Middle-East Journal of Scientific Research 6 (3): 293-304, 2010
ISSN 1990-9233

Function and Expression Pattern of Terminal Flower 1(*TFL1*) Homolog Genes in Dicot Plants

[1]*Yaghoob Tahery,* [2]*Nor-Aini Ab-Shukor,* [2]*Hazandy Abdul-Hamid,*
[3]*Mohd Puad Abdullah,* [4]*Norlia Binti Basherudin and* [1]*Farshid Kafilzadeh*

[1]Islamic Azad University, Jahrom branch, Iran
[2]Institute of Tropical Forestry and Forest Products Universiti Putra Malaysia,
43400 Serdang, Selangor, Malaysia
[3]Department of Cell and Molecular Biology, Faculty of Biotechnology and
Biomolecular Sciences, Universiti Putra Malaysia, 43400, Serdang, Selangor, Malaysia
[4]Genetic Unit, Forest Research Institute Malaysia (FRIM), 52109 Kepong, Selangor, Malaysia

Abstract: Terminal flowering1 (*TFL1*) is a key gene in charge of flowering time in *Arabidopsis thaliana*. During the past decade, genetic studies have found out several *TFL1* like genes in dicot plants. The main issues addressed in this paper are current advances in *TFL1* homologs isolated from different dicot species and their function in flowering. Taking advantage of previous studies of cloning, in this paper we have evaluated function of these genes in regulating flowering time. It will then go on to place or parts of plants in where these genes express. 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 most important developmental switch in plants. This event causes a phase transition at a certain point of plants life, resulting switch from vegetative growth to reproductive growth in plants. Through the last decade, molecular mechanism of flowering have been studied widely in herbaceous ''model'' plants such as *Arabidopsis thaliana* and snapdragon (*Antirrhinum majus*). Genetic models of flowering time, floral meristem identity and flower differentiation have been proposed upon the detection of numerous transcriptional regulator genes [1-3]. The shoot apical meristem (SAM) is a set of indeterminate stem cells, positioned at tip of the shoot axis. Meristems 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)*, designate inflorescence shoot apical meristem as indeterminate and repress 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 phosphatidylethanolamine-binding proteins (PEBPs), a family that is extensively conserved along with eukaryotes [12,15,16].*TERMINAL FLOWER 1* (*TFL1*) is considerable gene influences phase expansion and inflorescence architecture in Arabidopsis [12,17]. This gene regulates the onset of flowering in Arabidopsis. There are several members belong to *TFL1* family both move forward and delay onset of flowering in Arabidopsis. *TFL* mRNA has been detected 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

Corresponding Author: Yaghoob Tahery, Islamic Azad University, Jahrom branch, Iran.
Tel: 6-01-7229-9708, E-mail: yaghoobtahery@yahoo.com.

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 of *LFY* and *AP1* occurs [18]. *TFL1* repress flowering in an antagonistic manner with *FT* [28]. Mutations of *TFL1* effect in the inflorescence meristem being converted into a terminal flower [19]. In addition, the vegetative and early reproductive phases have been considerably shortened in *tfl1* mutants and in plants with over expressing *FT* [20]. In spite of their sequence similarity, *FT* and *TFL1* [21-23] 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 [24-26] . *TFL*1 has also been cloned and its structure has revealed that *TFL1* and *CEN*; another homolog in *Antirrhinum majus*; encode a similar protein [24, 12, 15, 26]. It has been detected that the TFL1: CEN proteins are homologous to a protein similar to a family of mammalian phosphatidylethanolamine-binding (PEBP) proteins [27, 28]. These proteins have been suggested to be found in membranes and interact with phospholipids and GTP-binding proteins in animals. *TFL1* encodes a protein that probably plays a role in signaling, maybe as an inhibitor of mitogen-activated protein kinase pathways [29]. TFL protein is also known as Raf-1 kinase inhibitor protein (RKIP). The molecular action of the PEBP proteins is not entirely clarified yet. Some studies support the hypothesis that they are involved in the regulation of a range of intracellular signaling cascades through their association with proteins of several functional classes. In mammals, they fix hydrophobic ligands, such as phosphatidylethanolamine and nucleotides, like GTP. it has detected that human PEBP facilitates heterotrimeric G protein-coupled signaling [30-32]. In past decade numerous attempts have been made to cloned *TFL1* homolog in different species plant, however, far too little attention has been paid to collect and summarized these data with respect to difference and similarity between their structure, as well as their expression and function. The purpose of this paper is to review recent research on collection of *TFL1* homolog gene in dicot plants: *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.).*

Expression Pattern: Expression analysis has revealed that genes closely related to *TFL1* are expressed mainly in the shoot apical meristem in the region below the terminal meristem. *TFL* mRNA was detected in the set of cell lying just below the apical vault of meristem.In wild-type Arabidopsis high levels of *TFL1* is observed in inflorescence apex while *LFY, AP1* that are antagonists of *TFL1* express in peripheral floral meristems but in *tfl* mutants Arabidopsis *LFY, AP1* genes are up regulated in inflorescence apex meristems, leads to early flowering [12]. Also it has been detected that *FT* express in leaves but can move to the shoot apex. However, unlike *CEN*, *TFL1* is also expressed during the vegetative phase. The *ATC* gene in Arabidopsis that also belongs to the *TFL1*-like subfamily has a quite different expression pattern, being expressed in the hypocotyls of young plants but not in the meristem [33]. *FT* expresses in leaves but can move to the shoot apex. In *Antirrinum,* the Centroradialis is expressed in just below the inflorescence apex a few days after floral induction. The study of *TFL1* homolog expression in *Brassica.naapus* has shown that this homolog prevalently express in flowers [34]. In citrus, expression analysis of *TFL1* homolog show a positive correlation of *CsTFL1* transcript accumulation with juvenility and negative relation with RNA level of two floral integrator genes *AP1* and *LFY*. *CsTFL* transcripts accumulate in all organs of fully developed flowers but not in any of the citrus vegetative including leaves, stems and roots [35]. These data is inconsistent with studies using apple, rice, or ryegrass. In these plants, *TFL* RNAs has been detected in vegetative tissues of adult plants [36-38]. However, the RNAs for the TFL homolog from apple have also been detected in flowers [39]. *MdTFL1* concussively express in apple vegetative organs include: seedlings, roots, stems, apical bud but not in mature leaves. Expression will be peak approximately two weeks before floral bud differentiation [37]. *MdTFL1* mRNA was expressed in vegetative tissues, such as apical buds, seedling stem and roots, but not in reproductive tissues such as floral organs. The expression pattern of *MdTFL1* in different tissues similar to *TFL1*-like gene in tomato

