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RESEARCH ARTICLE

Genome sequencing and PEBP gene family analysis in Chinese yam (*Dioscorea polystachya*) identifies a candidate tuber inducing factor

Tatjana Ried · Marie Bolger · Jenny Riekötter · Toshiyuki Sakai · Janina Epping

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Abstract

Background and aims Phosphatidylethanolamine-binding proteins (PEBPs) are a class of ancient plant proteins involved in flowering, seed development and storage organ formation. The Flowering Locus T subgroup was shown to be involved in the initiation of flowering and tuberization. We aimed to characterize the PEBP family in the tuber crop Chinese yam (*Dioscorea polystachya*) and to identify FLOWERING LOCUS T (FT) homologs potentially involved in Chinese yam tuber formation.

Methods Based on a de novo genome assembly of Chinese yam, we investigated members of the PEBP family in silico. Expression analysis of FT homologs in yam tuber tissue revealed DpFT3a as a candidate for a tuber inducing FT. We then performed functional characterization of DpFTs by localization and interaction studies, as well as constitutive overexpression in *Arabidopsis thaliana* and *Solanum tuberosum*.

Results Analysis of the genome annotations revealed members of the PEBP-family in Chinese yams. Identified PEBPs were subjected to phylogenetic analysis and transcriptomic studies. Of the identified 9 FT homologs, DpFT3a, which was strongly expressed in yam tubers, was found to cause a severe tuberizing phenotype in transgenic potato (*Solanum tuberosum* cv. Désirée), indicating a role of DpFT3a in storage organ formation.

Conclusion We identified a Chinese yam specific FT homolog and provide strong indication for a role of this FT in tuber formation in yam as well as its potential to induce tuberous structures in potato. Our results complement the current knowledge on PEBP proteins in plants.

Keywords Chinese yam · Whole genome sequencing · Flowering Locus T · Tuber formation · *Solanum tuberosum*

Abbreviations

FT	FLOWERING LOCUS T
SP6A	SELF PRUNING 6A

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T. Ried
Cologne, Germany

M. Bolger
Institute of Bio- and Geosciences (IBG-4: Bioinformatics), Bioeconomy Science Center (BioSC), CEPLAS, Forschungszentrum Jülich GmbH, 52425 Jülich, Germany

J. Riekötter · J. Epping (✉)
Institute of Plant Biology and Biotechnology, University of Münster, 48143 Münster, Germany
e-mail: janina.epping@uni-muenster.de

T. Sakai
Crop Evolution Laboratory, Kyoto University, Mozume, Muko, Kyoto 617-0001, Japan

St	*Solanum tuberosum*
At	*Arabidopsis thaliana*
Dp	*Dioscorea polystachya*
FD	Flowering Locus D
TFL1	Terminal Flower 1
TSF	Twin Sister of FT
MFT	Mother of FT and TFL
BFT	Brother of FT
BiFC	Bimolecular Fluorescence Complementation
SAM	Shoot apical meristem
IM	Inflorescence meristem
CO	CONSTANS
PEBP	Phosphatidylethanolamine-binding protein
SD	Short day
LD	Long day
SP5G	SELF PRUNING 5G
TAC	Tuber Activation Complex
WT	Wild type

Introduction

Geophytes are plants that are able to produce storage organs in the form of tubers, corms, bulbs or rhizomes for reproduction and endurance of adverse environmental conditions (Khosa et al. 2021). A number of these storage organs serve as an important food source for calories and nutrients; they are produced by plant species such as the potato, sweet potato, carrot, cassava and yam. To date, most research concerning storage organ formation has been done in potato (*Solanum tuberosum*), the most important tuber crop globally (Xu et al. 2011). Several molecular factors were found to participate in tuberization, and special attention was paid to SELF PRUNING 6A (StSP6A), a FT homolog, which plays a crucial role in tuber induction in potato (Navarro et al. 2011). Initially, FT was shown to play a critical role in regulating floral induction in *Arabidopsis thaliana* as well as many other angiosperms (Turck et al. 2008; Pin et al. 2010). Dependent on day length, the transcription factor CONSTANS (CO) activates *FT* expression in the phloem companion cells in Arabidopsis leaves (An et al. 2004; Wigge et al. 2005). Several studies showed that protein and mRNA of FT are phloem-mobile and traffic through the phloem to the shoot apical meristem (SAM) (Corbesier et al. 2007; Lin et al. 2007; Tamaki et al. 2007; Yoo et al. 2013). In the SAM, FT interacts with the transcription factor FLOWERING LOCUS D (FD), mediated by 14–3-3 proteins, to induce the expression of floral identity genes, turning the SAM into an inflorescence meristem (IM) (Wigge et al. 2005). TERMINAL FLOWER 1 (TFL1), a protein with a high amino acid similarity to FT, acts antagonistically to FT by interacting with FD to repress floral identity genes at the tip of the IM. Thus, TFL1 maintains the meristemal identity of the IM, while floral meristems form at the sides (Koornneef et al. 1991; Shannon And Meeks-Wagner 1991, 1993; An et al. 2004; Abe et al. 2005; Lee et al. 2008; Taoka et al. 2011). In tobacco (*Nicotiana tabacum*) and sugar beet (*Beta vulgaris*), antagonistic FTs in floral development were identified (Pin et al. 2010; Harig et al. 2012). FTs with variations in the amino acid sequence of functionally conserved motifs, act as flower-repressing factors besides TFL (Pin et al. 2010; Harig et al. 2012). Both FT and TFL are members of the PEBP protein family, defining two of three subclades in angiosperms (FT-like, TFL-like and MFT-like) (Kardailsky et al. 1999; Kobayashi 1999).

Tuber induction in the strictly short day (SD) tuberizing potato subspecies *Andigena* was found to be similar to the flower inducing process of other plants (Navarro et al. 2011). Similar to flower development, a CO homolog in potato (*StCO*) is expressed higher under long days (LDs), but instead of inducing the expression of the tuber-inducing *StSP6A*, it induces the expression of the FT homolog *StSP5G*. In the leaf, StSP5G prevents tuberization by inhibiting *StSP6A* expression. As StCO is unstable under SD conditions, *StSP5G* expression is not induced and *StSP6A* is not repressed. The StSP6A protein moves through the phloem to the stolon, a modified underground shoot that develops into a tuber (Martinez-Garcia et al. 2002; González-Schain et al. 2012; Abelenda et al. 2016; Sharma et al. 2016). In the stolon, StSP6A interacts with FD, mediated by 14–3-3 proteins. This interaction results in the formation of the so-called tuber-activation complex (TAC), regulating the expression of tuber formation genes (Teo et al. 2017). FT involvement in storage organ formation was also investigated in the monocotyledonous crop onion (*Allium cepa*). Here, AcFT homologs were shown to initiate or inhibit bulb induction and regulate flowering time, dependent on daylength and vernalization (Lee et al. 2013).

Tuber crops play an important role in human nutrition and global food security (Scott et al. 2000). A

profound understanding of tuber development in these crops is a prerequisite for improved breeding strategies. One such important tuber crop is yam (*Dioscorea spp.*). Species commonly known as yams belong to the monocotyledonous genus *Dioscorea*. Yams are mostly annual, dioecious plants that produce starchy underground tubers, which emerge from the hypocotyl (Coursey 1967; Shewry 2003). Although mostly unknown in Europe, they are cultivated as staple crops, predominantly in Western Africa, but also Asia, Southern and Central America and the Pacific Islands (Irvine 1952; Ayensu and Coursey 1972; Opara 2003; Bhattacharjee et al. 2011; Tamiru et al. 2017).

