https://doi.org/10.17816/ecogen16141

DETERMINATE GROWTH HABIT OF GRAIN LEGUMES: ROLE IN DOMESTICATION AND SELECTION, GENETIC CONTROL

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Cite this article as: Krylova E.A., Khlestkina E.K., Burlyaeva M.O., Vishnyakova M.A. Determinate growth habit of grain legumes: role in domestication and selection, genetic control. *Ecological genetics*. 2020;18(1):43-58. https://doi.org/10.17816/ecogen16141.

Received: *18.09.2019* Revised: *10.01.2020* Accepted: *19.03.2020*

❀ This review is devoted to the analysis of molecular genetic mechanisms of controlling the type of growth habit of grain legumes (pea, soybean, common bean, vigna); it provides information about known homologous genes *TFL1*, *LFY*, *AP1*, *FUL*, *FT*, and *FD*. Significant changes in plant architectonics were during domestication of grain legumes. Many wild relatives of legumes are characterized by an indeterminate growth habit type, cultivated plants are characterized by indeterminate and determinate types. In plants with a determinate growth habit type, terminal inflorescence is formed at transition from the vegetative phase to the reproductive phase. These plants are characterized by a complex of features: simultaneous maturation of pods, resistance to lodging, etc. In indeterminate type of growth habit, the apical shoot meristem remains active during plant life. The main genes responsible for the plant transition to flowering are the homologs of the arabidopsis genes *LFY*, *TFL1*, *AP1*. *TFL1* gene is responsible for maintenance of growth of the shoot apical meristem; its homologs were identified in pea (*PsTFL1a*), soybean (*Dt1/GmTFL1*), common bean (*PvTFL1y*), cowpea (*VuTFL1*). The identification and characterization of the genes responsible for the type of stem growth habit are necessary for the successful selection of modern varieties suitable for mechanized cultivation. Design of molecular markers that diagnose this important breeding trait at early plant development stages, will help to determine the type of stem growth habit.

❀ **Keywords:** growth habit; grain legumes; *TFL1*; pea; soybean; common bean; cowpea.

ДЕТЕРМИНАНТНЫЙ ХАРАКТЕР РОСТА ЗЕРНОБОБОВЫХ КУЛЬТУР: РОЛЬ В ДОМЕСТИКАЦИИ И СЕЛЕКЦИИ, ГЕНЕТИЧЕСКИЙ КОНТРОЛЬ

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Для цитирования: Крылова Е.А., Хлесткина Е.К., Бурляева М.О., Вишнякова М.А. Детерминантный характер роста зернобобовых культур: роль в доместикации и селекции, генетический контроль // Экологическая генетика. – 2020. – Т. 18. – № 1. – С. 43–58. https://doi.org/10.17816/ecogen16141.

Поступила: *18.09.2019* Одобрена: *10.01.2020* Принята: *19.03.2020*

❀ Настоящий обзор посвящен анализу молекулярно-генетических механизмов контроля типа роста зернобобовых культур (горох, соя, фасоль, вигна), представлены сведения об известных генах-гомологах *TFL1*, *LFY*, *AP1*, *FUL*, *FT* и *FD*. В процессе доместикации зернобобовых происходили значительные изменения в архитектонике растений. Для многих диких родичей бобовых культур характерен индетерминантный тип роста, для введенных в культуру — ин- и детерминантный. У растений с детерминантным типом роста переход из вегетативной стадии в репродуктивную происходит при формировании терминальной цветочной кисти, флоральная меристема образуется из верхушечной. Они характеризуются комплексом ценных признаков: дружным созреванием бобов, устойчивостью к полеганию и др. При индетерминантном типе роста верхушечная меристема побега сохраняет свою активность на протяжении всей жизни. Основные гены, отвечающие за переход растения к цветению, — гомологи генов арабидопсиса *LFY*, *TFL1*, *AP1*. За поддержание роста апикальной меристемы побега отвечает ген *TFL1*, гомологи которого выявлены у гороха (*PsTFL1a*), сои (*Dt1/GmTFL1*), фасоли (*PvTFL1y*) и вигны (*VuTFL1*). Идентификация и характеристика генов, отвечающих за тип роста стебля, — необходимое условие для успешной селекции современных сортов, пригодных для механизированного возделывания. В связи с этим разработка молекулярных маркеров, диагностирующих данный селекционно важный признак, поможет на ранних стадиях определить тип роста стебля.

❀ **Ключевые слова:** тип роста; зернобобовые; *TFL1*; горох; соя; фасоль; вигна.

INTRODUCTION

Grain legumes account for 27% of the world agricultural crop production and provide 33% of global protein consumption [1]. According to FAO (Food and Agriculture Organization of the United Nations) [2], worldwide production of grain legumes has increased for the last half-century by more than 1.5 times, and was amounted to 71 million tons in 2013. Grain legumes take up 13–14% of global area farming. The majority of grain legumes are multipurpose crops. Varieties with determinate growth habit are often cultivated for seeds, they have food value, while varieties with indeterminate (not terminated) growth habit are grown for livestock feed and less for food. These plants are characterized by non-synchronous pods maturity, which makes mechanical harvesting impossible and the cultivation efficiency of these varieties for seed production is decreased. Legumes with indeterminate growth more often used as silage, fodder, green fodder, and green manure.