named SP9D, as both genes are expressed in shoot apices and roots, not in reproductive tissues [40]. In fact, MdTFL1 shows greater connection to SP9D (77%) than to SP (72%) in amino acids sequences. Recent study has been shown *MdTFL1* and *MdTFL1a* are found in the vegetative tissues in both the adult and juvenile phases. *MdCENa* is mostly expressed in fruit receptacles, roots and cultured tissues; *MdCENb* is silenced in most organs probably due to gene duplication by the polyploid origin of apple. In pea, *PsTFL1*a corresponds to *DETERMINATE (DET)* gene of Arabidopsis, expresses principally in root, in shoot apex only after initiation of flowering, flowering buds and flowers. *PsTFL1c* expresses in both vegetative and reproductive organs, corresponds to *LATE FLOWERING (LF)* gene of Arabidopsis and cause delaying in flowering induction. *PsTFL1b* is another homolog that is found in the apex, roots and dormant nodes of pea but not in flowers [41]. *VvTFL1A, VvTFL1B* and *VvTFL1C* of grapevine are express in first-season latent buds and detected in initial stages of inflorescence development but are not detect together with flower development [42, 43]. *Vv FT* is link with seasonal flowering induction in latent buds and to the development of inflorescences, flowers and fruits [42, 44]. Generally it is found that expressions of grapevine *FT/TFL1*-like genes are coupled with either meristem proliferation or determination processes. Whiles expression of genes such as *VvMFT* and *VvFT* is linked with meristem determination and differentiation of inflorescences, tendrils or flowers, *TFL1*-like gene expression is more related to meristem proliferation in shoot and apices [45]. *Ljcen1* is found in young root tip and reproductive shoot apical meristem of *Lotus japonicus* .This gene express ceaselessly in sub-doment of the primary inflorescence meristem and impermanent in secondary inflorescence meristem of Lotus japonicas [46]. *SELF-PRUNING* (*SP*), express in leaves and shoot apices in very early stages and then in inflorescence and floral primordial of tomato. It means in addition to leaf and floral primordial, *SP* occurs in all meristem including vegetative,floral, inflorescence and axillary meristems [47]. In tobacco, it has been found that expression of *CET2* and *CET4* occur in vegetative axillary meristem, but they are not express in main soot meristem. *NFL* (for *Nicotiana FLO LFY);* the likely tobacco homolog of *FLO* and *LFY;* express in main apex. Up regulating of floral meristem identity genes make changing of vegetatitive meristem to flowering shoots and will be coinciding with down regulating of *CET* genes. Despite of Antirrhinum and Arabidopsis in which *CEN* and *TFL1* are found in the primary shoot apex, *CET2* or *CET4* are not expressed in the primary shoot apical meristem of tobacco. The expression of both *CET2* and *CET4* was restricted to axillary meristems during the vegetative phase [48]. However in Arabidopsis, *TFL1* expression is also occurred in axillary meristems, which result in secondary inflorescences [3]. Moreover, floral meristem identity genes, such as *FLO* in Antirrhinum and *LFY* in Arabidopsis, are expressed in domains separate from *CEN* and *TFL1*, suggesting an antagonistic relationship between these genes [11, 12, 49, 10]. *CEN* and *TFL1* are expressed in the apical meristem, while *FLO* and *LFY* are limited to peripheral meristems [3, 10].The expression domains of *CET2* and *CET4* and *NFL* did not appear to overlap significantly. Development of axillary meristems correlates with a reduction in *CET2* and *CET4* expression and an increase in that of *NFL*. It has been found that *NFL* expression is recognized first in the main apex of tobacco, which may prevent *CET2* and *CET4* expression in the primary shoot. Though, in axillary meristems, expression of *CET2* and *CET4* may be established early to promote leaf development phase. When *NFL* expression increases in these meristems, expression of *CET2* and *CET4* becomes increasingly more limited to the central domain until the genes are down regulated upon flowering. As a result, *CET2*or *CET4* may expand the vegetative phase of axillary meristems so that they shape leafy branches rather than straight switching to flowers. Axillary meristems just below the terminal flower do not express *CET2* or *CET4* but have strong *NFL* expression from early in their development. This pattern leads to terminal flowers. In *Impatiens balsamina* expression of *IbTFL1* is very similar to *TFL1, CEN, CET2* and *CET4* genes. *IbTFL1*expression is correlated to early formation of axillary meristems and its transcripts is found in axillary shoot and axillary meristems but not detected in apex and axillary flower. Briefly, expression of *IbTFL1* is found in axillary meristems in the vegetative phase and early formed meristems in the inflorescence phase; it is never detected in the apex of the main shoot or in meristems of the terminal inflorescence [50]. Both *PtCENL-1, PtMFT* is express in all tissue of *populus*: except that there is no *PtMF* transcript in vascular tissues. *PtCENL-1* express stronger than *PtMFT*. Transcripts of *PtMFT* is chiefly seen in inflorescence buds while a *PtCENL-1* transcript is chiefly detected in vegetative buds [48]. In one study in Maloid family include Japanese pear, European pear, apple, quince Loquat, Chinese quince, all species examined, *TFL1* homologues have been shown that transcribed mainly in buds [51]. Both *TFL1* homologues, *TFL1-1* and *TFL1-2*, have been

expressed at high levels in buds before floral differentiation and their expression seemed to decrease after floral differentiation. Species-specific patterns of organ-specific expression are also observed, e.g. the presence of *MdTFL1-1* transcripts in hypanthiums of apple, *MdTFL1-2* transcripts in stamens of apple and those of *PpTFL1-2* and *PcTFL1-2* in peduncles of pears. It is unclear whether *TFL1* homologues are involved in other pathways in floral organs. RT-PCR on 13 tissues in both vegetative and reproductive phases has been shown the difference in temporal expression patterns of *CsTFL1b*, *CsTFL1c12* and *CsFT* in cucumber [52]. These genes were up regulated at flowering. *CsTFL1c2*, *CsTFL1d*, *CsTFL1c1* are expressed in both vegetative and reproductive. CsTFL1a is seen in ovary, flowering bud, cotyledon, stem, tendril, shoot apex.*CsTFL1b* is expressed in cotyledon, stem, root and shoot apex and *CsFT* has been detected in stigma, ovary, anther, sepal, petal, leaf, root and shoot apex of cucumber. In Cotton, *TFL1a* and *TFL1b* have a little different expression patterns. The *GaTFL1a* and *GhTFL1a* transcript is preferentially expressed in leaf, root and SAM, but absent in all the other tissues examined while expression of *GaTFL1b* and *GhTFL1b* is present primarily in root and secondary in SAM, leaf and flower [53]. In Pepper, it has been shown that higher levels of the *Casp* transcript accumulate in floral buds than in other organs [54]. This kind of expression pattern is similar to that displayed by *CaSP* ortholog genes expression, namely, *SP* of tomato and *TFL1* of Arabidopsis.