Chinese yam (*Dioscorea polystachya*) is cultivated in temperate climates, primarily Japan and China (O'Sullivan 2010). The tubers of Chinese yam show a geotropic response in the distal end. While the distal end grows downwards and thickens, the proximal end stops growing and hardens (Shewry 2003). Besides serving as a carbohydrate source, Chinese yam has many beneficial health ingredients. In several studies, whole tubers or separate compounds were shown to, amongst others, increase insulin sensitivity, suppress fat uptake and exhibit cholesterol-lowering effects (Kwon et al. 2003; Gao et al. 2007; Liu et al. 2009; Son et al. 2014; Fan et al. 2015). Despite its importance as a food crop and health benefits, yam is considered an orphan crop (Otoo 2017; Tamiru et al. 2017; Mabhaudhi et al. 2019). Challenging conditions such as labor-intensive cultivation, a long growth cycle, sparse and asynchronous flowering as well as prevalent asexual propagation slow down breeding attempts (Burkill 1960; Hahn et al. 1987; Asiedu et al. 1997; Mignouna et al. 2003, 2007). Furthermore, yams are polyploid and highly heterozygous, impeding investigations of the genetic background of tuber growth and traits (Mignouna et al. 2003).

Recent years have seen significant progress in yam (*Dioscorea* spp.) genomics, with several genome assemblies available for species such as *Dioscorea alata* (Cormier et al. 2019), *D. rotundata* (Tamiru et al. 2017), *D. dumetorum* (Siadjeu et al., 2020), *D. nipponica* (Hu et al., 2025), and *D. zingiberensis* (Li et al., 2022). These assemblies have advanced our understanding of yam genetics, diversity, and domestication. However, the species we focus on in this study has not yet been sequenced, and genomic differences across *Dioscorea* species highlight the need for species-specific reference genomes. Our de novo assembly thus complements existing genomic resources by providing a reference for this particular species, enabling targeted analyses such as the characterization of the *PEBP* gene family and its involvement in tuber development.

To improve our understanding of tuber development in yam, we investigated the PEBP family in Chinese yam with the aim to identify FTs potentially involved in the tuberization process. To identify PEBP homologs in silico, we generated and assembled a de novo whole genome assembly using PacBio Hifi reads. Intra-species ploidy variation has previously been described in many species of *Dioscorea* with diploid, triploid and tetraploid levels reported for *D. alata* (Arnau et al. 2009), a species closely related to Chinese yam. Two different cultivars of Chinese yam have been reported as having a chromosome number of 100 and 140 (Babil et al. 2013). Given that the basic chromosome number for *D. alata* is reported as 20 (x = 20), we expect Chinese yam to be pentaploid or heptaploid. In the present study, we used the de novo genome data to characterize the PEBP family in silico. Based on sequence analyses, we selected a FT homolog potentially involved in tuber formation and show its functionality as a potential tuber inducing protein *in planta*.

Materials and methods

De novo genome sequencing

Tubers of *D. polystachya* were provided by a local farmer (St. Calude de Diray, Loir-et-Cher, France) from a variant we titled 'F60' (Riekötter et al. 2023). F60 plants grown from seed tubers were cultivated in raised bed (1.2 × 0.8 × 1.4 m) in Münster, Germany (51°57′55.3"N 7°36′54.1"E) between April and September 2020. Leaf material of young leaves was flash-frozen in liquid nitrogen and sent to DNA Sequencing Center at Brigham Young University, Utah, US for DNA extraction and PacBio SMRT sequencing. Sequencing was performed on a PacBio Sequel II using three 8M SMRT cells and 30 h collection time. Sequencing data was assessed for length and quality using FastQC (www.bioinformatics.babraham.ac.uk/projects/fastqc).

Genome assembly

Raw PacBio circular consensus sequencing (ccs) reads were converted to fastq files using the PacBio pipeline. The assembly of the genome was performed using the Hifiasm assembler version 0.17.6. with default parameters. This assembler is specifically designed to handle long and accurate PacBio HiFi reads. Hifiasm employs an overlap-layout-consensus (OLC) strategy to construct a de novo assembly.

Structural and functional annotation

Structural annotation of the genes from the assembled genome was performed using Helixer, a novel state-of-the-art ab-initio gene caller which uses deep neural networks to structurally annotate genes in a genome (Holst et al. 2023). The default settings with the plant model was used to predict the genes. The resulting output was assessed using BUSCO and compared to the results of BUSCO on the genome. Protein function annotation was assigned to protein sequences using the online tool Mercator4 v5.0 (Schwacke et al. 2019; Bolger et al. 2021) (Online Resource 1).

In silico analysis of DpPEBP sequences

Multiple sequence alignment (MSA) of PEBP protein sequences was performed using the MUSCLE algorithm. A phylogenetic tree was constructed by a Neighbor-Joining method based on *p*-distance with 1000 bootstrap replicates using the MEGA11 software (Tamura et al. 2021). PEBPs from species other than *D. polystachya* had the following NCBI GenBank accession numbers: *Arabidopsis thaliana* (At), BAA77838.1, AAD37380.1, BAB10165.1, AAB41624.1, AAF03937.1; *Beta vulgaris* (Bv), ADM92608.1, ADM92610.1; *Nicotiana tabacum* (Nt), JX679067, JX679070, AAD43528.1; *Oryza sativa* (Os), BAB61028.1, BAB39886.1, XP_015634144.1 *Solanum tuberosum* (St), BAV67096.1, XP_006365457.1, NP_001274897.1, *Triticum aestivum* (Ta), BAK78895.1. MSA of FT protein sequences was visualized using the Jalview v2.11.2.7 program (Waterhouse et al. 2009). Visualization of gene structure of *DpPEBP* genes was performed with TBtools v1.123 (Chen et al. 2020).

Expression of PEBPs in tuber tissue

Expression of *PEBP* family members in Chinese yam tubers were analyzed using the recently published transcriptomic data of *D. polystachya* var. F60 (Riekötter et al. 2023) (Accession number: PRJNA942579). Raw sequencing data were filtered using fastp v0.12.4 to cut adapter sequences and to remove bad quality reads (Chen et al. 2018) with following parameters: −3 -q 15 -n 10 -t 1 -T 1 -l 20 -w 1.. Mapping of clean reads against the genome of *D. polystachya* var. F60 was performed using HISAT2 v 2.2.1 with following parameters: -k 1 –no-mixed –no-discordant (Liao et al. 2014; Kim et al. 2015). Counting of mapped reads per gene was performed using featureCounts v2.0.1 (Liao et al. 2014).

Generation and analysis of transgenic *S. tuberosum* plants

The coding sequence of DpFT3a was amplified from cDNA of F60 tuber tissue using primers DpFT3_NcoI_fwd and DpFT3_XbaI_rev (Table S1 in Online Resource 2) deduced from the genomic sequence. Amplified fragments were purified using agarose gel electrophoresis and the Gel and PCR clean-up-Kit (Macherey–Nagel, Düren, Germany) and ligated into plant expression vector plab12.10-Q35S (Xing et al. 2014; Stolze et al. 2017) for overexpression in *S. tuberosum* cv. Désirée resulting in plab12.10-Q35S-DpFT3a. The plab12.10-Q35S-DpFT3a was stably transformed into *S. tuberosum* cv. Désirée as described previously (Hoekema et al. 1983; Horsch et al. 1985) using the *Agrobacterium tumefaciens* strain LBA4404. Transformed leaves were cultivated in sterile culture on selective solid medium (4.4 g L^{-1} Murashige and Skoog salt solution (MS) including vitamins, 20 g L^{-1} sucrose, and 6.5 g L^{-1} agar, 75 mg L^{-1} kanamycin, pH 5.8), in sterile environment under long day conditions (16 h artificial light (100 µmol $m^{-2}s^{-1}$)/8 h darkness) at 24/17 °C. Regenerated plants were tested for transgene integration. For this purpose, genomic DNA was extracted from potato leaf material using an adapted protocol (Edwards et al. 1991). In brief, flash-frozen leaf material was milled in 500 µL Edward's extraction buffer using a Mixer mill MM400 (Retsch, Germany) for 90 s at 30 Hz. Samples were centrifuged at 21,300 × g for 5 min and 300 µL of the supernatant were mixed

