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Terminal Flower 1(*TFL1*) Homolog Genes in Dicot Plants

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Abstract: Terminal flowering1 (*TFL1*) is an important gene responsible for time of flowering in *Arabidopsis thaliana.* It belongs to phosphtidyl ethanolamine binding protein domain PEBP gene family. Throughout the past decade, genetic studies have found out several *TFL1* like genes in dicots and monocots plants. In this paper, current advances in *TFL1* homolog isolated from different dicot species, has been addressed. *Arabidopsis thaliana*, *Antirrhinum majus*, *Brassica naapus*, Citrus sinensis L, *Pisum sativum*, *Vitis vinifera* L, *Beta palonga, Lotus japonicus*, *Lycopersicon esculentum*, *Impatiens balsamina*, *populus trichocarpa*, *Malus xdomestica*, *Pyrus pyrifolia*, *Pyrus communis*, *Cydonia oblonga*, *Chaenomeles sinensis*, *Cucumis sativus*, *Gossypium hirsutum*,*Capsicum annuum L.*and *Eriobotrya japonica* are dicot plants which their TFL1 homologs will be discused here. Moreover, similarity and differences between them and other known genes, have been compared.

Key word: Flowering · TFL1 · Gene expression · Dicot · Arabidopsis

INTRODUCTION

Flowering is the significant developmental switch in plants .This leads to a phase transition at a certain point of plants life, resulting switch from vegetative growth to reproductive growth in plants. During the last decade, molecular mechanism of flowering have been studied extensively in herbaceous ‘‘model’’ plants such as *Arabidopsis thaliana* and snapdragon (*Antirrhinum majus*). Genetic models of flowering time, flower differentiation and floral meristem identity have been designed upon the detection of numerous transcriptional regulator genes [1-3]. The shoot apical meristem (SAM) is a set of indeterminate stem cells, located at tip of the shoot axis. Meristems which grew up in shoot apex can generate either shoots or flowers. This achievement depends on expression of two sets of meristem identity genes: first, floral meristem identity gene like *LEAFY (LFY*), *APETALA 1 (AP1)* and *CAULIFLOWER (CAL)* ,that appoint lateral meristem in Arabidopsis to convert into flowers rather than shoots or leaves [4-10]. Second, shoot meristem identity genes, like *TERMINAL FLOWER* 1*(TFL1)*, appoint inflorescence shoot apical meristem as indeterminate and inhibit flower creation from shoot [11-13]. Researchers have shown that there are two basic types of flowering architecture in plants: namely, determinate and indeterminate. In first case, growing of shoot is indefinitely and flowers are only produce peripherally. In second case, growth of apical meristem cease when a terminal flower is created on apex [14]. The indeterminate condition of the shoot apex is maintained by a cluster of proteins belonging to the family of phosphatidyl ethanolamine-binding proteins (PEBPs), a family that is extensively conserved along with eukaryotes [12, 15, 16]. *TERMINAL FLOWER 1* (*TFL1*) is significant gene effect phase development and inflorescence architecture in Arabidopsis [12, 17].This gene governs the onset of flowering in Arabidopsis. Several members of *TFL1* family have been detected in Arabidopsis; both move forward and delay onset of flowering in this plant. *TFL* mRNA has been located in the set of cell lie just below the apical vault of meristem. *TFL*1 acts as a meristem identity gene and leads down regulating of *LFY* and *AP1*, which are floral meristem identity genes therefore prevents expression of *LFY* and *AP1* in shoot apical meristem. Mutation in *TFL1* converts the apical shoot meristem and axillary shoot meristem to floral meristem [1]. In the meantime ectopically expression