Function: *TERMINAL FLOWER 1* (*TFL1*) is significant gene influences phase development and inflorescence architecture in Arabidopsis [12, 17]. This gene regulates the onset of flowering in Arabidopsis .*TFL1* is consider as a meristem identity gene and cause down regulating of *LFY* and *AP1*; the two floral meristem identity genes; and prevents their expression of in shoot apical meristem. *TFL1* has responsibility in inflorescence meristem identity as well as in floral initiation control as a repressor of flowering. It is anticipated that these two separate roles are in fact one, with *TFL1* controlling the length of both the vegetative and reproductive phases [13].*TFL1* encode a protein has a opposite effect with protein encode with *FT* [22]. *AtTFL1* promote flowering while *AtFT* inhibit flowering [55], *FT* endorses flowering development by acting on *LFY* and *AP1*; two floral meristem identity genes; whereas *AtTFL*1 repress their expression [22; 23]. As *TSF* and *FT* regulate in the same way under photoperiod condition, it suggests some abundance in their role for flowering endorsement [56]. *FT* has an interface with FD; b ZIP transcription factor. This causes activation of floral identity genes like *APETALA1* (*AP1*) in the SAM to begin development of flowering [57, 58]. In order to create flowers, *FT* also up regulate expression of *LFY* in the shoot apex. Consequently flowering will be promoted under long days [57-59]. Although *MFT* is a floral inducer but it works extremely with *FT* in Arabidopsis [26]. *AtTSF* has been shown to functions redundantly with *AtFT* to endorse flowering. It proposes *AtTSF* may be required in short-day condition. Although *ATC* can functionally alternative for *TFL1*, but that these genes have different responsibility in vivo. Since loss-of-function mutants of *ATC* show no flowering phenotypes whereas it's over expression have parallel effects as *TFL1* over expression, It suggests that *ATC* could be functionally redundant with *TFL1* [33]. *TSF*, the closest homolog of *FT*, also look as if to act as integrator of flowering time pathways and seems to promote flowering redundantly with *FT* [60, 56]. *MFT* as well as *FT* and *TSF* could also have a redundant function in flowering promotion [26]. As yet nothing is known about the role of the Arabidopsis *BFT* gene or its putative orthologs in other species. It has been shown that *tfl1* accelerate loss of ad axial trichomes in Arabidopsis [61] and the expression of a *TFL1*-like gene in Arabidopsis prevents the loss of adaxial trichomes. Hence, In Arabidopsis, vanishing of the trichomes from the ad axial surface of cauline leaves has been shown to be closely correlated to floral induction. *tfl* mutant in Arabidopsis converts the apical shoot meristem and axillary shoot meristem to floral meristem [1]. For the moment ectopically expression of *LFY* and *AP1* also occurs [18]. *tfl1* mutants cause a terminal flower formation in Arabidopsis and flowering earlier than the wild type. As a result it leads to decreasing in vegetative phase [12]. Over expression of *TFL1* keep plant onto vegetative state thus develops vegetative growth stage in Arabidopsis. Hence, Delaying in shift to flowering and making structure look like shoot in place of inflorescence and creating of a terminal flower is caused with over expression of TFL1. Expanded vegetative phase cause larger plant and massively branched inflorescences [11, 12].over expression of *FLOWERING LOCUS (FT)*; another *TFL1* family repress activity of *TFL1*. However *mft* mutant show normal flowering time. Over expression of *MFT,* although is not sufficient to form terminal flowers but show early flowering in Arabidopsis. Loss-of-function of *ATC* does not cause tfl1-like phenotypes. And over expression of *ATC* shows similar phenotypes to those illustrated for

over expression of *TFL1*.Overexpression of *TWIN SISTER OF FT* (*TSF*), has been revealed move ahead early flowering whereas over expression of *ATC* has a opposite effect [23, 33].It has been detected that over expression of *TFL1*and *ATC* delay flowering while inversely over expression of *MFT* and *TSF* progress early flowering [23,33,26,56]. Ectopically over expressing of *TFL1*homologs from other plants demonstrates phenotypes similar to observed in the 35S::*TFL1* transgenic *Arabidopsis*. Crystallography analysis has shown that CEN may be having interaction with a kinase [19]. AmCEN protein as well as AtTFL1 function in delaying flowering and is in charge of maintain indeterminancy of inflorescence meristem. *CEN* is involved in inflorescence architecture in snapdragon and has interacts with the floral-meristem-identity gene to regulate flower position and morphology [11].The centroradialis mutation leads to the conversion of the indeterminate inflorescence of Antirrhinum to terminal flowering formation. Ectopically expression of *TFL1* homolog in *Brassica.naapus* has an effect on inflorescence development. Ectopically expressed *CsTFL* in Arabidopsis lead to late flowering phenotypes and its severity linked with amount of *CSTFL* transcripts. It has been shown 35: *CsTFL* transgene can complement *tfl1-2* mutant [35, 62]. *MdTFL1* has a role in the maintenance of the vegetative phase in apple and it functions analogously to *TFL1*. Over expression of *MdTFL1* in Transgenic Arabidopsis shows maintenance of inflorescence meristem, delayed flowering and morphological change as have been observed in 35S::*TFL1* transformants. It has also been detected that *MdTFL1* is responsible for vegetative phase maintenance and functionally is analog to*TFL1* [37]. MdTFL1 transgene delays Arabidopsis flowering. *PsTFL1*a has constant role in indeterminacy maintenance of apical meristem during flowering in Pea [41]. *VvTFLA1A, VvTFLB1* and *VvTFLC1* are tree *TFL1* homolog in grapevine associate with vegetative development and maintaining of meristem indeterminancy in grapevine. VvFT and VvMFT are involved in flowering promotion; while VvTFL1A, VvTFL1Bnd VvTFL1C could be correlate with vegetative development and maintenance of meristem indetermination [42, 43]. When *VvFT* over expressed in transgenic Arabidopsis plants it makes early flowering phenotypes as those produced by *FT*. It supports a role for this gene in flowering promotion. It has been reported over expression of *VvTFL1A* does not influence flowering time but affects on determination of flower meristems, strongly altering inflorescence structure. *VvFT* and *VvTFL1A* can be orthologs of Arabidopsis *FT* and *TFL1* respectively. Arabidopsis with over expressing *VvFT* flower significantly earlier than wild type plants .They show a reduction in their flowering time of up to one week and flower with approximately half the number of leaves than the wild type plants, showing a significant reduction in leaf number both in rosettes and inflorescences. Leaves of transgenic plants were generally narrower and smaller than wild type leaves and displayed a curled phenotype. Furthermore, plants from the earliest 35S::VvFT415 transgenic line often show the development of terminal flowers resulting from the differentiation of inflorescence meristems as flower meristems .Arabidopsis ectopically expressing *VvTFL1A* are significantly delayed in flowering time with respect to wild type plants. But just a few one has been showed a significant increase in the total number of leaves, as a consequence of a significant higher number of inflorescence leaves. Thus, the delay in flowering time could be more related to an increase in the plastochron length than to the production of additional leaves. It has been seen, in transgenic plants, over expression of *VvTFL1A* cases a reduction of apical dominance promoting the growth of lateral inflorescences from rosette leaves axillary meristems [42, 43]. Tomato has similar architectures like tobacco, producing terminal structures and making further shoot growth through lower axillary meristems. In wild-type tomato, the shoot meristem has a vegetative stage that terminates with the formation of an inflorescence. A new axis of growth expands from an axillary meristem and creates three leaves before again terminating in an inflorescence. This process repeats itself indefinitely and represents a sympodial growth pattern. The role of the *SP* gene in tomato correlated to regulation of the cycle of vegetative and reproductive growth inherent in the sympodial system. Over expression of the *SP* as same as ectopic over expression *CEN* in tomato cause 'indeterminate' phenotype, means the replacement of flowers by leaves in the inflorescence. It also represses the transition of the vegetative apex to a reproductive shoot that result in an extended vegetative phase of sympodial shoots [47]. Over expression of *CET* gene suppresses flowering and extends vegetative stages in tobacco. It has been although seen over expression of *CEN* in tobacco does not delay flowering by directly changing the expression of *NFL*. But by extending the vegetative phase, the 35S–*CEN* transgene delay the down regulation of *CET2* and *CET4* in axillary meristems. Furthermore over expression of *TFL1* does not considerably delay flowering time in tobacco [48].