with 310 µL isopropanol in a new reaction tube. After 10 min incubation at RT, extracts were centrifuged at 21,300×g for 10 min and supernatant was discarded. Pellet was washed with 70% (v/v) ethanol, air-dried and dissolved in 50 µL H_2O. DNA was used for PCR analysis using primers 35SP-fw and DpFT3-rv. Regenerated transgenic plants were moved from tissue culture to the greenhouse upon rooting. For expression studies of transgenes, plant material was frozen in liquid nitrogen immediately after harvest and RNA was extracted using innuPrep Plant RNA Kit (IST Innuscreen, Berlin, Germany) with DNaseI-digest as described by the manufacturer. Subsequently, 500 ng of isolated RNA were transcribed into cDNA using the PrimeScript RT Master Mix (Takara Bio Europe, Saint-Germain-en-Laye, France) accordingly to the manufacturer's instructions. For quantitative real-time PCR the SYBR™ Green PCR Master Mix (KAPA Biosystems, Wilmington, Massachusetts, USA) and the primers DpFT3_qPCR1_fwd/DpFT3_qPCR1_rev and qRT_StGAPDH_fw/qRT_StGAPDH_rev (Table S1 in Online Resource 2) were used. A 10 µL reaction mixture containing 5 µL KAPA SYBR FAST qPCR Master Mix (2×) Kit (Roche, Basel, Switzerland), 2.5 µL cDNA (diluted 1:5 or 1:10) and 2.5 µL primer mix (2 µM) was prepared and qRT-PCR was performed on a CFX96 Touch Real-Time PCR Detection System (Bio-Rad Laboratories, Hercules, CA, USA) with following program configuration: 95 °C for 3 min, followed by 44 cycles of 95 °C for 3 s, 60 °C for 20 s and 95 °C for 5 s. Melt curve analysis was performed in 0.5 °C increments from 58 to 95 °C to confirm gene specific amplification. Reactions were carried out in technical triplicates for each biological replicate. The housekeeping gene *StGAPDH* served as internal control and was used for gene expression normalization. Relative gene expression was calculated using the $2^{-\Delta\Delta Ct}$ method (Livak And Schmittgen 2001).

Further methods can be found in the Online Resource 2 file.

Results

De novo genome sequence

The three Hifi libraries were found to be of high quality both in terms of quality and length and quality (Online Resource 3). The resulting assembled genome was assessed using several metrics, including N50, assembly length, and number of contigs (Table 1). Due to the high ploidy of the *D. polystachya* genome, hifiasm struggled to create a high quality, contiguous genome despite the use of high quality PacBio Hifi reads. The draft assembly was however assessed as satisfactory for the purpose of gene exploration. The completeness of the genic component was assessed with BUSCO (Simão et al. 2015; Manni et al. 2021) and showed a 98% overall gene completeness with a large duplication rate (97.4%) when using the embryophyta_odb10 dataset. This large duplication rate is expected due to the extreme ploidy level of this plant.

The PEBP-family has 75 members in Chinese yam

In plants, the PEBP-family is divided into the three subclades of MFT-like, TFL-like and FT-like, based on their function and conservation of essential motifs (Kardailsky et al. 1999; Kobayashi 1999). To gather information about the PEBP-family in Chinese yam, the functional annotation of the genome was screened for members of this family. Overall, 75 genes with annotation as PEBP were found based on the functional annotation obtained by Mercator4 (with protscriber and swissprot enabled) (Online Resource 1). Based on the annotations, multiple sequence alignment (Online Resource 1) and phylogenetic analysis with sequences from known PEBPs (Fig. 1), the DpPEBPs were grouped into 22 MFT-like genes, 19 TFL-like genes and 34 FT-like genes and named and grouped accordingly. DpFTs were further grouped into three sub-groups. 22 DpPEBPs were annotated as "protein mother of ft and tfl homolog" (Online Resource 1) in the functional annotation of Mercator4

Table 1 Quality of de novo *D. polystachya* genome assembly

Assembly name	yam_v0.16.1.bp.p_ctg
Length (bp)	1,807,892,738
Number of contigs	2,462
Contig N50 length (bb)	9,966,655
Genome BUSCO (embryophyta_odb10)	C:98.7%[S:1.3%,D:97.4%],F:0.6%,M:0.7%,n:1614
Protein BUSCO (embryophyta_odb10)	C:98.0%[S:2.2%,D:95.8%],F:1.2%,M:0.8%,n:1614

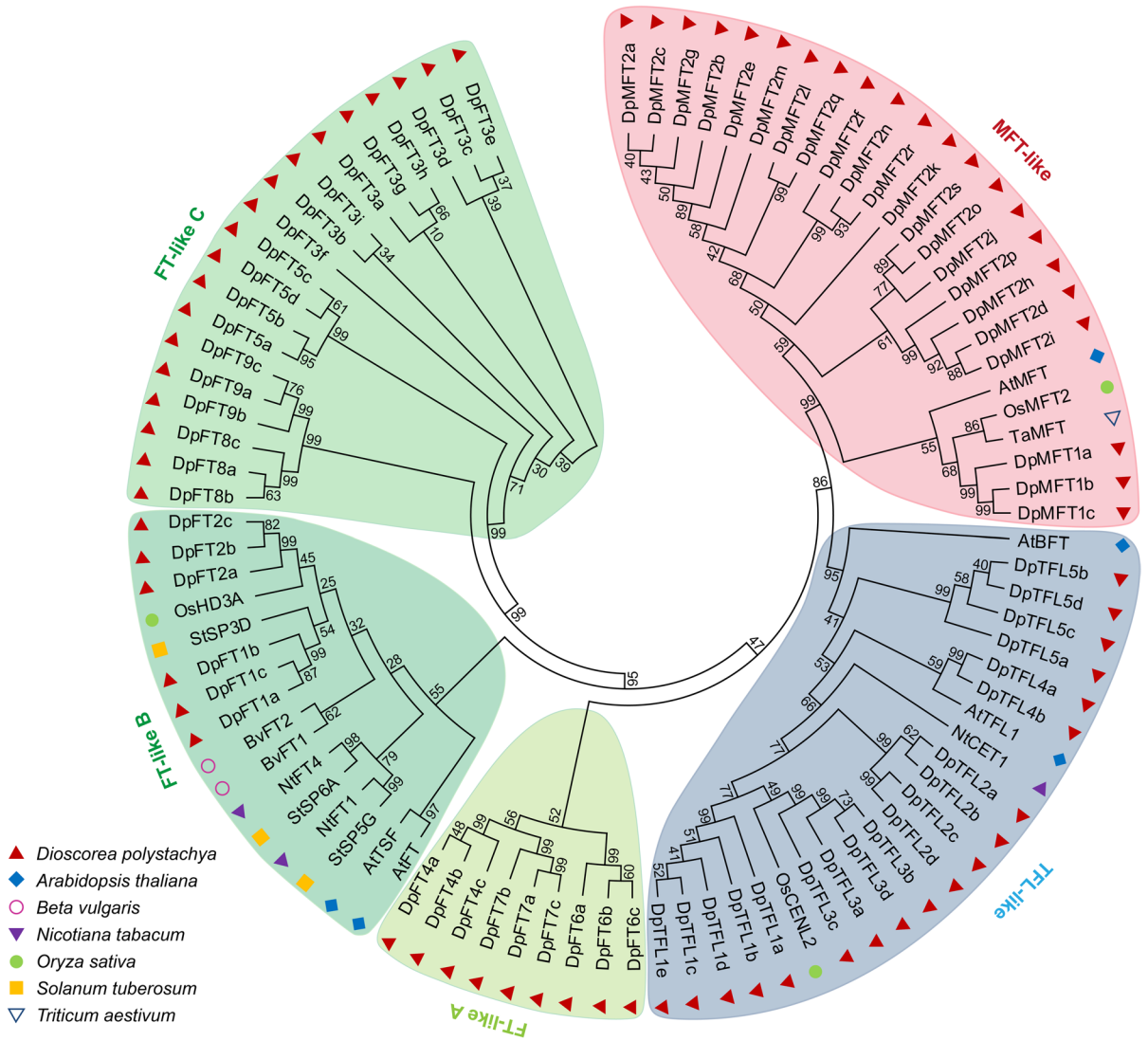


Fig. 1 The PEBP family in *D. polystachya*. Phylogenetic analysis of all 75 identified *DpPEBP* genes in the *D. polystachya* genome plus sequences from PEBPs with known functions from other plant species. Protein sequences were aligned using MUSCLE algorithm. Phylogenetic tree was generated using Neighbor-Joining method with 1000 bootstrap replication. Bootstrap values are shown at each node in percent. Genes were assigned to the MFT-like-, TFL-like-, and FT-like-subclades (and named accordingly) based on the functional annotation obtained by Mercator4 (with prot-scriber and swissprot enabled) (Online Resource 1) and their similarity to the reference sequences from known PEBPs in the phylogram

and thus classified as MFT-like. In our phylogenetic analysis based on the MUSCLE algorithm, these PEBPs grouped together with Mother of FT and TFL1 from Arabidopsis, (AtMFT), rice (OsMFT2) and wheat (TaMFT) on a separate branch. Of the 22 DpMFTs, three DpMFTs (DpMFT1a-c) clustered together with known MFTs from other plant species. The other 19 DpMFTs clustered together on a different sub-branch and were designated DpMFT2a-s.