Cultivated species differ from their wild relatives in many features – constituents of "domestication syndrome" [3]. One of the features of domestication syndrome of agricultural crops is a compact bushy shape of plant. In grain legumes, it is expressed in the reduction of branching, fewer nodes, reduced twining of the main shoot apex, and determinate growth habit which is typical for a number of legumes species [4]. The wild relatives of grain legumes are generally climbing, herbaceous plants with numerous branches and nodes. The climbing habit allows wild legumes to compete with surrounding plants for light in the shrubby or arboreal vegetation, where they grow naturally [5, 6]. Cultivated plants should have determinate growth habit which is suitable for harvesting with using primitive ancient tools or modern mechanical machinery. Plants with determinate growth habit (so is called "bush-type" in the case of the common bean and *Vigna*) are adapted for mechanical harvesting much better than climbing plants with indeterminate growth habit. Therefore determinate growth habit can be considered as one of the important traits of "domestication syndrome" of grain legumes.

An understanding of the genetic basis of the traits, which promoted domestication and distribution of grain legumes, is useful to improve the efficiency of their breeding. It is also important for broadening of species cultivation areas, as the demand for them as a source of food and feed is increasing in the Russian Federation. Additionally knowledge of "domestication genes" can be useful for more effective involvement of the wild species of secondary and tertiary gene pools in breeding.

DOMESTICATION OF GRAIN LEGUMES

Grain legumes are cultivated in moderate, subtropical, and tropical climates. The wide range of variability of morphological and economically important traits allows them to be included in different systems of arable farming all around the world. A majority of grain legumes are self-pollinating plants. Some species are cross-pollinating.

According to J. Harlan [7], members of *Fabaceae* family might have been among first domesticated crops. The main centers of crop development were connected with distribution of the main centres of human culture. Pea (*Pisum sativum* L.), faba bean (*Vicia faba* L.), lentil (*Lens culinaris* Medik.), grass pea (*Lathyrus sativus* L.), chickpea (*Cicer arietinum* L.) were the first domesticated legume crops [1]. These legumes together with cereals formed main diet of ancient civilizations in the Near East and the Mediterranean. N.I. Vavilov associated the origin of these crops with the Central Asiatic centre. He noticed the importance of this area "as a native land of all the most important grain legumes <...> that are represented by the exceptional abundance of genes" [8, p. 28]. N.I. Vavilov considered Asia Minor as a secondary centre of origin of pea and chickpea. He also assumed the Mediterranean as the secondary centre of origin for many important cultivated plants, including grain legumes [8]. He stated that "many cultivated plants of the Mediterranean, for example, flax, barley, faba bean, chickpea, are characterized with large size of grains and of pods in contrast to the small-grain forms of the Middle Asia, where is the main location of their origin and where most of dominant genes of these plants is concentrated. A big human contribution can be traced in selection of the most cultivated forms of the Mediterranean region" [8, p. 36]. Besides,

N.I. Vavilov considered Abyssinian centre as one of the foci of origin of chickpea, lentil, pea and faba bean.

Archaeological evidence dates the existence of pea back to 10,000 BC in the Near East and Central Asia. In Europe, pea has been cultivated since the Stone Age [9]. Faba bean is also historically important crop and it is ancient cultivated plant. Their remains have been found in archeological sites in northwest Syria, which have been dated back to 10 millenium BC. Large-seeded faba bean remains were found in the Mediterranean region, which it is highly likely a secondary center of their domestication [1]. Faba bean distributed to Europe from Mediterranean region. Lentil is also an ancient cultivated plant. Lentil seeds dating to the 8 and 7 millennia BC were found in the early farming settlements in the Near East [1].

The origin of soybean (*Glycine max* (L.) Merr) is associated with China. Evolution of the cultivated soybean species is closely connected with the history of ancient Chinese civilization. Soybean is mentioned in many ancient Chinese books. Namely the Chinese centre of origin considered by N.I. Vavilov as the primary focus for soybean; he indicated great variety of forms of this crop in this region [8]. Currently the precise location of soybean domestication in China is still being discussed.

The foci of origin of the common bean (*Phaseolus vulgaris* L.) are also still being discussed. N.I. Vavilov considered that the South Mexican and the Central American foci were the centers of origin of the common bean [8]. He stated that "here <...> is the native land of the main American common bean species" [8, p. 41]. He considered the South American focus as the secondary center of origin of the common bean. Currently, two geographically isolated gene pools of common bean exist: Andean and Central American. Based on data of morphological and molecular studies it was hypothesized that the domestication of the common bean was independent in the Central and South America [10]. Early archaeological remains in the caves of Ayacucho and Guerrero regions of Peru and Mexico, respectively, suggest that the domestication of common bean could have occurred as early as 10,000 years ago in the Andes and around 7,500 years ago in Central America [1]. Wild *Phaseolus* species occur from northern Mexico to northwestern Argentina [11]. Columbia is considered as an independent center of domestication [12].

The domestication of *Vigna* Savi, the most closely related genus to *Phaseolus* took place in countries of the Old World [13]. Varieties of *Vigna unguiculata* suspb. *sesquipedalis* (L.) Verdc. are the most interesting. They are characterized by high yield. N.I. Vavilov distinguished three foci of *Vigna* origin, namely Chinese, Indian, and Abyssinian [8]. The Chinese focus is considered as secondary center of the origin for asparagus bean *V. unguiculata* suspb. *sesquipedalis*.