As there is no relations between *IbTFL1* and floral identity genes in main apical meristem, hence induction of flowering carry out with different way require constant amount of leaf-drived signal. *IbTFL1* is not required for maintaining the terminal meristem and prevention of terminal flowering. *IbTFL1* participate in specifying the phase and identity of axillary meristems. *IbAG* is able to specify the identity of floral determinacy and floral organs in Arabidopsis but is not able to specify floral determinacy in Impatiens [50]. Similar to *TFL1*, *IbTFL1* can control both the transition from the vegetative to the inflorescence phase and the transition from the inflorescence phase to flowering. It has been shown that *IbTFL1* is involved in the maintenance of the inflorescence state of axillary shoot meristems and axillary inflorescences; it is not expressed in later developing inflorescences or in meristems which are developing as flowers. *IbTFL1* is not, however, involved in the conservation of the apical meristem of the determinate line in non-inductive conditions, or in the avoidance of terminal flowering in the indeterminate line. Ectopic expression of *IbTFL1* shows a delay in bolting and the conversion of floral meristems into inflorescence-like structures. The phenotypes of plants over expressing *IbTFL1* and *IbAG* are similar to over expressing of *ATC* which is able to complement the *tfl1* mutant phenotype [33] and another closely related genes like STK and SHP1/2 [63]. In Arabidopsis, flower to inflorescence reversion has detected that involves the ectopic expression of shoot meristem identity genes including *TFL1* and a *CEN* homologue [64, 65]. But In Impatiens, *IbTFL1* is not involved in specifying indeterminacy in the terminal meristem, so processes leading to reversion may are different. In the Arabidopsis inflorescence *TFL1* is up regulated prior to *LFY* in order to prevent *LFY* from specifying the terminal apex as floral [13, 3]. In the Impatiens, *IbLFY* has been observed in the apex during both vegetative and floral development [58]. It is expressed in the developing primordia but not in the centre of the meristem and is not up regulated in flowering conditions. Regarding *IbTFL1* no expression has been detected in the apex. The level and/or position of *IbLFY* expression are therefore not enough to specify these meristems as floral even in the absence of *IbTFL1*. This lack of ability of *IbLFY* to specify the terminal meristem as floral may describe why *IbTFL1* is not necessary for the avoidance of terminal flowering. The expression of *IbTFL1* is parallel to the pattern of expression have been observed for the tobacco CEN-like genes *CET2* and *CET4* [48]. In both plants expression is linked with early development of axillary meristems intended to form inflorescences. Although *CET2* and *CET4* are not expressed in the terminal meristem, but like the determinate Impatiens line, tobacco develops a terminal flower. The expression pattern of *IbTFL1* shows more similarity to *TFL1*, *CEN* and *CET1/2*. Similar to *IbLFY*, tobacco *NFL* is expressed in the terminal meristem during vegetative and floral development [66, 67]. Tobacco, however, has not been reported to revert to leaf production, which may be a reflection of its day-neutral character, where floral signals are not dependent on day length. Terminal flowering in Impatiens has been suggested that is not controlled by direct up regulation of *IbLFY* and its antagonism with *IbTFL1*. This explains the quantitative requirement for the leaf-derived floral signal. There is no interaction between *IbLFY* and *IbTFL1* in the main apex but there is a requirement for the induction of flowering by a different, quantitative pathway, which requires a constant supply of leaf-derived signal. The deletion of this signal leads to a reversion to leaf production. Also pattern of ovule initiation requires that *IbAG* expression does not specify the floral meristem as determinate; it means the control of floral determinacy in Impatiens must be downstream of ovule production and involve a factor that is properly regulated in the zygomorphic axillary flowers but not properly regulated by the quantitative pathway controlling the terminal inflorescence. Three *PsTFL1* genes present different Patterns of expression. *DET* similar to *CEN* [11] is express only after the floral transition, whereas *TFL1* also is expressed during the vegetative phase [12]. *TFL1* antagonizes *LFY* in Arabidopsis, as does *CEN* with *FLORICAULA* in snapdragon. Double mutants (*tfl1 lfy* or *cen flo*) have an *lfy* or *flo* phenotype, respectively [11, 12]. The same interaction pattern is detected in pea between *DET* and *UNIFOLIATA*, the *LFY* ortholog. The double mutant *det uni* has a *uni* phenotype [68]. Two *TFL1* homologs in pea have two separate functions: *LF* is involved in the control of the vegetative phase by delaying the transition from the vegetative to the I1 inflorescence meristemit cause delaying in floral initiation, hence and *DET* is responsible to control the floral phase by preventing the transition from the I1 inflorescence meristem to the flower. This type of regulation is not same as in Arabidopsis, in which only one *TFL1* gene controls the length of both the vegetative and floral phases. Similar to *DET*, *CEN* also has only one function during the vegetative phase in snapdragon [11]. As a result, pea and Arabidopsis have different strategies to control flowering time, which may symbolize dissimilar strategies to answer