19 DpPEBPs were annotated as "effector protein *(TFL/BFT/CEN)" in Mercator4 and clustered on the TFL-like-branch with CEN-like protein 1 from tobacco (NtCET1), CENL2 from rice (OsCENL2) and Terminal Flower 1 (AtTFL1) and Brother of FT and TFL (AtBFT) from Arabidopsis in our

phylogenetic analysis. Based on sequence similarities, they were designated DpTFL1a-e, DpTFL2a-d, DpTFL3a-d, DpTFL4a,b and DpTFL5a-d. The largest group of DpPEBPs could be assigned to the FT-like class based on functional annotation and clustered on a sperate branch in the phylogram together with FT proteins from Arabidopsis, tobacco, sugar beet, potato and rice (Fig. 1). Six DpFTs, designated DpFT1a-c and DpFT2a-c, clustered on a sub-branch with known FTs from other plant species. The other DpFTs clustered on separate sub-branches with DpFT4a-c, DpFT6a-c and DpFT7a-c on one sub-branch and DpFT3a-f, DpFT5a-d, DpFT8a-c and DpFT9a-c on a separated sub-branch. The examination of the predicted intron–exon structure of *DpPEBP* genes revealed the presence of four introns in most of the *PEBP* genes (Fig. S1 in Online Resource 2).

A phylogram of DpPEBPs and known PEBP protein sequences of several other mono- and dicots was created to investigate similarities of DpPEBPs with PEBPs with known functions (Fig. 1). In the MFT-like subclade, DpMFT1 is close to the MFTs of the rice, wheat and Arabidopsis, while DpMFT2 showed greater distance. DpTFL1, DpTFL2 and DpTFL3 grouped very close with OsCENL2, a TFL-like homolog, while DpTFL4 was closest to Arabidopsis AtTFL1 and DpTFL5. Within the FT-like subclade, only DpFT1 and DpFT2 showed high similarity to known FT homologs. All other DpFTs are grouped further apart indicating lower sequence similarity to plant FT homologs described in literature.

Five *DpFTs* are expressed in tuber tissues

Several studies have revealed the importance and function of amino acid motifs of FT-proteins (Hanzawa et al. 2005; Ahn et al. 2006; Ho And Weigel 2014). The best studied motifs of FTs are REY, YAPGWRQ and LYN (highlighted in Fig. 2). Several studies showed that a repressing FT function was associated with a severe alteration or absence of the YAPGWRQ motif (Pin et al. 2010; Navarro et al. 2011; Harig et al. 2012; Lee et al. 2013; Manoharan et al. 2016; Wang et al. 2019; Yang et al. 2019). The LYN triad is described to be essential for an inducing FT function (Hanzawa et al. 2005; Ahn et al. 2006;

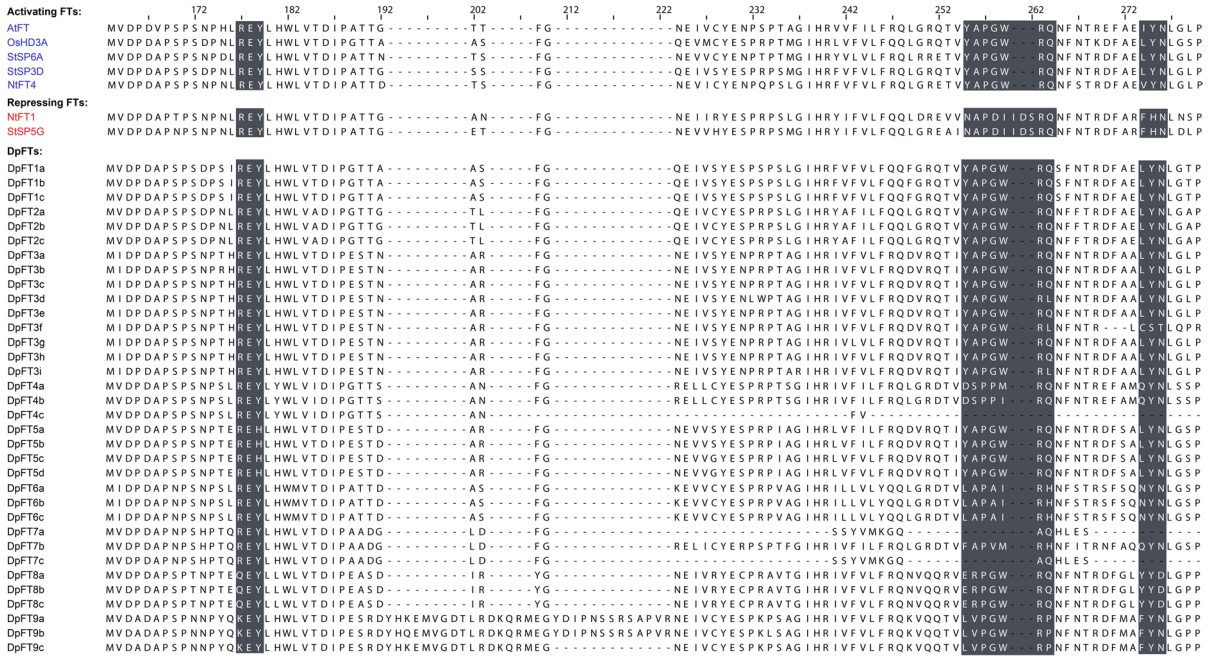


Fig. 2 Partial amino acid alignment of FT homologs. DpFTs were aligned to inducing and repressing FTs from Arabidopsis (AtFT), rice (OsHD3A), tobacco (NtFT4, NtFT1) and potato (StSP6A, StSP3D, StSP5G) which were grouped and colored according to their function described in literature. Activating FTs are colored in blue, repressing FTs are colored in red. Conserved motifs are highlighted in grey. The alignment was performed using MUSCLE algorithm

Ho And Weigel 2014). While the tyrosine residue in this motif is described to be conserved in FTs, a histidine is conserved in TFLs. Swapping these amino acids with each other reversed the roles of FT and TFL in Arabidopsis (Hanzawa et al. 2005). We aligned the amino acid sequences of DpFTs to inducing and repressing FTs from Arabidopsis (AtFT), rice (OsHD3A), tobacco (NtFT4, NtFT1) and potato (StSP6A, StSP3D, StSP5G) (Fig. 2). AtFT is a floral activator in Arabidopsis (Kardailsky et al. 1999; Kobayashi et al. (Kobayashi, 1999) and OsHD3A is a floral activator in rice (Tamaki et al. 2007). Both contain the REY and the YAPGW motif, as well as LYN triad, with isoleucine and leucine at the first position, respectively. StSP6A and StSP3D are activators of tuberization and floral development, respectively, and also contain the three beforementioned motifs. NtFT4 is a floral activator in tobacco (Harig et al. 2012), which contains the REQ and YAPGW motif and a slightly altered LYN triad with a valine instead of a leucine at the first position. In contrast the floral repressor NtFT1 from tobacco (Harig et al. 2012) and the tuberization repressor StSP5G from potato (Abelenda et al. 2016), lack the YAPGW motif as well as the tyrosine at the second position of the LYN triad. The tyrosine residues of the REY and LYN motif are conserved in all DpFTs, except for DpFT5, which showed the characteristic REH motif for TFLs. The YAPGWRQ motif, described in inducing FTs, was present in DpFT1-3 and DpFT5. In DpFT4, DpFT6, DpFT7, DpFT8 and DpFT9, alterations of the YAPGWRQ were detected, similar to FTs of repressing function (Pin et al. 2010; Harig et al. 2012). Taken together, DpFT1, DpFT2, DpFT3 and DpFT5 contained all of the amino acid motifs, described as essential for a flower- or tuber-inducing function. Next, we investigated the gene expression of potential tuber-inducing DpFTs in Chinese yam tuber tissue since, based on literature, tuber-inducing FTs were shown to be expressed in storage organ tissue.