The origin of adzuki bean (*V. angularis* (Willd.) Ohwi & Ohashi) was associated by N.I. Vavilov with the Chinese focus of origin [8]. Japan was one of the possible domestication centers of adzuki bean. Seed residues dating to 5,000 BC were found in Japan. The residues dating to 3,000 BC were found in China [14]. Discussion of the exact location of the adzuki domestication is not yet complete.

Vigna species such as mung bean (*V. radiata* (L.) R. Wilczek), black gram (*V. mungo* (L.) Hepper), and others were domesticated in the South-East Asia [1]. These species also have the long history of cultivation. N.I. Vavilov considered the Indian and Central Asian foci as the places of origin of these crops [8]. Residues of the Asian *Vigna* species dating to 3,500–3,000 BC were found in archaeological excavations in Central India [1].

Significant changes in plant architectonics and photoperiod response took place during the process of domestication and plant distribution from the centers of origin. Morphological and physiological features of seeds (size increase, loss of seed dormancy, and change of spreading mechanisms) also were altered. Changes also affected the growth habit. Many internodes, heavy branching and climbing growth habit are typical for many wild relatives of grain legumes. Growth of these plants continues after flowering until senescence. This type of growth is called indeterminate. In contrast, stems of plants with determinate growth habit have finite length, the transition from

Fig. 1. Plants with different types of growth habit: *a* – growth habit types of common bean [17]; *b* – diagrams of growth habit types. *1* – indeterminate, *2* – determinate

vegetative to reproductive stage is marked by the appearance of well-developed terminal inflorescence (Fig. 1). Varieties with determinacy form fewer number of pods with greater seed weight, plants have shorter growing period before flowering, they are resistant to lodging, and are suitable for mechanical harvesting.

Wild species of common bean are characterized by many long internodes, the stem is very thin and it can be up to 3 m in length [15]. Both growth habits, determinate and indeterminate, are recognized in cultivated species of common bean. [16]. If transition from vegetative growth to reproductive phase occurs early in the plant's development, a dwarf plant with few nodes (<10) is produced. If the transition is significantly delayed, a plant with many internodes (>20) is formed [15]. The simplest classification system of common bean on the basis of the morphological stem growth features was proposed by S.P. Singh [16]. Four types of growth habit were distinguished. Plants of type I are determinate and have few short internodes. Plants of types II, III, and IV are characterized by indeterminate growth habit, but they differ from each other in stem length, its strength, and the number of branches [16].

Farmers who grow cowpea (*Vigna unguiculata*) for seeds prefer improved varieties which have bushy type and determinate growth habit. These varieties are characterized by a short period to maturation (65–75 days) instead late maturing varieties (90 day to flowering) [18]. Plants with indeterminate growth are characterized by long reproductive phase and pods do not mature simultaneously. It requires an additional harvesting and it is not suitable for mechanical harvesting.

GENETIC CONTROL OF DETERMINATE GROWTH HABIT

The molecular mechanisms and structure of loci controlling determinate growth in grain legumes were unclear till the beginning of XXI century. Investigation of these problems has progressed in many crops following to the molecular study of genetic factors that initiate transition from vegetative development to reproductive phase in the model plant *Arabidopsis thaliana* (L.) Heynh.

Plant architectonics is directly connected with functioning of shoot apical meristem. The most of above-ground plant organs derive from shoot apical meristem. As the plant develops and the transition to flowering takes place, the shoot apical meristem gives rise to meristems of inflorescence and flowers. The transition from the vegetative to reproductive phase is controlled by the interaction of positive and negative regulators [19, 20]. There are several stages of flower formation – flowering induction, determination of floral meristem, and determination of the floral organs (Fig. 2). Flowering induction is the start of the genetic program

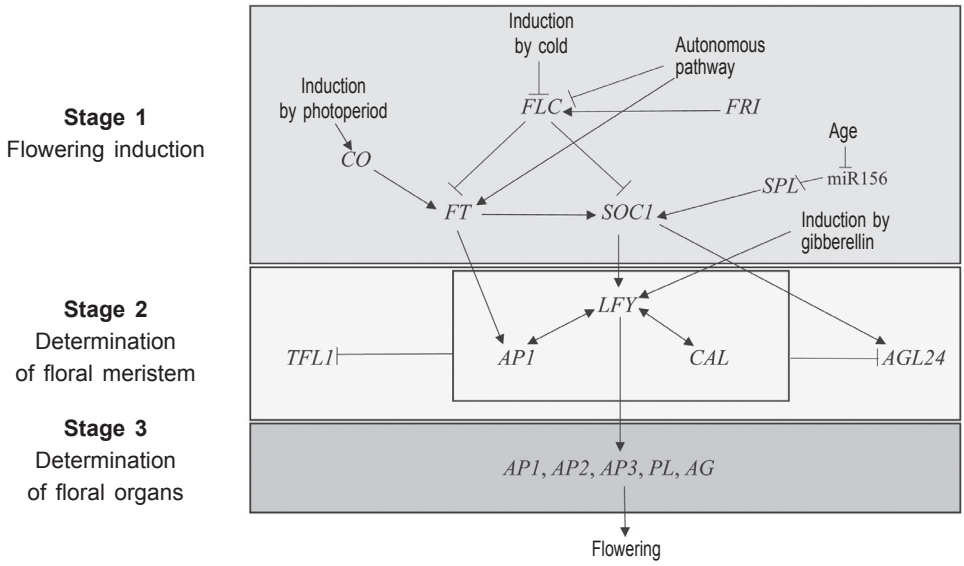

Fig. 2. Stages of floral development in *Arabidopsis thaliana* and the main controlling genes [19]

of next step of plant development. At this stage a cascade of physiological processes takes place in plant cells, the basis of which is molecular genetic interactions [19].