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of *LFY* and *AP1* occurs [18]. *TFL1* repress flowering in an antagonistic manner with *FT* [19].Mutations of *TFL1* effect in the inflorescence meristem being converted into a terminal flower [20].In addition, the vegetative and early reproductive phases have been considerably shortened in *tfl1* mutants and in plants with over expressing *FT* [21]. In spite of their sequence similarity, *FT* and *TFL1* [22- 24] have a antagonistic roles. *FT* induces floral transition, while *TFL1* suppresses it. As a result, among flowering time genes, *TERMINAL FLOWER* 1 (*TFL*1) plays a significant role in determination of floral meristem identity in *A*. *thaliana*. A deficient mutant in the function of this gene forms a terminal flower at the apex of its inflorescence after developing a few flowers [25, 26,27] .*TFL*1 has also been cloned and its structure has revealed that *TFL1* and *CEN* ; another homolog in *Antirrhinum majus* ; encode a similar protein [25, 12, 27,15] . this paper review recent research on collection of *TFL1* homolog genes in dicot plants: those include: *Arabidopsis thaliana*, snapdragon (*Antirrhinum majus*) ,*Brassica.naapus*, citrus (Citrus sinensis L.), pea (*Pisum sativum*) , grapevine (*Vitis vinifera* L.), *Beta palonga, Lotus japonicus*, Tomato (*Lycopersicon esculentum*) , Tobacco (*Lycopersicon esculentum*), *Impatiens balsamina, populus trichocarpa* , cereals , apple (*Malus xdomestica*), Japanese pear (*Pyrus pyrifolia*), European pear (*Pyrus communis*), quince (*Cydonia oblonga*), Chinesequince (*Chaenomeles sinensis*), loquat (*Eriobotrya japonica*), *cotton* (*Gossypium hirsutum*) , cucumber , (*Cucumis sativus*) and pepper (*Capsicum annuum L.)*

MATERIAL AND METHOD

Tfl1 Homolog Gene in Plants and Their Structure

Tfl1 in Dicot Plants: Studies have shown that several genes are present in Arabidopsis genome encoding PEBPs: *TFL1 (TERMINAL FLOWERING LOCUS 1), FLOWERING LOCUS T (FT), CEN* homolog in Arabidopsis *(ATC), BROTHER OF FT AND TFL1 (BFT), MOTHER OF FT AND TFL1 (MFT), TWIN SISTER FT (TSF)* [24, 28]. Among all of them *TFL1* and *FT* are more described functionally. The opposite functional roles of FT and TFL1 proteins have been related to the presence of critical amino acid residues. Eleven amino acid residues in the plant PEBP sequences have so far been identified as essential for a functional protein by crystallography [20] or by mutations [12, 15, 29]. According to Banfield and Brady [20] there are six essential amino acids necessary for ligand binding in one of TFL1 homolog protein in *A. majus* named CEN. Difference between TFL1 and FT