Yam tubers exhibit a developmental gradient from head to tip. In a previous study, we investigated the gene expression in different yam tuber parts (harvested three months after sprouting) and could show that the tuber head, middle and tip comprise highly different gene expression patterns (Riekötter et al. 2023). This indicates that the transcriptomic differences in the tuber parts might be related to different developmental phases of tuber tissues. Based on these data, we had a closer look at the expression pattern of DpPEBPs in the different tuber parts and calculated the normalized read counts (Liao et al. 2014) of all *DpPEBPs*. Expression was analyzed in the tuber head, middle and tip, to reveal differences in the expression pattern along the tuber growth gradient, as the tuber tip is the actively growing tuber part, while the tuber head is the oldest tuber part (Fig. 3). Differences in expression profiles were observed between the identified *DpFTs*. Highest expression was detected for variants of *DpFT7*, followed by *DpFT3* and *DpFT5* variants, respectively. All the three *DpFTs* expressed in tuber tissue showed highest expression in the head, declining towards the tip. These differences in expression between the tuber parts were shown to be significant in the differential expression analysis (Fig. S2 in Online Resource 2). For *DpFT2*, *DpFT4* and 2 variants of *DpFT1* and *DpFT6*, respectively, no expression was detected in the tuber tissue at this developmental stage. Of *DpMFTs* only *DpMFT1* was expressed in tuber tissue with *DpMFT1b* showing the highest expression in the tuber head. Of the *DpTFLs* identified *DpTFL2a-d*, *DpTFL3a-d, DpTFL4a,b* and *DpTFL5a-d* were expressed in tuber tissue with *DpTFL4b* showing high expression in the tuber head, declining toward the tip.

DpFT3a is a functional FT with inducing function

In search of a tuber inducing yam FT, we then focused on DpFT3a, since it contains all conserved motifs of inducing FTs and was expressed in tuber tissue. Interaction of FT with FD and the generation of a TAC is reported to be vital for the inducing and repressing functions of FT-like proteins, which also implies that the proteins must not be secluded within different compartments of the cell. Hence, we studied the interaction of DpFT3a with a potential DpFD protein, that we named DpFD1, which was isolated from tuber tissue (Online Resource 1). Cellular localization of both proteins was also performed. Both approaches were investigated upon transient expression in *N. benthamiana* leaves. To monitor DpFT3a and DpFD1 localization within cells, the N-terminal region of DpFT3a and DpFD1 were fused with the fluorophore Venus. A previous study showed that FD localizes to the nucleus, while FT localizes to the nucleus and the cytoplasm. Upon protein interaction, the FD-FT complex localizes to the nucleus (Abe et al. 2005).

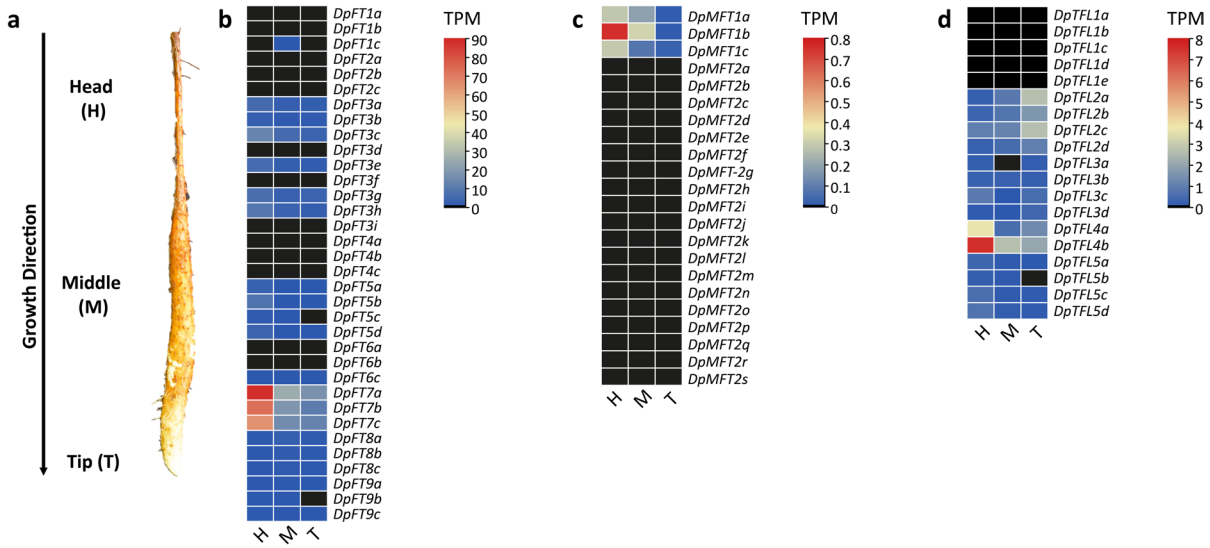


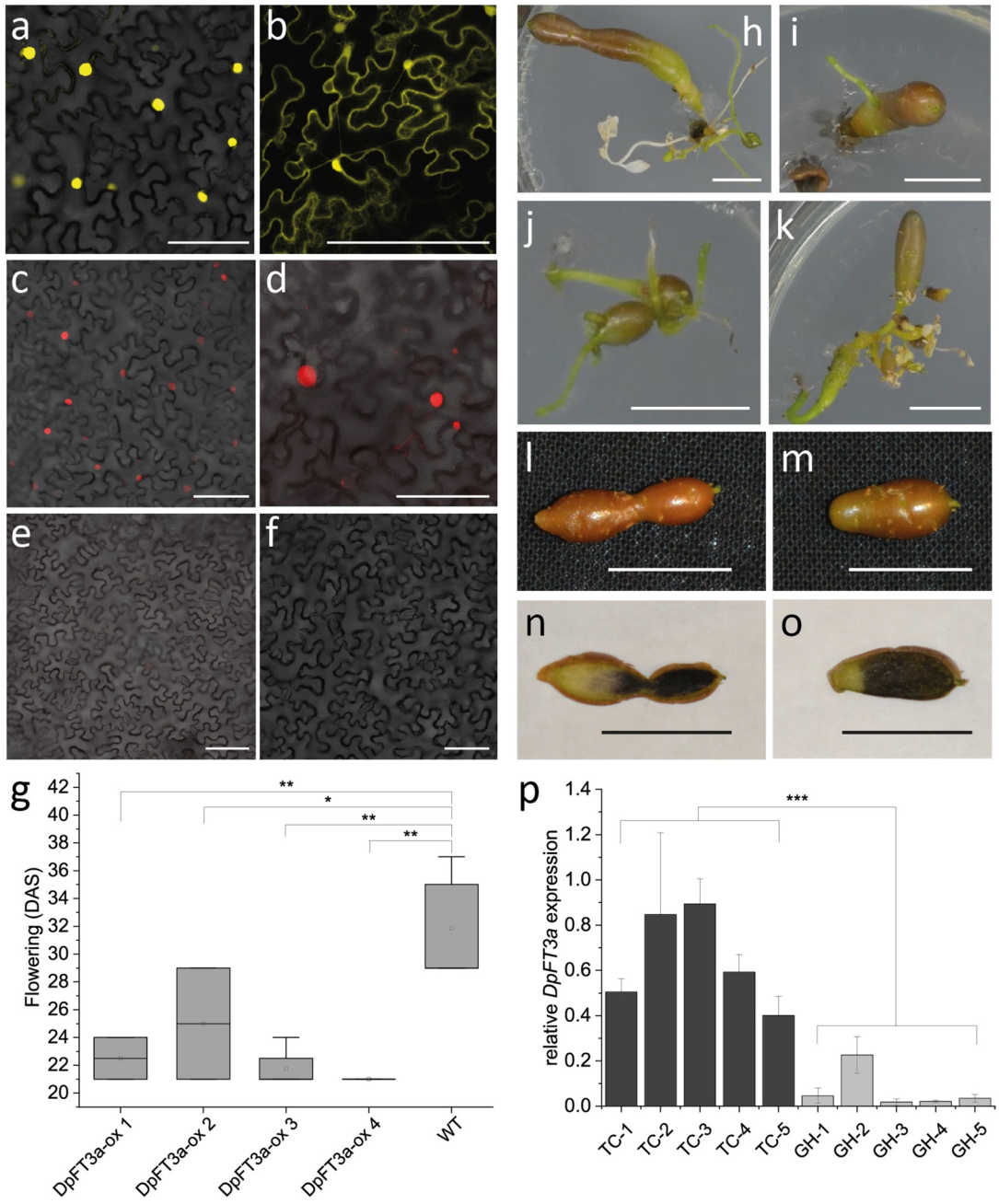
Fig. 3 Expression of *DpPEBPs* in tuber tissue. Expression levels were calculated in the head (H), middle (M) and tip (T) region of a growing tuber as shown in **a**. Based on tuber transcriptome data of three biological replicates (Riekötter et al. 2023) the expression levels of *DpFTs* (**b**), *DpMFTs* (**c**) and *DpTFLs* (**d**) were analyzed. TPM: transcripts per million (Raw data can be found in the Online Resource 1)