Shoot apical meristem consists of non-differentiated cells, whose further development is controlled by a number of exogenous and endogenous factors. Photoperiod and temperature are the main exogenous factors. However endogenous factors such as phytohormones, circadian clock, and senescence are also important. Signal ways responding to different exogenous and endogenous factors come down to several integral genes that control plant transition to flowering. These are floral meristem identity genes *LFY (LEAFY)*, *TFL1 (TERMINAL FLOWER1)*, and *AP1 (APETALA1)* [19]. The next plant development stage is initiation of floral meristem formation. The shoot apical meristem of a plant with indeterminate growth habit preserves its activity during the entire plant life cycle, wherein floral meristems are formed on the periphery of shoot apical meristem. Plants of determinate type stop its growth when the floral meristem is formed from vegetative apex.

TFL1 is an antagonist of *LFY* gene. *LFY* acts as a main integrator of the information about pathways controlling flowering time and the initiation of floral meristems. *TFL1* function is to maintain indeterminacy of shoot apical meristem during the life plant cycle. During vegetative stage the level of *TFL1* expression is low and it increases upon transition to flowering. *TFL1* acts as repressor for flowering initiation through suppression of *LFY* expression, so *TFL1* is a negative regulator. In wild-type plants, *TFL1* expression is at low levels in the cells of the shoot apical meristem during vegetative stage. Mutation in *TFL1* changes indeterminate type to determinate habit in *Arabidopsis*, and an early transition to flowering is typical for such plants [21].

In contrast to *AP1* and *LFY*, the product of *TFL1* is not a transcription factor. TFL1 is homologous to the phosphatidylethanolamine binding proteins (PEBPs) that are involved in signalling pathways controlling growth and differentiation in animals, yeast and bacteria. *TFL1* belongs to a small gene family *CENTRORADIALIS / TERMINAL FLOWER1 / SELF–PRUNING (CETS)*, which controls time of the developmental transition from indeterminate to determinate growth. *CETS* family in *Arabidopsis* consists of six genes participating in regulation of flowering control: *TERMINAL FLOWER1 (TFL1)*, *TWIN SISTER OF FT (TSF)*, *BROTHER OF FT AND TFL1 (BFT)*, *ARABIDOPSIS THALIANA CENTRORADIALIS HOMOLOGUE (ATC)*, *MOTHER OF FT AND TFL1 (MFT)*, and *FLOWERING LOCUS T (FT)*. These genes are involved in regulation of flowering control and in other processes. For example, *TSF* regulates stomatal opening via the blue light-dependent activation of H^+-ATPase in guard cells [22]. *BFT* regulates transition to flowering under conditions of high

salinity [23]. *MFT* regulates seed germination via gibberellic and abscisic acid signalling pathways [24]. *CENTRORADIALIS* from snapdragon (*Antirrhinum majus* L.), *SELF–PRUNING* (*SP*) from tomato (*Solanum lycopersicum* L.) [25] and *CET* in the tobacco (*Nicotiana tabacum* L.) [26] are homologous to *TFL1*. In tomato, the product of gene *SP* can interact with a range diverse proteins and is involved in signal processes [27].

The first studies of the inheritance of legume stem growth habit were at the beginning of the last century. R.A. Emersen was one of the first who studied inheritance of three the most important (as it was believed at that time) morphological traits of cultivated common bean: plant length, climbing or erect habit, and position of pods (terminal or lateral) [28]. He stated Mendelian type of inheritance of observed traits in 3 : 1 proportion. In 1915 J.B. Norton conducted further studies of inheritance of common bean growth habit [29]. In his work Norton adhered to the research patterns previously conducted by Emersen, however, he designated each trait by "letter" and observed inheritance of each trait. So plant length was designated as "L", which corresponded to plants with long stem; letter "l" corresponded to plants with short stem. The inheritance of this trait was determined using numerous crosses. Based on the results of his studies, Norton concluded that existence of terminal inflorescence on the plant shoot restricted the growth of the whole plant. The formation of numerous lateral inflorescences was observed during unlimited growth of the main stem. Norton supposed that the plant length controlled by two or more factors, which he designated as L_1, L_2, etc. Norton considered that other factors control stem growth nature (climbing or erect). Thus, Norton was one of the first who supposed monogenic inheritance of growth habit, and stated that incomplete growth habit was dominant trait.

