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Identification and verification of DTF9.4, a QTL that promotes flowering in common bean (*Phaseolus vulgaris L.*) under long day photoperiod.

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IDENTIFICATION AND VERIFICATION OF DTF9.4, A QTL THAT PROMOTES FLOWERING IN COMMON BEAN (*PHASEOLUS VULGARIS* L.) UNDER LONG DAY PHOTOPERIOD.

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Abstract

Flowering time and maturity are important agronomic traits for common bean (*Phaseolus vulgaris L.*), a short-day species in order to adapt to different latitudes and achieve optimal yield. In 2021, a QTL for flowering time, named as DTF-9.4, was mapped on chromosome 09, explaining more than 30% phenotypic variance. Although the studies indicated functional genes exist in this region that controls flowering time, it has not been deciphered at high resolution. In this study, genotyping, and phenotyping of recombinant plants within the QTL region allowed us to test the effect of narrowed QTL at 200 kb and with only two candidate gene annotated, *PvFUL1* and *PvE1*, in Long Day environment. The development of near isogenic lines has allowed us to eliminate the effect of other major genes that segregated in the population (such as *PvCOL2*) with a major effect on flowering time. The line developed named as dtf-9.4 (*Pve1Pvful*) had a lower flowering node and early flowering time (node 8 and 40 d) compared with DTF-9.4 line (*PvE1PvFUL*) (node 15 and 54 d) in long day conditions (14 h light). This finding showed the possible involvement of other circadian clock gene in flowering time regulation in common bean. To determine the effects of these candidate genes underlying QTL, more analyses will be necessary in an effort to link markers, RNA expression, and the phenotype.

Contents

1. Introduction

1.1. Description and biology of *Phaseolus vulgaris* species

Phaseolus vulgaris L. (common bean) belongs to the Fabaceae family. The genus *Phaseolus* contains about 70–80 species (George et. al, 2003), distributed exclusively in the America (Delgado-Salinas et al., 2006) but with a clear focal point in Mexico and Central America. Only five *Phaseolus* species were domesticated. Of these five species, common bean is the one with the broadest geographic distribution and largest agronomic, nutritional, and economic impact (Gepts, 2014a). Other domesticated species are runner bean (*P. coccineus*), tepary bean (*P. acutifolius*), lima bean (*P. lunatus*), and year bean (*P. dumosus*) (Gepts, 2014b). Common bean is a diploid species with 2n= 22 chromosomes and a medium-sized genome (Mc clean et al. 2020). Common bean comprises numerous cultivars with a wide range of morphological and agronomic characteristics (Purseglove, 1968; Singh et al., 1991a). Germination is epigeal and requires 5–8 days. The wild relatives are viny, herbaceous plants, with a high level of branching, many nodes, long and twining internodes, and diageotropic branch growth (Debouck et al., 1993). Cultivated forms are herbaceous annuals with determinate or indeterminate growth habits. Singh (1982) based on morphological growth characteristics classified into four discrete growth habits: type I is determinate and have few short internodes; types II, III, and IV are characterized by indeterminate growth habit, but they differ from each other in stem length, strength, and number of branches (Figure 1).

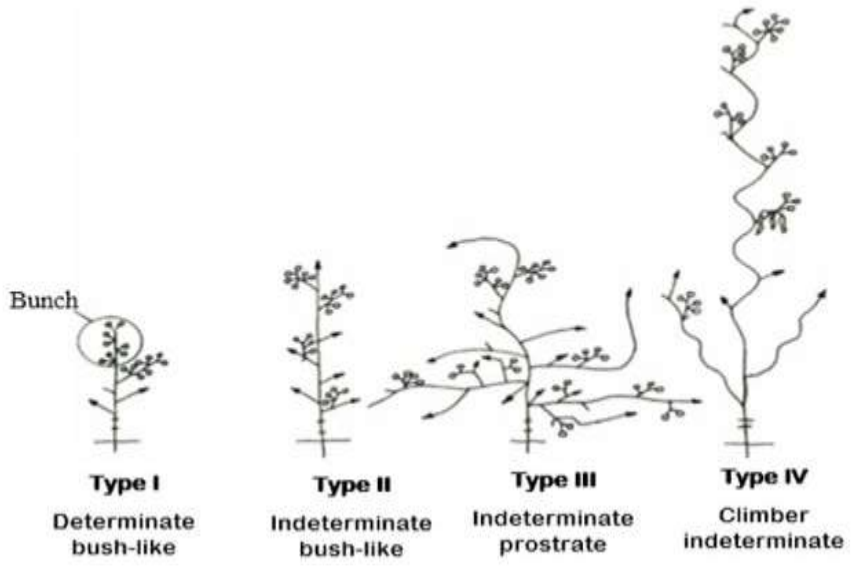


Figure 1 *Phaseolus vulgaris* growth habit. Modified from Debouck and Hidalgo (1984).