DpFD1 was indeed found to localize to the nucleus, while DpFT3a localized to the nucleus and the cytoplasm in *N. benthamiana* epidermal cells (Fig. 4a, b).

Next, we investigated the capability of DpFT3a to form a protein complex with DpFD1. Here we performed a BiFC assay, in which the N-terminal part of mRFP was fused to the N-terminus of DpFT3a and the C-terminal part of mRFP was fused to the N-terminus of DpFD1, resulting in red fluorescence upon interaction of DpFT3a and DpFD1. Detection of fluorescence of the reporter protein in the nucleus indicated interaction between DpFD1 and DpFT3a (Fig. 4c-f). Furthermore, we investigated the function of DpFT3a upon overexpression in *A. thaliana*. Systemic overexpression of *DpFT3a* in *A. thaliana* plants resulted in significantly earlier flowering of transgenic lines compared to wild type (WT) control plants, indicating that DpFT3 is a functional FT with an inducing function *in planta* (Fig. 4g).

DpFT3 induces a tuberous phenotype in potato

To investigate whether DpFT3a influences storage organ formation, *DpFT3a* was overexpressed in *S. tuberosum* cv. Désirée under control of the CaMV 35S promoter. Several transgenic lines started to form tuberous organs during regeneration in tissue culture and showed strongly impaired shoot, leaf and root growth (Fig. 4h–k). Consequently, these plants could not be transferred to the greenhouse and stayed in tissue culture (TC-lines). The development of organs in these lines was characterized by the initial formation of shoots with small leaves, which were suitable for expression studies. However, subsequent growth was marked by rapid thickening of the shoots into tuberous structures, accompanied by the death of the limited number of leaves that had formed (Fig. 4h and k). The produced tuberous structures had an elongated shape and Lugol-staining revealed starch accumulation in these organs (Fig. 4l-o). The absence of roots precluded successful transplantation to soil, and the tuberous organs could not be propagated or maintained through replanting or storage. Other lines could be transferred to the greenhouse (GH-lines) and showed no phenotypic differences compared to WT plants (Fig. S3 in Online Resource 2). Expression analysis on leaf tissue in tissue culture showed that TC lines had an overall significantly higher *DpFT3a* expression, indicating that the phenotype was dosage dependent (Fig. 4p).



Discussion

Genome sequence of *D. polystachya*

Despite the use of high-quality long reads, assembling of the genome to chromosome scale was not possible with the current data and available assemblers. We can see that the *D. polystachya* has a high overall BUSCO score which is comparable to *D. alata* (Bredeson et al. 2022) but with an extremely high level of duplication. On closer examination of the BUSCO duplication data, we can see that the gene duplication is largely 4x (which would roughly correspond to the 4 × genome size versus *D. alata*). Since the main hifiasm assembly typically merges parental chromosomal copies, this suggests that the

◂**Fig. 4** DpFT3a acts as a functional activating FT *in planta*. **a-b**: Cellular localization of DpFD1 and DpFT3a. CLSM images of *N. benthamiana* epidermal cells transiently expressing DpFD1 and DpFT3a. For visualization of localization, the YFP variant Venus was fused to the N-terminus of DpFT3a and DpFD1. Nuclear localization of Venus-DpFD1 (**a**); Cytoplasmatic and nuclear localization of Venus-DpFT3a (**b**). Scale bar: 100 µm. **c-f**: Interaction of DpFD1 and DpFT3a. CLSM images of *N. benthamiana* epidermal cells transiently expressing DpFD1 and DpFT3a proteins. To visualize a potential interaction between DpFT3a and DpFD1, the split-mRFP system was used: The N-terminal and C-terminal regions of mRFP were fused to the N-terminus of DpFT3a and DpFD1, respectively. Detection of red fluorescence in the nucleus of epidermal cells expressing N-mRFP-DpFT3a and C-mRFP-DpFD1 (**c**), and N-mRFP-AtFT and C-mRFP-AtFD (positive control) (**d**), respectively, indicating protein–protein interaction. Single infiltrations served as negative controls. No fluorescence signal was detected in epidermal cells expressing C-mRFP-DpFD1 (**e**) or N-mRFP-DpFT3a (**f**). Scale bar: 100 µm. **g**: Overexpression of DpFT3a induces an early flowering phenotype in transgenic Arabidopsis compared to wild type Col-0 lines (DpFT3a-ox, $n=4$; WT, $n=6$). Flowering time in days after sowing (DAS). Difference in flowering time between lines was calculated via Mann–Whitney test ($n=4$). Asterisks indicate statistical significance: * p-value ≤ 0.05, ** p-value ≤ 0.01. **h–k**: Transgenic potato lines with DpFT3a overexpression showed a tuberous phenotype with tuberous structures instead of shoots and produced neither functional roots nor leaves. Exemplarily, this phenotype is shown for three independent lines, TC-4 (**h**), TC-5 (**i**), TC-1 (**j**) and TC-2 (**k**) in tissue culture. **l-o**: Lugol-staining of the tuberous structures showed the accumulation of starch. l and m show the tuberous organs before cutting and o and p show the organs cut in half and stained with Lugol-staining. Scale bar = 1 cm. **p**: The observed phenotypes appeared in a dosage-dependent manner. While lines with high *DpFT3a* expression (TC) showed the tuberous phenotype, lines with lower *DpFT3a* expression levels (GH) could be transferred to the greenhouse and showed no phenotypic differences compared to WT plants. Shown is the relative *DpFT3a* expression in leaf tissue of five independent TC and GH lines regenerated in tissue culture ($n=5$). Expression was quantified via quantitative real-time PCR in technical triplicates for each sample. Difference in gene expression was calculated between all TC-lines and GH-lines via Mann–Whitney test. Asterisks indicate statistical significance: *** p-value ≤ 0.001

genome is likely octoploid ($2n=8x=160$). Upon checking the hifiasm haplotype phased assemblies, which try to keep parental copies separate, a roughly $7\times$ in both BUSCO copy number and overall genome size was observed, indicating that cultivar F60 is septaploid ($2n=7x=140$) as has previously been reported for this species (Babil et al. 2013).

