deposited in the Sweetpotato database. In agreement with the results presented (**Figure 7**), only the *ItfMo*2 and *ItbMo*1 genes showed scale of expression. The *ItfMo*2 gene stands out in leaf tissue with higher gene expression. By comparing the expression in *I. triloba* the gene that stood out was *ItbMo*1 expressed (*in silico*) in flower (**Figure 7**). (**Figure 7**). Its expression was relatively lower in root2 and stem tissues (**Figure 7**).

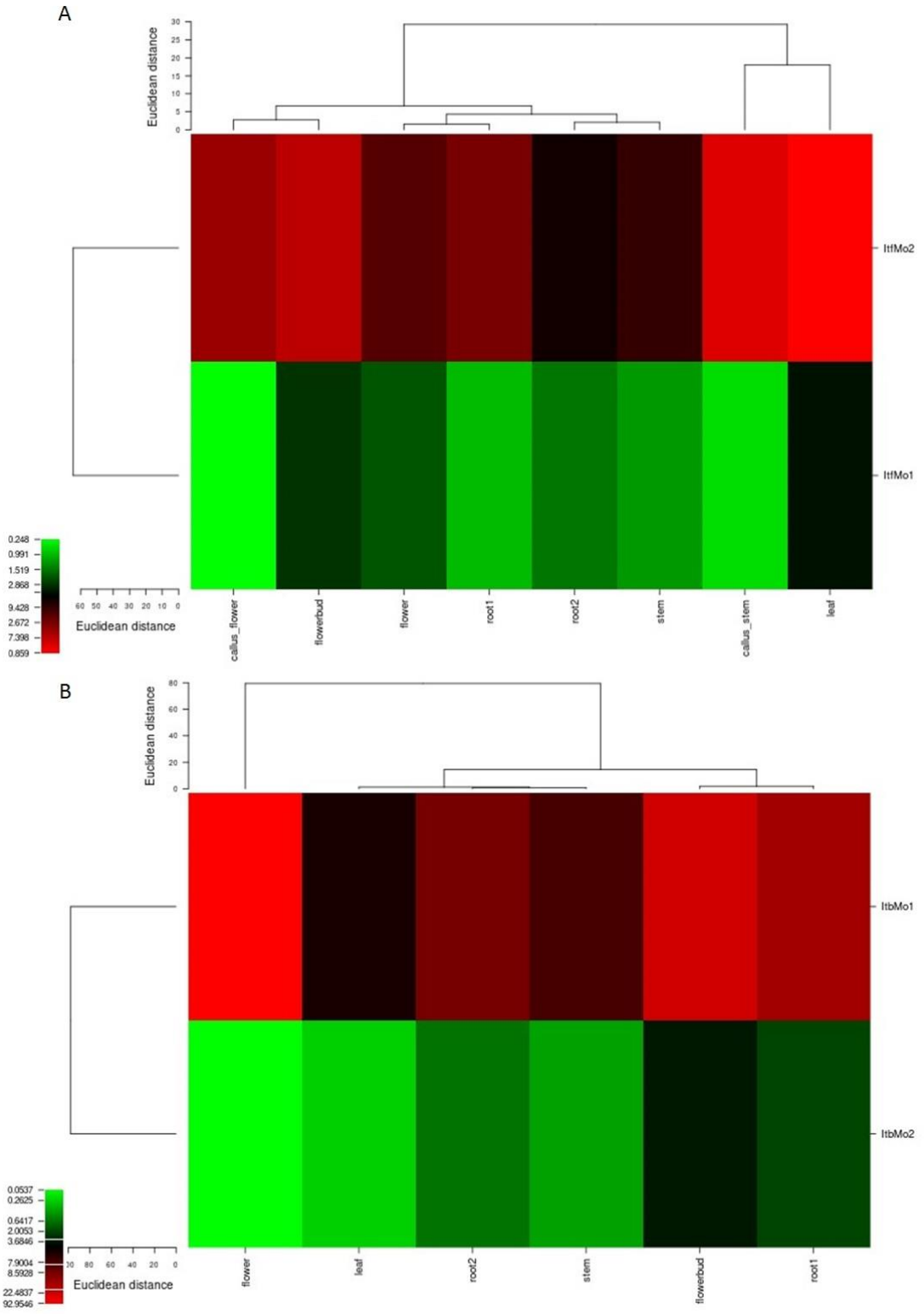

Figure 7. Tissue-specific expression of *Mo* genes in different organs in *Ipomoea* (FPKM). The tissues studied were: (callus_flower, callus_stem, flower, flower bud, leaf, root1, root2, stem, in **(A)** *I. trifida*), and (flower, flower bud, leaf, root1, root2, stem in **(B)** *I. triloba*).

In *Ipomoea* species, there still needs to be more information about the essential elements involved in the growth and development, particularly the Mo transporter. Additionally, despite some variations, molecular and physiological studies are needed to verify the role of some elements involved in plant nutrition. In effect, the *in silico* characterization approach in the different tissues present in this study establishes a scientific base for understanding where Mo transporter can be active in *Ipomoea*.

4. Conclusion

The results presented here demonstrate the relevance of *in silico* studies in identifying essential genes. In summary, four Mo transporter sequences were identified in the ancestors of the sweet potato: *I. trifida* (two Mo transporters) and *I. triloba* (two Mo transporters). It was evident in this study that two types can mediate Mo transporters. Phylogenetic comparisons with other species revealed the presence of two groups (A-B) and one outgroup. Synteny events comparisons of the *Mo* genes between *I. trifida* and *I. triloba* showed orthologous genes and were conserved in both species. In addition, the transcriptional profile was different between *I. trifida* (*ItfMo*2-leaf) and *I. triloba* (*ItbMo*1-flower). This study provides the basis for future investigations into the roles played by Mo transporters.

Author contributions: Conceptualization, TBdS; methodology, TBdS, CCdS, LGGL and SGHdS; formal data analysis, CCdS, LGGL and SGHdS; investigation, TBdS, CCdS, LGGL and SGHdS; writing—original draft preparation, TBdS and SGHdS; writing—review and editing, TBdS and SGHdS. All authors have read and agreed to the published version of the manuscript.

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