The next block of inheritance investigations of many morphological features of common bean was performed by German scientist H.Lamprecht. For the first time he marked gene controlling growth habit of common bean as *FIN* (from Latin *finitis* – limited) [30]. It was supposed that namely this locus was responsible for determinacy in most varieties of common bean. As for climbing varieties the control of gene *Tor* (from Latin *torquere* – climbing) was proposed [31]. Later the active investigations of inheritance of growth habit of common bean continued and it was shown that *FIN* also controls plant growth with a climbing stem habit, *FIN* has been mapped to chromosome of Pv01 [32]. It was detected that determinate growth habit was controlled by the only recessive allele of gene *fin*. Indeterminate growth habit was a dominant trait.

One more genetically well-studied grain legume crop is soybean. The most of researchers distinguish three soybean stem growth habits: indeterminate, determinate, and intermediate or semideterminate, where termination of growth of main shoot occurs later than in determinate varieties. These plants are less susceptible to lodging than indeterminate varieties and at the same time they produce more pods than determinate ones [33].

The first studies of inheritance of soybean growth habit used the methods of classic genetic analysis [34]. C.M. Woodworth studied F2 of crossing between Ebony variety (complete growth habit) and Manchu variety (incomplete growth habit) and it was observed Mendelian type of inheritance (F2 ratios of 3 indeterminate: 1 determinate). Inheritance of soybean growth habit was suggested as monogenic. C.M. Woodworth proposed the name for growth habits, such as indeterminate (dominant) and determinate (recessive) and gene pair *Dt* and *dt* for them [34]. Later plants with intermediate growth habit type (*dt1dt1* genotype) were detected. Termination of growth occurs later than in determinate varieties. R.L. Bernard [35] hypothesized the inheritance of two gene pairs affecting stem termination. The second gene was designed as *Dt2*. Bernard called intermediate stem type as semideterminate. The stem growth of soybean is regulated by an epistatic interaction of two genes *Dt1* and *Dt2* [35, 36]. *Dt1* (=*Dt* according to Woodworth [34]) determines indeterminate growth habit, while *dt1dt1* genotypes produce determinate phenotypes. *Dt2* in the presence of the dominant allele *Dt1* results in the semideterminate type. Because *Dt1* is incompletely dominant over *dt1*, heterozygotes *Dt1dt1* also have semideterminate

growth habit. Allele *Dt2* is completely dominant over *dt2*.

The examples of dependence of growth habit on cultivation conditions of members of the tribe *Phaseoleae* Bronn. (common bean, cowpea, soybean, lablab bean, and others) are known. Determinate growth habit of cowpea (*V. unguiculata)* changed to indeterminate at the night temperature of 24 °C and daylength of 12 h [37]. Similarly lablab bean (*Lablab purpureus* (L.) Sweet) changed growth habit determinate to indeterminate at 13 h day at 25 °C and at 10–11 h day at 30 °C. Meanwhile at 20 °C in any daylight lablab bean growth habit did not change [38]. Two groups of soybean varieties were found in photoinsensitive varieties. Some varieties had a stable determinate growth habit. Number of internodes during transition to flowering was also stable (=10) at different daylengths and different temperatures. However, some varieties changed stem growth habit to indeterminate under high temperatures, and the number of internodes of these plants increased [39].

Gene *FT* is the member of *CETS* family. It initiates the transition to determinate growth and flowering. Genes *TFL1* and *FT* in *Arabidopsis* have opposite effect on flowering initiation: *TFL1* is repressor, while *FT* is an activator [20, 33]. Products of both genes interact with the product of other gene *FLOWERING LOCUS D (FD)*, which belongs to bZIP transcription factor family. It is expressed mainly in the shoot apex. Protein binding leads to the formation of a heterodimer. Under non-inductive conditions of a short day, the FT protein is not generated, while complex FD with TFL1 is generated. This complex blocks activator function of FD, and flowering is delayed. In the short-day conditions, protein FT forms heterodimer with FD, which activates expression of genes responsible for development of floral meristem and transcription of gene *AP1* is initiated.

The most of dicots have one copy of *TFL1* in their genomes. *TFL1/CEN* paralogs were described in monocots. *ROOTS CURL IN NPA* (*RCN1* and *RCN2*) perform similar functions and have similar expression patterns with *TFL1* [40]. Genes *FT* and *TFL1* are result of duplication of one ancestral copy and they encode small proteins containing 175 and 177 amino acids, respectively. These proteins have only 60% identity [41, 42]. Studies of protein structure demonstrated that single base change could alter protein function. Thus substitution of Tyr85His in FT and His88Tyr in TFL1 leads to a change in the functional significance of proteins to the opposite. Genes *FT* and *TFL1* are highly conserved and they have four exons and three introns [42]. Exons 1–3 have highly conserved sequences. Exons lengths were found to be constant; no significant differences were detected between paralogs. The fourth exon is the most variable [40, 42]. In contrast to exons, introns lengths were highly variable between dicots and monocots. *RCN1* of monocots had relatively short but constant intron lengths compared with other paralogs. Furthermore, *RCNs* of different representatives of monocots had a higher number of intron length polymorphisms than eudicot *TFL1/CEN* [40].