can be explained with presence of Tyr85/Gln140 in FT versus His88/Asp144 in TFL1 [19, 22] Like Arabidopsis, in another model plant; antirrhinum; it has been found an anologe named CEN that is functionally identity to TFL. Although using southern hybridization it has detected that there are four copies of *TFL1* homolog in *Brassica.naapus,* but just three clones; *BNTFL1-1, BNTFL1-2 and BNTFL1-3,* have been identified with 1.4kb Length, four exons and three entrons. Deduced amino acid sequences from *BNTFL*1-1, *BNTFL*1-2 and *BNTFL*1-3 are nearly identical to that of *A*. *thaliana TFL*1 (87.1, 84.8 and 86.5% homology to *TFL*1, respectively). The three *TFL*1 -like genes which have identified in *B*. *napus* are nearly identical, it seems that they are distinguishable by sequence difference in their first introns and 3' UTR regions as well as by those in the coding regions leading to amino acid substitutions. Homologies of *BNTFL*1-1 to *BNTFL*1-2 and *BNTFL*1-3 in nucleotide sequence have been reported 97% and 99.3%, respectively. While four substitutions in the deduced amino acid sequences have been found between proteins encoded by *BNTFL*1-1 and *BNTFL*1-2 and one between those encoded by *BNTFL*1-1 and *BNTFL*1-3; there have been cleared nucleotide sequence changes in the first introns and the 3' UTRs. *BNTFL*1-1 and *BNTFL*1-3 have six nucleotides GAGAGA and two nucleotides TA in a part of the first intron (577 and 597 bp downstream of the putative initiation codon, respectively), whereas *BNTFL*1-2 has none of them. Also, at 13 bp downstream of the putative termination codon of the 3% UTR, a specific sequence has been found in *BNTFL*1-2 but not in both *BNTFL*1-1 and *BNTFL*1-3. These marks point to that *BNTFL*1-3 is more strictly related to *BNTFL*1-1 than to *BNTFL*1-2. These explanations suggest that *BNTFL*1-1 and *BNTFL*1-3 have originated from duplication of an ancestral gene, whereas *BNTFL*1-2 may have a different origin. It means *BNTFL*1-2 may have been originated from AA genome and the *BNTFL*1-1 and *BNTFL*1-3 from CC genome [30]. In Cucumber six homolog with difference length and exon and intron have been detected [31]; *CsTFL1a*, *CsTFL1b*, *CsTFL1c1*, *CsTFL1c2*, *CsTFL1d* and *CsFT* with 1046, 2624, 1272, 763, 1190, 2524 bp Length, respectively. Also 4, 4, 3, 3, 4, 4 exon and 3, 3, 2, 2, 3, 3 intron for each of them have been observed respectively. Proportion of amino acid sequence relationship of CsTFL1a, CsTFL1b, CsTFL1c1, CsTFL1c2 and CsTFL1d to TFL1 of Arabidopsis are 79 %, 83 %, 75 %, 77 % and 76 %, respectively and CsFT to FT is 84 %. *CsTFL1 is* a single-copy TFL1 homolog in citrus that has about