Diversity of PEBP-family in Chinese yam

In the present study we investigated the genetic diversity of PEBPs in Chinese yam on the basis of a de novo genome sequence. Overall, 75 PEBP sequences were found in the genome. Sequence alignment and phylogenetic studies enabled grouping of PEBP genes into 22 MFT-like, 19 TFL-like and 34 FT-like genes. The PEBP family in *D. polystachya* exhibits a high degree of diversity, with a relative distribution of MFT, TFL, and FT members similar to that found in other monocotyledonous species, and consistent with previous studies on PEBP families in plants (Kardailsky et al. 1999; Chardon And Damerval 2005; Karlgren et al. 2011; Zheng et al. 2016; Dong et al. 2020; Zhang et al. 2021).

Phylogenetic analyses showed that FTs have diversified into up to 12 individual clades with 5 main lineages. *Dioscoreales* were shown to have three of these groups (Bennett And Dixon 2021), fitting with our phylogenetic analysis on DpFTs. The high number of FTs compared to TFL and MFT is likely a result of gene duplication followed by positive selection, sub-, or neofunctionalization of FT function, which has driven the expansion of the FT family in other monocots (Zheng et al. 2016). A similar distribution of PEBP family members was also found in the White yam *D. rotundata*, where 10 PEBPs (8 FT, 1 TFL, 1 MFT) were identified in the genome (Susila And Purwestri 2023).This expansion is thought to enable FTs to contribute to adaptations to environmental stimuli by integrating signals and fine-tuning developmental processes through their tissue-specific expression (Bennett And Dixon 2021; Liu et al. 2023). This is supported by previous studies on FT homologs in other species, such as SP3D, SP5G and SP6A in potato, as well as the floral activator and repressor in sugar beet, which indicated a neofunctionalization of FTs (Abelenda et al. 2014; Bennett And Dixon 2021; Pin et al. 2010). Albeit the sharing high sequence similarity, the high copy number of DpPEBPs in Chinese yam might as well fine tune developmental processes such as timing of flowering transition and tuberization, which has been postulated for other species and needs to be further investigated in the future.

Phylogenetic relationship to known PEBPs

We analyzed the phylogenetic relationship of DpPEBPs to functionally characterized PEBPs from other plant species. DpFT1 and DpFT2 grouped with StSP3D and OsHd3a, both known to induce flowering in potato and rice respectively (Tamaki et al. 2007; Navarro et al. 2011), but not with other Solanaceae FTs. This is consistent with Chardon and Damerval, who hypothesized that PEBPs have undergone independent evolution within species (Chardon And Damerval 2005). In search for a potentially tuber-inducing FT ("tuberigen"), we took closer look at the protein motifs described to be relevant for their function. Four DpFTs (DpFT1, DpFT2, DpFT3, DpFT5) contained the conserved YAPGWRQ motif, which was found in several studies to be crucial for a flower- or tuber-inducing function (Ahn et al. 2006; Pin et al. 2010; Navarro et al. 2011; Harig et al. 2012). In onion, it was found that the bulb promoting AcFT1 has the slightly altered YAPnWRQ motif (Lee et al. 2013). However, in soy bean it was shown that even a slight modification of the motif in GmFT1a (pPGWRQ) is sufficient to determine its function as a floral repressor (Liu et al. 2018). More generally, a repressing function was shown to be associated with a severe alteration or absence of the YAPGWRQ motif (Pin et al. 2010; Navarro et al. 2011; Harig et al. 2012; Lee et al. 2013; Manoharan et al. 2016; Wang et al. 2019; Yang et al. 2019).

Another well studied motif is the LYN triad, which is described to be essential for an inducing FT function (Hanzawa et al. 2005; Ahn et al. 2006; Ho And Weigel 2014). Besides containing the YAPGWRQ motif, DpFT1, DpFT2, DpFT3, DpFT5 are also the only DpFTs that contain the LYN triad, indicating that these four FTs could be potential candidates for inducing FTs. The other DpFTs show alterations in both the YAPGWRQ motif, as well as the LYN triad, directing towards a potentially repressing function. In DpFT5, the REY motif, which is the third well-studied FT motif, the tyrosine is substituted by a histamine, resulting in REH at this position. While the Y residue is described to be conserved in FTs, a H is conserved in TFLs. Swapping these amino acids with each other reversed the roles of FT and TFL in *A. thaliana* (Hanzawa et al. 2005). However, FTs from banana which contain a REH motif were able to rescue an *ft-10* mutant in Arabidopsis (Chaurasia et al. 2017), indicating that the REY motif might not be entirely necessary for an inducing function.

DpFT expression in Chinese yam tubers

Based on the previously published tuber transcriptome (Riekötter et al. 2023), we analyzed the expression pattern of all DpPEBPs. Of the 75 identified PEBPs in this study, 21 FTs and 14 TFLs and 3 MFTs were expressed in the tuber tissue, underlining the diverse roles of PEBPs in growth and development in plants (Carmel-Goren et al. 2003; Chardon And Damerval 2005; McGarry And Ayre 2012; Zheng et al. 2016; Jin et al. 2021; Liu et al. 2021; Tribble et al. 2021). For most *DpPEBPs* expressed in tuber tissue, the highest expression was found in the tuber head. This is interesting, because the yam tuber head is assumed to enter a dormant stage early on, while the tip is still growing, and is assumed to be metabolically less active (Orkwor et al. 1998; Ile et al. 2006; Kawasaki et al. 2008). *DpFTs* with detectable expression in tubers showed the highest transcript levels in the head or middle part of the tubers. The expression of StSP6A increases gradually in early potato tuber development (Sun et al. 2024) and a regulatory feed-back loop is described for StSP6A that elevates *StSP6A* transcript levels in potato tuber development (Navarro et al. 2011). Similar to the mechanism described in potato, we speculate that elevated transcript levels of *DpFTs* in the upper tuber parts might be caused by longer transcriptional activity compared to the tuber tip. The developmental role of this transcriptional gradient is unclear and will have to be investigated further in future studies.

Interestingly, *DpTFL2* showed an expression pattern contrary to the other *DpPEBPs* with the highest expression in the tip, gradually decreasing towards the head. TFL-like proteins were described to maintain meristem identity (Carmona et al. 2007; Serrano-Mislata et al. 2016) and as the yam tuber tip contains a meristem and constitutes the actively growing part of the tuber, DpTFL2 might be involved in keeping meristem identity. Furthermore, in potato, expression of the TFL homolog *StTFL1* was observed in stolons with increasing mRNA levels onward tuberization but low levels in mature tubers (Guo et al. 2010). A putative role of StTFL1 in potato tuberization was suggested based on increased tuber numbers in transgenic *StTFL1* overexpressing lines (Guo et al. 2010).

The expression pattern of *DpTFL2* with elevated transcript level in the young tissue (tuber tip) therefore resembles *StTFL1* expression indicating a putative similar function. Interestingly, overexpression of another TFL homolog *StCEN* decreased sprout growth rate in comparison to control plants in potato. However, no clear evidence on its role controlling the timing of tuber bud dormancy release was apparent (Morris et al. 2019). Thus, DpTFL4 might fulfill a similar role in controlling sprout growth as StCEN. Whether it controls sprout growth and even tuber dormancy of Chinese yam could be an objective for future research.

DpFT7a-c variants showed the highest expression of all *DpPEBPs* in tuber tissue but was excluded from further analysis here, because it does not contain the amino acids described to be necessary for an activating function. However, it will be interesting to investigate its function in yam tubers in future studies.