When studying the overexpression of chimeric proteins in different plants, it was shown that the fundamental difference in the structure of FT and TFL1 proteins is in the composition of a small section (128–145th amino acids), within which a segment of 14 amino acid residues is localized. This section forms a loop with variable conformation. It has been suggested that replacing an amino acid in a loop may change the protein function to the opposite. Analysis of protein structure of *FT* and *TFL1* orthologs was conducted in many plants. The external loop evolved rapidly in TFL1 orthologs, however it is almost unchanged in FT orthologs. Substitution of one amino acid (Gln140 in FT and Asp144 in TFL1) reversed protein function. These amino acids are located at the beginning of the loop, which is likely a ligand binding site. Gln140/Asp144 directly connect with functionally important amino acids Tyr85/His88. Thus, interacting pairs Tyr85–Gln140 and His88–Asp144 in FT and TFL1 have the key role for determination of protein function [41, 42].

The search for *FT* and *TFL1* orthologs was conducted in different systematic groups [43]. *TFL1* orthologs of pea (*Pisum sativum*), soybean (*Glycine max*), and common bean (*Phaseolus vulgaris*) are studied best of all from grain legumes.

Three *TFL1* homologs were isolated in pea, which were designated *PsTFL1a*, *PsTFL1b*, and

PsTFL1c [43, 44]. Genes *PsTFL1a* and *PsTFL1c* encode proteins of 174 and 173 amino acids, respectively. These proteins have high homology level between each other (approximately 70%) and high identity to protein TFL1 of *Arabidopsis* (72% and 65%, respectively). Based on the phylogenetic analysis the *TFL1* homologs were combined in several groups. Both *PsTFL1a* and *PsTFL1c* clustered with *TFL1*, while gene *PsTFL1b* formed one group with genes *CEN* and *SP*. Expression patterns of three pea genes were different. Thus, no expression of *PsTFL1a* was detected in shoot apex before floral initiation. The accumulation of transcripts was detected in apex only after floral transition and it continued during the reproductive plant stage. Expression of *PsTFL1b* was detected in apex during the vegetative and reproductive phases. Gene expression was also found in roots and nodes, but it was not detected in flowers. Expression of *PsTFL1c* was detected in all studied tissues [44]. *PsTFL1a* corresponds to *DETERMINATE (DET)*. Phenotype of *det* pea mutants was similar to those of *tfl1* and *cen* mutants. All three mutant plants have determinate growth habit [45]. Gene *PsTFL1c* corresponds to the gene *LATE FLOWERING (LF)* and is a paralog of *DET/PsTFL1a*. In pea the protein LF likely delays the transition to flowering induction by prolongation of vegetative phase. Low level of *PsTFL1c* transcript accumulation stimulated earlier transition to flowering, while high level of gene expression delayed this transition. *lf* mutants had an earlier transition to flowering. *det lf* double pea mutants demonstrated an earlier floral transition and these plants had determinate growth habit; this phenotype is similar to *tfl1* mutants of *Arabidopsis*.

Thus, control of transition from vegetative stage to floral initiation is regulated by two genes (*DET/PsTFL1a* and *LF)* in pea in contrast to *Arabidopsis* [44].

Russian researchers described two genes, *DET* and *DEH*, which mutations are connected to the determinate stem growth habit of pea [46–51]. The apical meristem of mutants of the gene *DET* (*DETERMINATE*) is completely converted in terminal inflorescence. Results of numerous crosses demonstrated that gene *DET* is localized in linkage group 7 and it is closely linked with gene *R*. *det r* mutants have determinate stem growth habit and seeds with rough surface [46, 50]. Mutants in gene *DEH* (*DETERMINATE HABIT*) beginning from the first productive node have small stipules. As result in the upper shoot part due to reduction of photo-assimilating surface, vegetative poorly developed bud is formed. The bud dies in unfavorable conditions, thus resulting in plant growth termination [48]. This type of determinate growth is called by Russian researchers as "samara type" [48]. Plants of this type are resistant to lodging and have apical location of pods. Gene *DEH* is presumably localized in chromosome 3, its structure is unknown, and current data on the type of inheritance are contradictory.

It should be noted that in addition to an apical inflorescence meristem, there are the secondary meristems, which identity connected to functioning of the gene set *VEG1*, *GIGAS,* and *VEG2* (see Table 1, Fig. 3). Gene *VEG1* belongs to the group of genes *AP1/SQUA/FUL* and it is *AGL79*-like gene [52]. *VEG1* specifies identity of secondary inflorescence meristem and it is expressed after transition to flowering in the inflorescence apex area. The *veg1* pea mutants do not flower, floral organs do not develop and transition to the flowering stage is blocked [52]. *DET* expression was detected in *veg1* mutants in the lateral meristems at the flanks of apical meristem. *VEG1* expression is required for activation of such lateral meristems via direct and indirect repression of *DET* expression.

Three groups of *FT* genes – *FTa*, *FTb,* and *FTc* were detected in pea, and the complex regulation of dependence of floral initiation on daylength was determined [53]. Probably there is a mutual transcriptional regulation within this gene family [54]. Expression of *FT* homologs was detected in leaves, as well as in the plants' apex. Only *FTb2* was expressed in leaf tissue in the transition to flowering. Expression of *FTa1* and *FTa2* was also observed in leaves; however, in contrast to *FTb2* expression, it was independent from day length. Two main genes of *FT*-group, *FTa1,* and *FTb2,* are expressed in leaves but they have different functions in the process of plant development. Finally, gene *FTc* is expressed only in the shoot apex and becomes an

integrator of signalling from other *FT* genes whose expression is determined in the leaves. Gene *GIGAS* of pea corresponds to *FTa1* and it is an ortholog of gene *FT* in *Arabidopsis* (see Table).