to environmental conditions. In Arabidopsis, variation in flowering time is described principally by response to vernalization, while in pea it appears it mostly correlated with photo period. In both cases, the transcript level of the repressor, *FLC* or *LF*, determines flowering time. Like that what is seen about *TFL1* and *FT* in Arabidopsis, *PtCENL-1*and *PtMFT* have antagonistic role in flowering regulation in poplar. *PtCENL-1* aids to delay flowering and extend bud dormancy in poplar trees. Since over expression and suppression of *PtMFT* have been showed no effect on flowering development, it is possible that *PtCENL-1*, but not *PtMFT* could advance and perhaps postpone flowering and alter time of post-domancy bud flushing in poplar. It has been detected that in transgenic poplar, flower formation under long photoperiod is induced when suppress *PtCENL-1* activity. Although over expression of the *PtCENL-1* lead to delay in shoot emergence bud flushing. But over expression and suppression of *PtMFT* has no effect on flowering development [69].Data have observed from some Maloid species including loquat, European pear, apple, quince, Chinese quince and Japanese pear could support the idea that *TFL1* homologues play a significant role in floral differentiation. By comparing the coding sequences of determinate and indeterminate pepper, it has been detected a single nucleotide (C) insertion in the first exon of *CaSP* cDNA [54]. The mutation has been occurred in 151 bp downstream from the ATG start codon and lead to a non-functional CaSP protein. Thus it has been suppose that the determinate form of pepper is the result of the insertion of a single C nucleotide in the coding region of *CaSP*. *CaSP* over expression in tobacco displays late-flowering phenotypes similar to the phenotypes have been shown by over expression of its orthologs in other plants. It has suggested that pepper *CaSP* is an ortholog of *SP* in tomato. *sp* mutant in tomato has shown that fewer nodes forms on its stem before terminal flower formation and indeterminate flowers alter to determinate flowers on the branches of plant. Inactivation of *SP* either by mutation or the suppression by antisense RNA has been found results in the premature switch of the sympodial vegetative apex into a terminal determinate inflorescence shoot but has neither influence on the architecture of the inflorescence itself nor on the morphology of the flowers [47].

DISCUSSION

In both Antirrhinum and Arabidopsis whose inflorescences are indeterminate, *CEN/TFL1* delays up-regulation of floral meristem identity genes by retarding phase development. They are expressed at high levels in the inflorescence apex [11, 12] and they can prevent a response to even high-level expression of *LEAFY* and *AP1* [3]. However, studies have shown that *Arabidopsis TFL1* and *Antirrhinum CEN* are not closely related [46]. *CEN* is induced during floral initiation [11], whereas *TFL1* expression also is found during the vegetative phase; this expression could explain the role of *TFL1* in delaying flowering in Arabidopsis [12]. Mutations in either TFL1 or CEN show the production of an inflorescence with a terminal abnormal flower, while wild-type plants normally develop an "indeterminate" inflorescence without terminal differentiation [24, 11, 36, 70, 71]. Although indeterminate inflorescences converts to determinate flowers in *tfl1* and *cen* mutant plants, but *tfl1*mutants in Arabidopsis have a terminal flower and flowers earlier than the wild type [12]. Moreover early-flowering phenotype is not observed in snapdragon. In contrast with similarity in sequence between *TFL/CEN* homolog family, they are different in function, even some of them have opposite function .Like *Arabidopsis* in which two kind of *TFL1* family with opposite function can be seen;*TFL1* with role in suppressing flowering and *FT* with promotion of flowering; in some another species *FT* homolog have been detected, for example in Citrus [72], apple trees [37] and grapevine one *FT* related gene has been detected, while duplication and divergence of this sequence has been observed in other families such as Brassicaceae [23], Solanaceae [40,73] or Salicaceae [74] and Populus [69]. However in some specious homolog with *FT* role like is absent. Similarity in expression pattern and function with *AtTFL1* gene can be observed in another species too. Most of homolog shows a conservation of the amino acid residues and regions distinctive of this subfamily and vital for their function. transgenic Arabidopsis plants over expressed them nearly show similar symptoms but results have been suggested that functional variance of the roles in phase transition may have happened between *TFL1* homolog throughout evolution in dicots as well as monocot. Another considerable issue is that difference in residue at some position in *TFL1* homolog could be in some measure responsible for the variety in the severity of their phenotypes.

However different in size but most TFL1- like genes in dicot and monocot species such as ryegrass, *Arabidopsis thaliana*, *Brassica.naapus*, Cucumber, grapevine, *Lotus japonicus*, *Lycopersicon esculentum*, *Nicotiana tabacum,* rice, *Impatiens balsamina* poplar, apple, Vitis and cotton present the same four exon, three