1.9 kb in Length with, 4 exons and 3 introns which that has a conserved location among TFL homolog relative to the protein sequence [32]. *CsTFL* encoded a 19-kD protein with 74% and 70% amino acid identity to *Arabidopsis* TFL1 and *Antirrhinum majus* CEN, respectively, but shared the highest identity (80%) with the *O. sativa* TFL homolog. All of [20] six essential amino acids necessary for ligand binding are conserved in CsTFL with the exception of Ile-110. Studies have been shown that Ile-110 corresponded to Met-115 in the AmCEN protein. Difference at this place has been observed in Arabidopsis and some monocots as well [15, 33] has demonstrated that the residue at position 110 could be in some measure responsible for the variety in the severity of phenotypes in transgenic Arabidopsis plants ectopically expressing the *TFL* homolog. The deduced amino acid sequence of CsTFL has been shown 65% identical to the Arabidopsis TFL1 protein. Kotoda and Wada [34] isolated a c DNA homolog to TFL1 in dicot plant apple. Named, *MdTFL1*. Coding region of the *MdTFL1* cDNA shows 76%, 73%, 71% and 58% sequence identity to *TFL1*, *CEN*, *SP* and *FT*, respectively. And phylogenic comparison has been shown that MdTFL1 is grouped with FT-like, CEN-like (dicot), TFL1-like (dicot) and CEN/TFL1-like (monocot) proteins. The protein product expect for the MdTFL1 sequence consists of 172 residues and with comparison to other CETS family members demonstrates that it groups with TFL1 and four *Brassica* proteins. However recently; Mimida *et al*. [35] has described four *TFL1*/*CEN*-like genes; *MdTFL1*, *MdTFL1a*, *MdCENa* and *MdCENb* in apple (*Malusxdomestica* Borkh.) that mapped by a similar position on putatively homoeologous linkage groups. Constitutively expression of *TFL1* in transgenic Arabidopsis plants indicate that the Apple *TFL1*/*CEN*-like genes functions equivalently to *TFL1*, proposing that they be able to be complement the *TFL1* function. Since *MdTFL1* and *MdTFL1a* are expressed in the vegetative tissues in both the adult and juvenile phases, it can consider they act redundantly as a flowering repressor and a regulator of vegetative meristem identity. But *MdCENa* is largely expressed in fruit receptacles, cultured tissues and roots, so it could be involved in proliferating tissues development but not in be in charge of the transition from the juvenile to the adult phase. *MdCENb* is silenced in most organs maybe because of gene duplication by the polyploid origin of apple. These expression patterns also have been supported using heterologous expression of β-glucuronidase fused with *MdTFL1* and *MdCENa* promoter regions in transgenic Arabidopsis. Results have been suggested that functional variance of the roles in the regulation of vegetative meristem identity may have happened between four *TFL1*/*CEN*-like genes throughout evolution in apple. *PsTFL1*a, *PsTFL1b, PsTFL1c* are the tree homologs have been seen in pea. Both *PsTFL1a* and *PsTFL1c* has been cluster with *TFL1*. *PsTFL1b* belongs to another cluster of genes that includes *CEN*, *SP* and *ATC* [36]. Using the computer software, it has been suggested that PsTFL1a and *PsTFL1c* are expected to encode proteins of 174 and 173 amino acids, respectively, indeed they show 70% amino acid identity and 72 and 65% identity with TFL1, respectively. The predicted protein for Partial sequence of *PsTFL1b* clone, which is incomplete in 5 ends, covers 90 amino acids and show 73% identity with TFL1. All of three predicted protein have large regions that are conserved across TFL1 homolog from other species and Intron/exon boundaries also are extremely conserved across these genes. *PsTFL1a* has been mapped and found to be located in a region shown previously to contain *DET* [37]. Mapping study has determinate that *PsTFL1a* is closely linked to *DETERMINATE (DET)* gene; a gene involve in maintain the indeterminacy. Also *PsTFL1b* has been recognized in a region containing no obvious candidate flowering loci. But *PsTFL1c* has been shown to be located in a region containing *LATE FLOWERING (LF)*; a gene delays the induction of flowering [38, 39] and important quantitative trait loci for flowering time. Indeed, mutation study in pea has been shown that *det* and *lf* mutation shown a substitution in the predicted amino acid sequence of *PsTFL1a* and an important modification in *PsTFL1c* sequence respectively. These finding suggests that *PsTFL1a* and *PsTFL1c* corresponds *to DET* and *LF* respectively. Although it has been found five homolog in grapevine (Vitis vinifera) but they have been grouped in three major cluster; the *FT, MFT* and *TFL1*, the last one including three of the Vitis sequence named *VvTFL1A, VvTFL1B, VvTFL1C* [40, 41]. All of five genes *VvTFL1A, VvTFL1B, VvTFL1C, VvFT and VvMFT* preserved the characteristic genomic organization for this gene family, with four exons and three introns in the same positions. VvFT displays all the characteristic features of the FT protein subfamily [22] which consist of the conservation of Tyr85 (but Tyr84 in VvFT) and Gln140 (but Gln139 in VvFT), also the conserved 11 amino acid residues in exon 4, critical for FT activity, as well as the highly conserved LYN triad present in exon 4. VvFT is related with Arabidopsis FT and TSF as well as other FT orthologous proteins recognized in other dicot species. In second cluster (MFT), the essential Tyr and Gln residues are substituted by Trp and Ser,