Time of flowering varies with cultivar, temperature, and photoperiod (Singh et al., 1991a). Flowering is usually initiated 28–42 days after planting, but significantly delayed among climbing varieties grown at higher elevation. Flowering in cultivars of growth habit I is concentrated over a very short period, while indeterminate cultivars produce additional nodes after initial flowering, leading to longer flowering periods (CIAT, 1975). Papilionaceous flowers are borne in axillary and terminal racemes and may bear one to many flowers. The flowers are zygomorphic with a bi-petalled keel and two lateral wing petals and are large (Doutt, 1932). The flower contains ten stamens and a single multi-ovuled ovary, is predominantly self-fertilized, and develops into a straight or slightly curved pod. Seed filling periods may also vary between 23 and 50 days in determinate cultivars and indeterminate climbing varieties. Physiological maturity (the stage beyond which no further increase in seed dry matter takes place) may occur in 60–65 days after planting in early maturing varieties grown under short growing seasons or may extend to 200 days in climbing varieties grown in cooler upland elevations (Graham & Ranalli, 1997). Seeds may be round, elliptical, somewhat flattened, or rounded elongate in shape, and a rich assortment of coat colors and patterns exists. Seed size ranges from 50 mg seed in wild accessions collected in Mexico, to more than 2,000 mg seed in some large-seeded Colombian varieties (Singh et al., 1991b).

1.2. History of the origin and distribution of common bean

The origin of the wild common bean remains a topic for debate. The wild forms, which grow from northern Mexico to north-western Argentina (Toro & Tohme, 1990), are characterized

by three eco-geographic gene pools. The Andean and Mesoamerican gene pools are the major ones, and include both wild and domesticated forms (Bitocchi et al., 2013). The third gene pool is represented by wild populations that grow in northern Peru and Ecuador (Debouck et al., 1993), and that are characterized by a specific phaseolin type, known as 'Inca', which is not found in individuals outside of this geographic location (Kami et al., 1995).

Domestication took place after the formation of these gene pools in independent events (Bitocchi et al., 2013; Kwak & Gepts, 2009; Mamidi et al., 2011). The geographical and ecological separation over millennia have combined to achieve marked differences between both major gene pools at the morphological (Gepts & Debouck, 1991) and molecular levels (Koenig & Gepts, 1989; Singh et al., 1991b). In this way, the two major gene pools have been divided into seven races. The Mesoamerican gene pool contains four races: Durango (D), Jalisco (J), Mesomaerica (M), and Guatemala (G), and the Andean gene pool contains three races: Chile (C), New Granada (N), and Peru (P) (Singh et al., 1991a) (Figure 2).

Common bean was introduced into Europe in the early 16th century and spread rapidly from Europe to the Middle East, West Asia, and other regions in the 16th and 17th centuries. Ultimately, centers of origin were formed in Europe (Angioi et al., 2010; 2011; Santalla et al., 2002), Brazil (Burle et al., 2010), South Africa (Asfaw et al., 2009; Blair et al., 2010), and China (Zhang et al., 2008).

Figure 2 characteristics of dry seeds from different races of Common Bean. Right: Mesoamerican races, left: Andean races. Source: Photo courtesy from SP Singh, University of Idaho, USA.

1.3. Common bean: economic importance and relevance

Common bean is the most important grain legume in the world, only second to soybean. It is not only used a dry grain and snap bean as vegetable but is also as canned products in the market. Beans provide 16–33% proteins; 50–60% carbohydrates, of which 14–19% is dietary fiber; 1–3% lipids; and numerous micronutrients, such as zinc, iron, magnesium, phosphorus, calcium, sodium, copper, potassium, thiamine, riboflavin, niacin, vitamin B6, and folic acid (Augustin et al., 1981; Campos-Vega et al., 2010; Hayat et al., 2014; Wainaina et al., 2021). Global production as a dry grain is 26.8 million tons, while production as a vegetable or snap bean is 23.5 million tons according to the database of the Food and Agriculture Organization (FAO) in 2018. The yields as dry grain and snap bean are 913 kg per ha and 1515 kg per ha, respectively (FAOSTAT). Because of their high protein, mineral and fiber content, beans are consumed instead of meat in underdeveloped and developing countries (Reyes-Moreno & Paredes-López, 1993). However, especially in the last decade, the benefits of beans have been better understood in terms of high protein, important minerals, dietary fiber and some vitamins, so consumption has also increased in developed countries (Lucier et al., 2000). As the common bean is easy to produce, flavorful and versatile, it has gained its popularity also help the farmers to generate great sources of income.