intron organization. Exception for this pattern of exone and intron is found in Cucumber *CsTFL1c1* and *CsTFL1c2* genes with 3 and 2 exone and intron respectively. The location where *TFL1* like genes expressed in species is not completely same. In addition to *Arabidopsis,* in some another species *TFL1* like gene express only or preferably in vegetative tissue; for example; apple, grapevine, tobacco, poplus Japanese pear, european pear, apple, quince, Loquat, Chinese quince. Expression of some *TFL1* like genes in vegetative tissue and before flowering , can be consider as sign of systematic mechanisms to inhibit floral promotive signaling resulting to inhibit precocious flowering before appropriate flowering time. In addition to vegetative tissue, in some species, these homologies can be seen in another part of plant as well. In Antirrhinum, in addition to the apical meristem, CEN mRNA is found in other tissues too [11; 15, 26]. In tomato *SP* expression is found throughout development in all the primordial organs [47]. *RCN2* in rice, *LpTFL1* in ryegrass and *PsTFL1* genes in pea are expressed in both vegetative and reproductive tissues [75, 36, 38, 15, 26]. The L. perenne and Brassica *TFL* like genes are expressed in a variety of vegetative tissues in addition to floral organs [36, 38]. In contrast with two mentioned expression pattern, in some plants these homolog just find in floral organs. For example *CsTFL1* is not found in adult vegetative part of plant, such as leaf, stem and root and seed but they were detectable in all floral organs of citrus. [35]. In term of responsibility of *TFL1* like gene(s) in phase transition we can grouped species to three categories: first group include species only one homolog of *TFL1* is involved in flowering control; *Antirrinum,* citrus, *Lotus.*japonicus, tomato, Capsicum. Annuum and *Beta palonga* are species in which one *TFL1* control phase transition. In second group more than one homolog functions for example in *Arabidopsis* besides of *TFL1* that inhibit flowering, *ATC* also has redundant function in with *TFL1*.in contrast, another homolog like *FT* chiefly ,and *MFT*, *TSF* redundantly with *FT*, together promote flowering. This cooperation of two or more *TFL1* homolog to be responsible in flowering control can be seen in *Brassica.naapus*, Cucumber, apple, pea, grapevine, tobacco, populus, maloid species and *cotton*. However it needs to be clear that in certain species with more than one *TFL1* homolog how many of them is responsible in phase control. It means only one of them is effective or they share together in function. In Arabidopsis, only the *TFL1* gene controls the length of both vegetative and floral phases [60]. Differently, in pea, two *TFL1/CEN*-like genes shared the functions: LATE FLOWERING (LF, also named PsTFL1c) is involved in the control of the vegetative phase by delaying the transition from the vegetative to the I_1 inflorescence meristem and *DETERMINATE* (*DET*, also named *PsTFL1a*) is involved in the control of the floral phase by preventing the transition from the I_1 inflorescence meristem to the flower. However, it is still a question whether four copies of *Oscen* genes in the rice genome are all needed in the processes. Last one group include species have homolog of TFL1 but they are not in charge of phase transition, or act different of TFL1 function. Differently, despite of similarity in sequence with *TFL1* family, some genes has not any role in flowering development; example for this case is *Impatiens balsamina.* There is no interaction between *IbLFY* and *IbTFL1* in the main apex but there is a requirement for the induction of flowering by a different, quantitative pathway, which requires a constant supply of leaf-derived signal. The deletion of this signal leads to a reversion to leaf production. In indeterminate species floral meristem identity genes not to be expressed in the shoot apical meristem but are restricted to primordia or meristems arising from the periphery. But in many determinate species, such as tobacco, tomato, petunia and Impatiens balsimina, there are *FLO*- and *LFY*-like genes that are expressed powerfully in the shoot apical meristem from very early in development [66, 47, 67, 76]. In Antirrhinum, Arabidopsis and tobacco, the production of flowers or shoots most likely depends on the relative expression patterns of *TFL1/CEN*-like genes and floral meristem identity genes such as *LFY*and *AP1* [48,3]. With agreement to this the seasonal expression level of *MdTFL1* in apple apices appears to be complementary to that of *AFL1*, which progressively increases during flower development. Hence, the induction of flowering may also correlated with relative expression of *MdTFL1* and *AFL1* in apple. Previous study has shown that *LFY* and *AP1* repress the expression of *TFL1* in Arabidopsis [3]. Hence, in species such as tobacco, *TFL1*-like gene activity may be repressed in the apical meristem, causing production of terminal flowers rather than shoots. As a result there is a model for Arabidopsis, Antirrhinum and tobacco in which the production of shoots or flowers depends on the relative expression patterns of *TFL1*-like genes and floral meristem identity genes. However, unlike in Antirrhinum and Arabidopsis, in wild-type tomato, *SP* expression occurs in all meristems, overlapping with the expression of floral meristem identity genes. Therefore this expression patterns give no sign as to how the activities of these two groups of genes might be separated in tomato.

REFERENCES

1. Liljegren, S.J., C. Gustafson-Brown, A. Pinyopich, G.S. Ditta and M.F. Yanofsky, 1999. Interactions among APETALA1, LEAFY and TERMINAL FLOWER1 Specify Meristem Fate. The Plant Cell Online, 11: 1007-1018.
2. Parcy, F., O. Nilsson, M.A. Busch, I. Lee and D. Weigel, 1998. A genetic framework for floral patterning. Nature, 395: 561-566.
3. Ratcliffe, O.J., 1999. Separation of shoot and floral identity in Arabidopsis. Develop., 1266: 1109-1120.
4. Bowman, J.L., J. Alvarez, D. Weigel, E.M. Meyerowitz and D.R. Smyth, 1993. Control of flower development in Arabidopsis thaliana by APETALA1 and interacting genes. Develop., 119(3): 721.
5. Gustafson-Brown, C., B. Savidge and M. F. Yanofsky, 1994. Regulation of the arabidopsis floral homeotic gene APETALA1. Cell., 76: 131-143.
6. Kempin, S.A., B. Savidge and M.F. Yanofsky, 1995. Molecular basis of the cauliflower phenotype in Arabidopsis. Sci., 267: 522-525.
7. Mandel, M.A., C. Gustafson-Brown, B. Savidge and M.F. Yanofsky, 1992. Molecular characterization of the Arabidopsis floral homeotic gene Apetalai. Nature-london, pp: 273.
8. Mandel, M.A. and M.F. Yanofsky, 1995. A gene triggering flower formation in Arabidopsis. Nature, 377: 522-524.
9. Weigel, D., J. Alvarez, D.R. Smyth, M.F. Yanofsky and E.M. Meyerowitz, 1992. LEAFY controls floral meristem identity in Arabidopsis. Cell, 69: 843-859.
10. Weigel, D. and O. Nilsson, 1995. A developmental switch sufficient for flower initiation in diverse plants. Nature, 377: 495-500.
11. Bradley, D., R. Carpenter, L. Copsey, C. Vincent, S. Rothstein and E. Coen, 1996. Control of inflorescence architecture in Antirrhinum. Nature, 379: 791-797.
12. Bradley, D., O. Ratcliffe, C. Vincent, R. Carpenter and E. Coen, 1997. Inflorescence Commitment and Architecture in Arabidopsis. Sci., 275: 80.
13. Ratcliffe, O.J., 1998. A common mechanism controls the life cycle and architecture of plants. Develop., 1259: 1609-1615.
14. Weberling, F., R.J. Pankhurst and R.J. Pankhurst, 1989. Morphology of flowers and inflorescences. Cambridge University Press .
15. Ohshima, S., M. Murata, W. Sakamoto, Y. Ogura and F. Motoyoshi, 1997. Cloning and molecular analysis of the Arabidopsis gene Terminal Flower 1. Mol. Gen. Genet, 254: 186-194.
16. Yeung, K. T. Seitz, S. Li, P. Janosch, B. McFerran and C. Kaiser, 1999. Suppression of Raf-1 kinase activity and MAP kinase signalling by RKIP. Nature, 401: 173-177.
17. Ruiz-Garcia, L., F. Madueno, M. Wilkinson, G. Haughn, J. Salinas and J.M. Martinez-Zapater, 1997. Different roles of flowering-time genes in the activation of floral initiation genes in Arabidopsis. The Plant Cell Online, 9(11): 1921..
18. Eiro, M. and G. Coupland, 1998. The Control of Flowering Time and Floral Identity in Arabidopsis. Plant Physiology 117(1): 1-8. Am. Soc. Plant. Biol.,
19. Banfield, M.J. and R.L. Brady, 2000. The structure of Antirrhinum centroradialis protein (CEN) suggests a role as a kinase regulator. J. Molecular Biol., 297: 1159-1170.
20. Hsu, C.Y., Y. Liu, D.S. Luthe and C. Yuceer, 2006. Poplar FT2 shortens the juvenile phase and promotes seasonal flowering. The Plant Cell Online, 18: 1846.
21. Ahn, J.H., D. Miller, V.J. Winter, M.J. Banfield, J.H. Lee and S.Y. Yoo, 2006. A divergent external loop confers antagonistic activity on floral regulators FT and TFL1. The EMBO J., 25(3): 605-614.
22. Kardailsky, I., V.K. Shukla, J.H. Ahn, N. Dagenais, S.K. Christensen and J.T. Nguyen, 1999. Activation Tagging of the Floral Inducer FT. Sci., 286: 1962.
23. Kobayashi, Y., H. Kaya, K. Goto, M. Iwabuchi and T. Araki, 1999. A Pair of Related Genes with Antagonistic Roles in Mediating Flowering Signals. Sci., 286: 1960.
24. Alvarez, J., C.L. Guli, X.H. Yu and D.R. Smyth, 1992. Terminal flower: a gene affecting inflorescence development in Arabidopsis thaliana. The Plant J., 2: 103-116.
25. Schultz, E.A., 1993. Genetic analysis of the floral initiation process (FLIP) in Arabidopsis. Development, 119(3): 745-765.
26. SoYeon, Y., I. Kardailsky, L. JongSeob, D. Weigel and A. JiHoon, 2004. Acceleration of flowering by overexpression of MFT (MOTHER OF FT AND TFL1). Molecules and Cells, 17: 95-101.
27. Bucquoy, S., P. Jolles and F. Schoentgen, 1994. Relationships between molecular interactions (nucleotides, lipids and proteins) and structural features of the bovine brain 21-kDa protein. European J. Biochemistry, 225: 1203-1210.