DpFT3a is a candidate gene for a yam tuber-inducing factor

DpFT3a was investigated as a potential tuber-inducing FT ('tuberigen') due to its expression in tuber tissue and presence of necessary motifs described for an inducing function. Our results in tobacco revealed that DpFT3a localized to the nucleus, which is in accordance with the nuclear localization described for other FTs (Abe et al. 2005; Liu et al. 2018; Kim et al. 2022). Interaction of DpFT3a with DpFD1 was shown in a BiFC assay, indicating its potential to form a TAC (Abe et al. 2005; Harig et al. 2012; Teo et al. 2017; Beinecke et al. 2018; Zhang et al. 2020). Upon overexpression of *DpFT3a* in *A. thaliana*, transgenic lines flowered significantly earlier than WT, indicating a flower promoting function of DpFT3a in Arabidopsis (Navarro et al. 2011; Chaurasia et al. 2017; Yang et al. 2019). This is in agreement with the previous observation that StSP6A can induce flowering in the non-flowering Arabidopsis *ft-1* mutant (Navarro et al. 2011). To analyze its function in a tuber producing plant, we also expressed DpFT3a in potato. Interestingly, overexpression of *DpFT3a* induced a strong, dosage-dependent, tuberous-storage-organ-inducing phenotype without promoting flowering, indicating that DpFT3a can function as a tuber-inducing FT. Although StSP3D has been first described to play an important role in flowering as florigen, only recently a tuber-inducing activity was suggested for StSP3D in potato (Jing et al. 2023). Thus, further investigations will be required to show if DpFT3a also has a dual activity as florigen and tuberigen. Our results furthermore indicate that storage organ promoting FTs depend on other geophyte-specific factors (not present in Arabidopsis) to reveal their storage organ inducing function. Even in the well-studied potato, downstream transcriptional regulators of the TAC are elusive, underlying the importance of future research on the function of FTs for tuberous crop improvement strategies.

Our results further suggest an effect on meristem identity and plant architecture, since the strong tuber-inducing phenotype of constitutively overexpressing *DpFT3a* potatoes was characterized by the absence of leaves and roots. In accordance with our results, members of the PEBP-family, especially TFLs and the FT:TFL ratio, are described to play an important role in plant architecture (Carmel-Goren et al. 2003; McGarry And Ayre 2012; Jin et al. 2021; Liu et al. 2021). Furthermore, the starch accumulation in tuberous organs of transgenic potatoes with overexpression of DpFT3a suggests a role of DpFT3a in sugar flux regulation. A regulatory role in assimilate allocation from source to sink organs has been proposed for StSP6A as leaf/stem-specific overexpression of StSP6A resulted in more efficient transport of esculin, a sucrose analogue, into the phloem for long-distance transport compared to the WT control (Lehretz et al. 2019, 2021). Furthermore, these transgenic lines revealed a reduced shoot growth due to the inhibition of stem elongation and secondary growth as well as repressed bud outgrowth as a proposed consequence of low sucrose levels, while tuber number was elevated (Lehretz et al. 2019, 2021). In addition, StSP6A was found to interact with the sucrose efflux transporter StSWEET11 to enhance sucrose transport to the stolon by blocking apoplast leakage thereby promoting tuber swelling (Abelenda et al. 2019). DpFT3a could possess a similar function in sugar transport: inhibiting sucrose efflux from phloem to parenchyma cells and increasing the long-distance transport resulting in reduced shoot growth. High gene expression levels in the more mature upper tuber part (head) could lead to the directed transport of sucrose towards the actively growing tip. Elevated sugar levels in the sink tissue might have promoted tuber development, which then served as storage

organ of the newly synthesized starch that was detectable in the TC-lines. Taken together, our results strongly suggest that DpFT3a has tuber-inducing activity in geophytic plants.

It is essential to acknowledge that our findings are limited to heterologous plant systems, as an efficient transformation protocol of Chinese yam has yet to be developed. Future studies should involve knockout or overexpression of DpPEBPs to give more insight into their roles in plant development. Additionally, it is crucial to mention that the analyzed transcriptomic data represent a specific developmental stage of Chinese yam tubers, and selection of *DpFT3a* as candidate gene of tuberization is restricted to this data. We cannot exclude the possibility that other DpPEBP family members, which were not expressed at this stage, may be expressed at different time points and thus be potentially involved in tuber development. Therefore, future studies should address the expression profiles of *DpPEBP* family members over time in Chinese yam tubers and investigate potential functional redundancies among DpPEBPs. Especially the high transcript level of *DpFT7* rises the intriguing question whether an interplay of DpFT7 and DpFT3 might coordinate tuber formation in Chinese yam which would be worth investigating in future research studies.

Impact on yam breeding and future research prospects

The advent of next-generation DNA sequencing technologies has revolutionized the field of plant genomics, enabling the sequencing of genomes from numerous important crops. This development is of high importance for crop improvement programs (Darkwa et al. 2020). The availability of genome sequences provides invaluable insights into the underlying genetics of complex traits in plants, facilitating the identification of key regulatory genes and their genetic variability among cultivars (Edwards And Batley 2010). Despite the significance of yam as a staple crop, only a limited number of genomes from yam species have been sequenced to date. Notable examples include the reference genome sequences of *D. rotundata* (Tamiru et al. 2017) and *D. alata* (Bredeson et al. 2022).

Being one of the most important global tuberous crops, yam plays a major role in food security for millions of people especially in West Africa. More than 95% of the world's yam are produced in "West African yam belt" including countries like Nigeria, Ghana, Côte d'Ivoire, Benin, and Togo (FAO 2022, 2023; Scarcelli et al. 2019).

Yam production faces significant challenges, including high costs for planting materials and labor, low yield potential of local varieties, and a shortage of quality seed yams (Darkwa et al. 2020; Owusu Danquah et al. 2022). To address these issues, improving yam productivity and yields through effective cultivation management and breeding is crucial. However, breeding in yam is a complex process due to various factors such as unpredictable flowering, non-synchronous flowering, a long growth cycle, low multiplication rates, polyploidy, and high heterozygosity (Orkwor et al. 1998). Our results contribute to our knowledge on molecular factors involved in yam tuber development as well as flowering. Future functional studies on the DpPEBPs identified in this study offer potential breeding targets to improve tuber yield. Based on our results it will also be interesting to investigate a potential role of PEBPs in yam tuber dormancy. This is of economic interest since dormancy influences post-harvest management and germination rate. The latter was shown to be a trait of high value for yam farmers (Kalu et al. 2023). In addition, flowering on a molecular level is a relatively unexplored process in Chinese yam and dioecy as well as asynchronous flowering of this species impede breeding attempts. Our studies provide candidate genes potentially involved in flower production, i.e. DpFT1, DpFT2 and DpFT4, which are not (with the exception of DpFT1c) expressed in tuber tissue and might be candidates for flower inducing/repressing FTs. Besides flowering, the development of functional molecular markers for sex determination is of high relevance for yam breeding (Darkwa et al. 2020). Recent studies have made progress in this area, with the development of SNP markers for *D. rotundata* (Tamiru et al. 2017) and the identification of a QTL for sex determination in *D. alata* (Cormier et al. 2019). Thus, the development of a sex marker in Chinese yam will greatly benefit from the availability of a genome sequence as provided by our study.

Further, food security is not only determined by food availability and quantity, but also by nutritional diversity in which underutilized orphan crops (Fahey 1998; Tadele 2019) such as yams also play an important role. Thus, efforts in crop improvement

by breeding projects could contribute towards economically efficient cultivation of yams on a global scale including the introduction of Chinese yam as potential crop in Europe. Consequently, our presented study has the potential to contribute to future breeding approaches for yam improvement. Last but not least, our results enhance our knowledge on Chinese yam and provides important insights for successful establishment of Chinese yam as a crop in Europe for diversification of agriculture and provision of food for healthy diet (Epping And Laibach 2020).

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Author contributions Tatjana Ried and Janina Epping designed the study. Tatjana Ried conducted all experiments except the genome assembly, which was conducted by Marie Bolger and the mapping of RNAseq reads against the genome, which was conducted by Toshiyuki Sakai. Jenny Riekötter contributed to the data analysis and figure design. The manuscript was written by Tatjana Ried, Janina Epping, Jenny Riekötter and Marie Bolger. All authors read and approved the final manuscript.

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Data availability The datasets generated during and/or analyzed during the current study are available at the European Nucleotide Archive (ENA), Project PRJEB82723 (https://www.ebi.ac.uk/ena/browser/view/PRJEB82723).

Declarations

Competing interests The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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