respectively; similar characteristics residues. In addition, the conserved triad sequence characteristic of the FT group is absent in VvMFT. VvMFT is related with Arabidopsis MFT and its putative orthologous proteins identified in tomato and Populus. Charged residues His88 and Asp144 have been conserved in third cluster in similar positions as TFL1, as well as the characteristic amino acid triad (ENE, END and DNG respectively for VvTFL1A, VvTFL1B and VvTFL1C) in exon 4. Third grapevine genes are related with Arabidopsis *TFL1*, *ATC* and *BFT*.

VvTFL1A is strictly correlated protein to the Arabidopsis TFL1and ATC as well as to the Antirrhinum CEN. VvTFL1C cluster with Arabidopsis BFT, Nicotiana CET1 and Populus PnFTl1a, in what could depict a clade of BFT orthologous sequences. Whereas, VvTFL1B associated to TFL1-like proteins is less correlated to those recognized in Arabidopsis and Antirrhinum. *Ljcen1* is a single copy gene in the genome of *Lotus japonicus* that has four exons and three introns. *Ljcen1*encodes 174 amino acids, which showed 72% identity to TFL1, 71% to CEN, 76% to FDR1 and FDR2, 70% to CET2 and 67% to SP[42]. The *SP* gene with three intron and four exon has been localized to position 106 on the genetic map of chromosome VI of tomato [43, 44, 29]. Tobacco genome has seven CEN-like homologs, yet only CET2 and CET4 were orthologs .*CET2* and *CET4* probably represent single-copy genes in the diploid progenitors of the allotetraploid tobacco. The *CET* genes have three introns in the same positions as those in *CEN* and *TFL1*, but these introns are of different sizes. CET2 and CET4 are orthologs, which show 97% DNA sequence identity to each other [45]. *CET5* and *CET6* have been shown 93% identical to each other and 74% identical to *CEN*. *CET7* is 93% identical to *CET1* and 67% identical to *CEN*. Comparisons indicate that CET2/CET4, SP and CEN are more closely related than are any of the others. Other *CET* gene products are more distantly related, while most trees suggested that CET5 and CET6 are more related to TFL1 from the distantly related species Arabidopisis. *IbTFL1* has detected in *Impatiens balsamina* with1137 bp Length so that genomic sequence includes a 215 bp upstream region, containing a 51 bp 5'UTR and 27 bp of the 3' UTR. The size and position of exons is conserved between *IbTFL1*, as well as the *TFL1* family and *CEN* [46]. The predicted 181-amino-acid protein of *IbTFL1* is 68, 72, 66% identical to TFL1, ATC and CEN respectively; and a lower identity to the other members of the TFL1 family in Arabidopsis (BFT, 61%; FT, 57%; MFT, 47%; and TSF, 54%). The protein contains a *His* residue at amino acid 92 which is a key residue separating TFL1 and ATC from FT and the other family members in Arabidopsis [19]. IbTFL1 is clustered with TFL1, ATC, CEN and the other TFL1/CEN homologues but it is not clear whether IbTFL1 is more like TFL1 or ATC. Its cDNA has 67% identity to TFL1, 67% identity to ATC and 64% identity to CEN and with lower identity to the other TFL1 family members BFT, 58%; FT, 58%; MFT, 58%; TSF,56%). In *populus PtCENL-1* and *PtMFT* have 525 and 522 bp full-length coding sequence respectively. But their entire genomic sequence spanned 0.9 kb and 2.2 kb, respectively. Like to other *TFL1* homolog they have four exons and three introns. Due to a much longer third intron, *PtMFT* is considerably longer than *PtCENL-1* [47]. *Pt*CENL-1 has all six amino acids identified by Banfield and Brady [20] as ligand-binding sites in *Antirrhinum majus* CEN (*Am*CEN) whereas only three residues are conserved in *Pt*MFT. Both *PtCENL-1* and *PtMFT* encoded 19 KD proteins, consisting of 174 and173 amino acid residues, respectively. 52% amino acid identity has been seen between them. *Pt*CENL-1 is 79, 76-79, 77 and 72%, identitical with *Md*TFL1, CET2, *Oryza sativa* CEN-like proteins , *Am*CEN and *At*TFL1 respectively and lowest identity with *At*MFT (50%) , *At*FT (56%), *At*TSF (56%) and *At*BFT (61%).On protein level, *Pt*MFT shows the highest homology with *At*MFT (78%), but the lowest homology with *At*TFL1 (50%) and *At*FT (45%). *Pt*CENL-1 clusters with TFL1/CEN-like proteins and *Pt*MFT with *At*MFT .Also six additional members of *CEN*/*FT*-like genes has been identified named *PtCENL-2*, *PtCENL-3* and *P. trichocarpa FT*-like *-1* to *-4* (*PtFTL-1* to *PtFTL-4*). All encoded deduced proteins of either 173 or 174 amino acid residues. A phylogenetic analysis shows *Pt*CENL-1 to -3 formed one cluster; and *Pt*FTL-1 to 4 formed another cluster with 80% and 76% homology to *Os*HD3a and *At*FT, respectively, whereas *Pt*MFT is independent of either group. *Pt*CENL-1 is more closely related to *Pt*CENL-2 (91%) than to *Pt*CENL-3 (70%). *Pt*FTL-1, -3 and -4 grouped together and shared 90% identity with *Pt*FTL-2. Poplar FT-like proteins are more similar to *Pt*CENL-1 (59%) than to *Pt*MFT (49%). *Pt*CENL-1 shared 78% and 79% identity with *Cs*TFL protein from the woody perennial citrus and *Md*TFL1 from apple, respectively. One study on several Maloid species has shown that two different types of cDNA for *TFL1* homologues were isolated from each species, namely *PpTFL1-1* and *PpTFL1-2* for Japanese pear, *PcTFL1-1* and *PcTFL1-2* for European pear, *MdTFL1-1* and *MdTFL1-2* for apple, *CoTFL1-1* and