28. Grandy, D.K., E. Hanneman, J. Bunzow, M. Shih, C.A. Machida and J.M. Bidlack, 1990. Purification, cloning and tissue distribution of a 23-kDa rat protein isolated by morphine affinity chromatography. Mol. Endocrinol., 4: 1370-1376.
29. Corbit, K.C., N. Trakul, E.M. Eves, B. Diaz, M. Marshall and M.R. Rosner, 2003. Activation of Raf-1 signaling by protein kinase C through a mechanism involving Raf kinase inhibitory protein. J. Biological Chemistry, 278: 13061-13068.
30. Banfield, M.J., J.J. Barker, A.C.F. Perry and R.L. Brady, 1998. Function from structure? The crystal structure of human phosphatidylethanolamine -binding protein suggests a role in membrane signal transduction. Structure, 6: 1245-1254.
31. Kroslak, T., T. Koch, E. Kahl and V. Hollt, 2001. Human phosphatidylethanolamine-binding protein facilitates heterotrimeric G protein-dependent signaling. J. Biological Chemistry, 276: 39772-39778.
32. Serre, L., B. Vallqe, N. Bureaud, F. Schoentgen and C. Zelwer, 1998. Crystal structure of the phosphatidylethanolamine-binding protein from bovine brain: a novel structural class of phospholipid-binding proteins. Structure, 6: 1255-1265.
33. Mimida, N., K. Goto, Y. Kobayashi, T. Araki, J.H. Ahn and D. Weigel, 2001. Functional divergence of the TFL1-like gene family in Arabidopsis revealed by characterization of a novel homologue. Genes to Cells, 6: 327-336.
34. Mimida, N., W. Sakamoto, M. Murata and F. Motoyoshi, 1999. TERMINAL FLOWER 1-like genes in Brassica species. Plant Sci., 142(2): 155-162.
35. Lynn, J.P., J.L. Carol and L.W. Linda, 2004. Isolation and Characterization of a TERMINAL FLOWER Homolog and Its Correlation with Juvenility in Citrus. Plant Physiol., 135: 1540.
36. Jensen, C.S., K. Salchert and K.K. Nielsen, 2001. A Terminal Flower1-Like Gene from Perennial Ryegrass Involved in Floral Transition and Axillary Meristem Identity. Plant Physiol., 125: 1517-1528.
37. Kotoda, N. and M. Wada, 2005. MdTFL1, a TFL1-like gene of apple, retards the transition from the vegetative to reproductive phase in transgenic Arabidopsis. Plant Sci., 168: 95-104.
38. Nakagawa, M. K. Shimamoto and J. Kyozuka, 2002. Overexpression of RCN1 and RCN2, rice Terminal Flower 1/centroradialis homologs, confers delay of phase transition and altered panicle morphology in rice. The Plant J., 29: 743-750.
39. Kotoda, N.M. Wada, H. Kato, H. Iwanami, T. Masuda and J. Soejima, 2001. The function analysis of MdMADS5 and MdTFL, apple homologues of Apetala1 and Terminal Flower1, in transgenic Arabidopsis. Hortscience, 36: 441.
40. Carmel-Goren, L., Y.S. Liu, E. Lifschitz and D. Zamir, 2003. The SELF-PRUNING gene family in tomato. Plant Molecular Biol., 52: 1215-1222.
41. Fabrice, F., Julie, M. Juliette Court and C. Sandrine, 2003. Determinate and Late Flowering Are Two Terminal Flower1/centroradialis Homologs That Control Two Distinct Phases of Flowering Initiation and Development in Pea. The Plant. Cell, 15: 2742.
42. Carmona, M.J., M. Calonje and J.M. Martinez-Zapater, 2007a. The FT/TFL1 gene family in grapevine. Plant Molecular Biol., 63: 637-650.
43. Carmona, M.J., P. Cubas, M. Calonje and J.M. Martinez-Zapater, 2007b. Flowering transition in grapevine (Vitis vinifera L.). Canadian J. Botany, 85: 701.
44. Boss, P.K., L. Sreekantan and M.R. Thomas, 2006. A grapevine TFL1 homologue can delay flowering and alter floral development when overexpressed in heterologous species. Functional Plant Biol., 33(1): 31
45. Carmona, M.J., P. Cubas and J.M. Martinez-Zapater, 2002. VFL, the grapevine FLORICAULA/LEAFY ortholog, is expressed in meristematic regions independently of their fate. Plant Physiol., 130: 68-77.
46. Guo, X., Z. Zhao, J. Chen, X. Hu and D. Luo, 2006. A putative Centroradialis/terminal Flower 1-like gene, Ljcen1, plays a role in phase transition in Lotus japonicus. J. Plant Physiol., 163: 436-444.
47. Pnueli, L., 1998. The Self-pruning gene of tomato regulates vegetative to reproductive switching of sympodial meristems and is the ortholog of CEN and TFL1. Development, 125(11): 1979-1989.
48. Amaya, I., O.J. Ratcliffe and D.J. Bradley, 1999. Expression of Centroradialis (CEN) and CEN-like genes in tobacco reveals a conserved mechanism controlling phase change in diverse species. The Plant Cell Online, 11(8): 1405.