Pea gene *VEG2* is an ortholog of transcription factor *FD* [55]. VEG2 interacts with GIGAS/FTa1, heterodimer is formed, which it likely upregulates *VEG1* expression.

Two orthologs of *TFL1*, *GmTFL1a* and *GmTFL1b,* were identified in soybean [56, 57]. Proteins have high level of homology with protein PsTFL1a (approximately 85%) (see Table). Analysis of the transcription profiles of*GmTFL1a* and *GmTFL1b* in various plant tissues detected differences in transcription level. *GmTFL1a* was expressed greatly in the immature seeds and slightly in cotyledons and shoot apex. Reverse tendency was detected for *GmTFL1b*. Both mapping and expression analysis suggest that *GmTFL1b* is candidate for *Dt1* [56]. Analysis of the sequence polymorphism of *GmTFL1b* in plants with different growth habit types detected four single nucleotide substitutions in exon 4. The transition from indeterminate to determinate growth habit type in soybean is associated with independent artificial selection of four point mutations in gene *Dt1* during soybean domestication. *Dt1* (=*GmTFL1b*) is an ortholog of *TFL1*, it is located on chromosome 19. *Dt2* is mapped to the distal end of chromosome 18 [57]. Intermediate growth habit type is connected with the dominant mutation, thus leading to increase of the *Dt2* expression level in the inflorescence apex [58]. *Dt2Dt2* genotypes produce semideterminate phenotypes, while the indeterminate growth habit is marked in genotypes *dt2dt2*.

Dt1 expression level in soybean with determinate growth was significantly reduced at floral transition, while plants with indeterminate growth had expression levels that were not changed after the beginning of the reproduction stage [59]. *Dt1* expression in the shoot apex of the 12-day old plants grown under short-day conditions was not changed at later growth stages. A significant increase of *Dt1* expression was observed in indeterminate lines at 7 days after conversion to long-day conditions, *Dt1* expression at relatively high level was detected until 21 days after conversion into other light conditions. *Dt1* expression is under control of genes *E3* and *E4* that encode isoforms of phytochrome A (phyA) *GmPHYA3* and *GmPHYA2,* respectively [59]. The main function of phytochrome is the ratio estimation of red (R) and far-red (FR) light at natural lightening. Different ratios of R–FR activate transcription of *E3* and *E4* in the long-day conditions.

Ten *FT* homologs were identified in soybean, they are combined in five pairs in different homoeologues chromosome regions [60]. Two *FT* genes, *FT2a* (*FTa* gene) and *FT5a* (*FTc* gene), are important promoters of flowering. Expression of both genes is induced in short-day conditions, it has daily pattern with maximum of 4 h after dark [60–62]. Under long-day conditions the daily expression pattern was not detected. High expression level was detected in the leaves under short-day conditions for the other two *FTa* genes, (*FT3a* and *FT3b*) [60]. Only one *FT4* blocked flowering. *FT4* expression was initiated under long-day conditions and was regulated by gene *E1* [63]. Gene *E1* belongs to gene complex

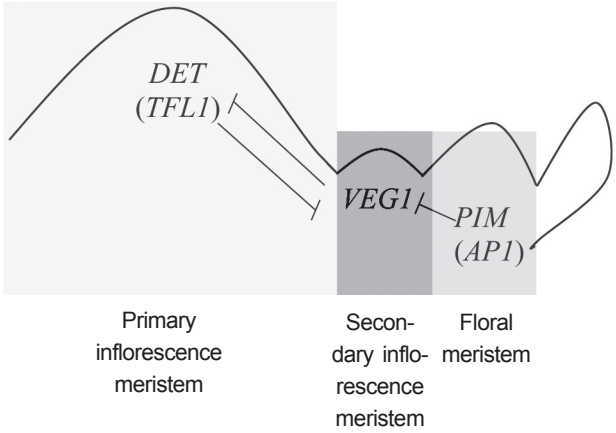

Fig. 3. Model of meristem identity in pea inflorescence [33]