CoTFL1-2 for quince, *CsTFL1-1* and *CsTFL1-2* for Chinese quince and *EjTFL1-1* and *EjTFL1-2* for loquat [48]. However, all homologues consisted of 172 deduced amino acid residues and a total of 25 substituted residues in the sequence alignment of Maloid homologues were found. Among them, 17 substitutions (positions 2, 3, 4, 5, 8, 33, 52, 69, 90, 96, 104, 105, 111, 128, 134, 159, 167) were species-specific, while 8 were specific to the type of TFL1 homologue (positions 23, 26, 59, 60, 73, 99, 127,140), TFL1-1 or TFL1-2. Briefly, The TFL1 homologues in Maloid species belonging to the two different clades, TFL1-1 and TFL1- 2, shared around 90% identity, while homologues within each clade has been shown identities of 98% (TFL1-1) and 97% (TFL1-2). *GhTFL1a* and *GhTFL1b* are isolated genes from cotton (*G. hirsutum and G. arboretum*) that keep the same exon–intron organization, with a final contig of 1838 bp and1510 bp for *GhTFL1a* and *GaTFL1b* respectively [49]. The genomic organization of *GhTFL1a* was similar to that of other *TFL1* genes from other plant species and consisted of four exons and three introns encoding for a 174 amino acid protein. Multiple alignments with a subset of proteins belonging to the PEBP family from other plant species has been revealed that TFL1b proteins associate with proteins from rice and Lolium perenne, whereas TFL1a proteins associate with proteins from poplar and Vitis, confirming similarities with TFL1-like proteins. Also, Key amino acids that distinguish TFL1from FT [22, 19] and MFT are conserved in TFL1a- and TFL1b-like proteins from cotton [17]. Genomic DNA analysis of *Capsicum. annuum* revealed that the *CaSP* gene is present in a single copy [50]. The *CaSP* genomic DNA sequence consisted of 2487 bp, a coding sequence of 528 bp and has four exons and three introns. The coding sequence of *CaSP* was predicted to encode a 175-amino acid polypeptide. *CaSP* is elucidated in linkage group 8 (chromosome 6) of the SNU2 pepper genetic map and is the closest neighbor of the *SP* gene of tomato in the *TFL1*-like gene group. It has 91, 88 and 89% identities with the SP gene of tomato (Solanum lycopersicum) and the CET2 and CET4 genes of tobacco (Nicotiana tabacum), respectively. Other orthologs that have highly homologous with the *CaSP* gene are including *TFL1, CEN, CET2, CET4, BRTFL1* and *BNTFL1*.The partial amplified *TFL1* homologue of *Beta. palonga*, has been detected a 238 bp sequence encode 79 amino acids, was renamed as *PTC-1* (*PTC*: Palong *TFL1/CEN*-like gene).The results showed that the *PTC* had above 65% identity at the amino acid level with *TFL1/CEN*-like genes isolated from different plants. The highest level of identity has been reported with *TFL1/CEN* homolog or ortholog proteins from *Pisum sativum.*

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