49. Shannon, S. and D.R. Meeks-Wagner, 1993. Genetic interactions that regulate inflorescence development in Arabidopsis. The Plant. Cell. Online, 5: 639-655.
50. Ordidge, M., T. Chiurugwi, F. Tooke and N. H. Battey, 2005. Leafy, Terminal Flower1 and Agamous are functionally conserved but do not regulate terminal flowering and floral determinacy in Impatiens balsamina. The Plant. J., 44: 985-1000.
51. Esumi, T., R. Tao and K. Yonemori, 2005. Isolation of Leafy and Terminal Flower 1 Homologues from six fruit tree species in the subfamily Maloideae of the Rosaceae. Sexual Plant Reproduction, 17: 277-287.
52. Sato, H., D. Heang, H. Sassa and T. Koba, 2009. Identification and characterization of FT/TFL1 gene family in cucumber. Breeding Sci., 59(1): 3-11.
53. Argiriou, A., G. Michailidis and A.S. Tsaftaris, 2008. Characterization and expression analysis of Terminal Flower1 homologs from cultivated alloteraploid cotton (Gossypium hirsutum) and its diploid progenitors. J. Plant Physiol., 165(15): 1636-1646.
54. Kim, D.H., M.S. Han, H.W. Cho, Y.D. Jo, M.C. Cho and B. Kim, 2006. Molecular cloning of a pepper gene that is homologous to Self-pruning. Molecules and Cells, 22(1): 89.
55. Hanzawa, Y., T. Money and D. Bradley, 2005. A single amino acid converts a repressor to an activator of flowering. Proceedings of the National Academy of Sci., 102: 7748-7753.
56. Yamaguchi, A., 2005. Twin Sister of ft (TSF) Acts as a Floral Pathway Integrator Redundantly with FT. Plant and Cell Physiol., 46(8): 1175-1189.
57. Abe, M., Y. Kobayashi, S. Yamamoto, Y. Daimon, A. Yamaguchi and Y. Ikeda, 2005. FD, a bZIP protein mediating signals from the floral pathway integrator FT at the shoot apex. Sci., 309(5737): 1052
58. Wigge, P.A., M.C. Kim, K.E. Jaeger, W. Busch, M. Schmid and J.U. Lohmann, 2005. Integration of Spatial and Temporal Information during Floral Induction in Arabidopsis. Sci., 309: 1056-1059.
59. Huang, T., H. Bohlenius, S. Eriksson, F. Parcy and O. Nilsson, 2005. The mRNA of the Arabidopsis Gene FT Moves from Leaf to Shoot Apex and Induces Flowering. Sci., 309: 1694-1696.
60. Michaels, S.D., E. Himelblau, S.Y. Kim, F.M. Schomburg and R.M. Amasino, 2005. Integration of Flowering Signals in Winter-Annual Arabidopsis 1. Plant Physiol., 137: 149-156.
61. Telfer, A., 1997. Phase change and the regulation of trichome distribution in Arabidopsis thaliana. Development, 124(3): 645-654.
62. Naozumi Mimida, W.S. M.M.F.M., 1999. Terminal Flower 1 -like genes in Brassica species. Plant Sci., 142: 155-162.
63. Favaro, R., A. Pinyopich, R. Battaglia, M. Kooiker, L. Borghi and G. Ditta, 2003. MADS-box protein complexes control carpel and ovule development in Arabidopsis. The Plant Cell, 15: 2603.
64. Okamuro, J.K., 1996. Flowers into shoots: photo and hormonal control of a meristem identity switch in Arabidopsis. Proceedings of the National Academy of Sciences National Acad Sci., 93(24): 13831-13836.
65. Parcy, F., K. Bomblies and D. Weigel, 2002. Interaction of Leafy, Agamous and Terminal Flower1 in maintaining floral meristem identity in Arabidopsis. Development, 129: 2519-2527.
66. Kelly, A.J., M.B. Bonnlander and D.R. Meeks-Wagner, 1995. NFL, the tobacco homolog of Floricaula and Leafy, is transcriptionally expressed in both vegetative and floral meristems. The Plant. Cell. Online, 7: 225-234.
67. Pouteau, S., 1997. The induction and maintenance of flowering in Impatiens. Development, 124(17): 3343-3351.
68. Singer, S., J. Sollinger, S. Maki, J. Fishbach, B. Short and C. Reinke, 1999. Inflorescence architecture: a developmental genetics approach. The Botanical Rev., 65: 385-410.
69. Mohamed, R., 2006. Expression and Function of Populus Homologs to Terminal Flower I Genes: Roles in Onset of Flowering and Shoot Phenology.Ph.D thesis. University Putra Malaysia.
70. Pillitteri, L.J., C.J. Lovatt and L.L. Walling, 2004. Isolation and characterization of a Terminal Flower homolog and its correlation with juvenility in citrus. Plant Physiol., 135: 1540-1551.
71. Shannon, S. and D.R. Meeks-Wagner, 1991. A Mutation in the Arabidopsis TFL1 Gene Affects Inflorescence Meristem Development. The Plant. Cell. Online, 3: 877-892.
72. Endo, T., T. Shimada, H. Fujii, Y. Kobayashi, T. Araki and M. Omura, 2005. Ectopic expression of an FT homolog from Citrus confers an early flowering phenotype on trifoliate orange (*Poncirus trifoliata* L. Raf.). Transgenic Res., 14: 703-712.

73. Lifschitz, E. and Y. Eshed, 2006. Universal florigenic signals triggered by FT homologues regulate growth and flowering cycles in perennial day-neutral tomato. J. Experimental Botany, 57: 3405.
74. Brunner, A.M. and O. Nilsson, 2004. Revisiting tree maturation and floral initiation in the poplar functional genomics era. New Phytologist, pp: 43-51.
75. Foucher, F., J. Morin, J. Courtiade, S. Cadioux, N. Ellis and M.J. Banfield, 2003. Determinate and Late Flowering Are Two Terminal Flower1/centroradialis Homologs That Control Two Distinct Phases of Flowering Initiation and Development in Pea. The Plant. Cell, 15: 2742-2754.
76. Souer, E., 1998. Genetic control of branching pattern and floral identity during Petunia inflorescence development. Development, 125(4): 733-742.