Homologs of main regulators of inflorescence development in legumes

Gene in *Arabidopsis thaliana*	Species	Homologous genes in legumes	Mutant	Phenotype of mutant	NCBI accession number	Reference
LEAFY (*LFY*)	*Lotus japonicus* L.	*LjLFY*	*proliferating floral meristem (pfm)*	Defects in formation of compound leaf. Adult plants have simple leaves. Inflorescence-like structures are formed. Morphology of flowers is anomal, petals and stamens are absent. Flowers are sterile	AY770393	[71]
	Medicago truncatula Gaertn.	*SGL1*	*single leaflet1 (sgl1)*		AY928184	[72]
	Pisum sativum	*UNI*	*unifoliata (uni)*		AF010190	[73]
	Vigna radiata	*VrLFY*	*unifoliate leaf (un)*		XP014491863	[74]
AP1	*Glycine max*	*GmAP1*	–	Morphology of flowers is anomal. The sepals of first flowers are replaced by bract-like organs, petals are absent. There are flowers consisting of external bracts, petals and cluster of central stamens. In the axil of modified sepals additional flowers with anomal morphology are formed	XM003547744	[75]
	L. japonicus	*LjAP1a, LjAP1b*	–		AY770395, AY770396	[71]
	M. truncatula	*MtPIM*	*mtpim*		DQ139345	[76]
	P. sativum	*PEAM4/PIM*	*proliferating inflorescence meristem (pim)*		AJ279089; AF461740	[77, 78]
TFL1	*G. max*	*Dt1 (GmTFL1)*	*dt1*	Indeterminate growth habit changes to determinate, plants flower earlier	AB511820, AB511821	[56]
	Phaseolus vulgaris	*PvTFL1y (FIN)*	*fin*		JN418219-418266	[30, 65]
	P. sativum	*PsTFL1a*	*det*		AY340579	[44]
	Vigna unguiculata	*VuTFL1*	–		KJ569520-KJ569525	[69]
	P. sativum	*DEH*	*determinate habit (deh)*	Plants have a short reproductive period, synchronous pods maturity. A small number of inflorescences, reduced stipules are formed. This mutation was noted in some Russian varieties (Orlovchanin 2, Batrak, Flagman 5, etc.)	Primary structure is unknown	[47–49, 51]
	G. max	*Dt2*	*dt2*	Semideterminate growth habit	KF908014	[58]
	P. sativum	*VEG1*	*vegetative 1 (veg1)*	Plants are not flowering; no floral organs are formed	JN974184	[52]
FT	*G. max*	*GmFT1a*	–	–	AB550124	[60]
	P. sativum	*GIGAS*	*gigas*	Plants are not flowering	HQ538822	[53]
FD	*P. sativum*	*VEG2*	*vegetative 2 (veg2)*	Flowering is delayed	KP739949	[55]

controlling duration of vegetative period and response to photoperiod.

Three *TFL1* homologs of *Arabidopsis* (*PvTFL1x*, *PvTFL1y,* and *PvTFL1z*) were identified in common bean. Using different approaches, the role of gene *PvTFL1y* was demonstrated in the determination of growth habit [64–66] (see Table). The protein PvTFL1y consists of 173 amino acids and it has 75% homology with protein TFL1 of *Arabidopsis*. *PvTFL1y* consists of introns and four exons. Unique haplotypes associated with determinate habit – 4,1-kb retrotransposon have been revealed in the fourth exon. The other accession had a T453A mutation at the end of exon two that was located in a putative splice site [66]. Various mutations in the *PvTFL1y* were identified in common bean accessions of different geographic origin (Central American and Andean) [65]. Single nucleotide substitutions were detected, as well as insertions and deletions. The 4171 bp insertion was observed in the fourth exon.

There are few studies of the molecular mechanisms of floral initiation control in species within the genus *Vigna*. Currently, genome sequencing of two *Vigna* species (mung bean (*Vigna radiata var. radiata VC1973A*) and adzuki bean (*Vigna angularis,* of variety Shumari) has been completed [67, 68]. A genome database of genus *Vigna* was presented for the first time: Vigna Genome Server ("VigGS", http://viggs.dna.affrc.go.jp). Genome sequenceing of other species is still underway. *Vigna unguiculata* is phylogeneticaly closest to *Phaseolus* genus. An ortholog of *TFL1* in accessions of *V. unguiculata* was identified for the first time in 2014 [69]. Nucleotide sequence of *VuTFL1* 1291 bp long is highly homologous (90%) to the sequence of common bean *PvTFL1y* and to the sequence of soybean *Dt1* (82%). Non-synonymous point mutation in the fourth exon was identified leading to amino acid substitution (proline to histidine) in determinate plants. This substitution leads to change of protein function.

The most of economically important traits are inherited as polygenic. The genetic control of domestication-related traits has been investigated in numerous crop species, including legumes, mainly by quantitative trait loci (QTL) mapping. QTL controlling important quantitative features (seeds weight, seed germination, days to flowering, etc.), as well as for four qualitative features (plant growth habit type, pod shattering, and pod color, root system architectonics) were identified in cowpea [70]. QTL controlling growth habit type was mapped on LG1 linkage group between markers SSR7079 and SSR7068. One of seven QTL for seed weight was found on this region too.

The correct differentiation of plant inflorescence requires the normal functioning of genes responsible for apex meristem activity, as well as genes responsible for floral meristem development. The meristem identity genes, *LFY*, *AP1,* and *TFL1,* are considered as the main genes of floral initiation. Expression of genes *LFY* and *AP1* is suppressed by TFL1, which blocks transcription activator FD. Cells of apical meristem continue proliferation and this process continues during the whole life cycle with indeterminate habit.

CONCLUSION

Identification and analysis of genes responsible for the type of stem growth are required for successful breeding of varieties. Stem growth type is an economically important trait. It interconnects with stem length, flowering duration, yield, resistance to lodging, and suitability of mechanized cultivation. For some varieties it can be difficult to distinguish between indeterminate and determinate stem types under short-day and under unfavorable growing conditions. In this regard, development of new molecular markers for identification of this important trait can help to determine the stem growth type at early stages. Detection of molecular mechanisms connected with plant development and transition to flowering will allow to move to a more efficient and faster creation of new varieties by means of marker-assisted selection.

The present review has been prepared within the framework of the VIR project No. 0481-2019-0001.

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