Dry beans are usually consumed as seeds cooked after soaking. Another type of dry bean is nuña or Peruvian popping bean (Pearson et al., 2012). At high altitudes, cooking dry beans by boiling becomes problematic because of the lowered boiling point of water and the extra time required to cook the food. Popping beans are heated directly and require less time to expand or puff into a soft edible state, thereby requiring less cooking fuel. Vegetable use of common beans includes immature pods (snap beans), high moisture seed, and leaves as greens (Wortmann, 2006). The snap bean is mainly consumed in developed countries, and they have been selected for reduced fiber in the green pod.

The common bean is produced in subtropical and tropical regions, most often by smallholders, and constitutes a major staple crop in both developing and developed countries. According to FAO estimates, the global bean production has risen from 16.6 million tonnes (Mt) in 1988-90 up to the record of 29.3 Mt in 2015-17. This significant growth results from the increase of both cultivation areas and yields over the past 30 years, with the Americas and Asia as the most important producing regions. The five top producer countries of dry beans during the

2013-17 period were, in annual average: India (5.8 Mt), Myanmar (4.9 Mt), Brazil (3.0 Mt), the United States (1.3 Mt) and Mexico (1.2 Mt) (FAOSTAT, 2019). Considering the global imports and exports of dry beans between 2012 and 2016, it seems that 12% to 18% of the world annual production (around 3.9 Mt on average) is traded internationally. China, Myanmar, and the United States are the main exporters, with India and the European Union being the largest importers (FAOSTAT, 2019).

1.4. Genomic resources in common bean

Common bean germplasm resources worldwide, including wild plant species, modern cultivars, and their wild crop relatives, are maintained in several collections: the International Centre for Tropical Agriculture (CIAT) in Colombia (about 32,000 accessions), United States Department of Agriculture Agricultural Research Service (USDA-ARS) (about 15,000 accessions), the Leibniz Institute of Plant Genetics and Crop Plant Research (IPK) in Germany (about 9,000 accessions), Brazilian gene bank (EMBRAPA) (about 27,700 accessions), in Beijing China (CAAS) (more than 5,000 accessions), and the National Center for Plant Genetic Resources in Alcala de Henares, Spain (with more than 5,000 bean accessions). The online global portal Genesys PGR is a free website (accessible at www.genesys-pgr.org) that contains over 135,000 accessions which are stored in several of the institutions mentioned above.

Genetic diversity has been extensively studied in bean using different types of markers, including seed protein (De La Fuente et al., 2012; Gepts et al., 1986) and isozyme analysis (Koenig & Gepts, 1989). Other molecular markers used for genetic diversity are DNA restriction fragment length polymorphism (RFLP) (Khairallah et al., 1990; 1992), nuclear RFLP (Velasquez & Gepts, 1994), allozymes (Santalla et al., 2002; Singh et al., 1991), and random amplified polymorphic DNA (RAPD) (Beebe et al., 2000; Freyre et al., 1998). Similar reports have also demonstrated genetic diversity through use of amplified fragment length polymorphism (AFLP) markers (Beebe et al., 2001; Papa & Gepts, 2003; Zizumbo-Villarreal et al., 2005), SSR markers (Blair et al., 2006; Gaitán-Solís et al., 2002), DNA sequencing (Gepts et al., 2008), and single nucleotide polymorphism (SNP) markers (Blair et al., 2013; Galeano et al., 2012). Numerous maps have been generated using these marker types (reviewed by González et al., 2017), although SNP markers have generally supplanted prior types of markers. A large number of studies have been carried out, involving both mapping of qualitative and quantitative traits in biparental populations, and more recently, through genome-wide association studies (GWAS) in diverse germplasm collections (reviewed by González et al., 2017).

More recently, the genomics era has led to a rapid increase in available sequence data, which has thus provided a more detailed picture of the genetic diversity and structure of crop germplasm. The current availability of high-throughput sequencing platforms has allowed the release of high-quality reference genomes of the Andean G19833 (Schmutz et al., 2014) and Mesoamerican BAT93 (Vlasova et al., 2016) genotypes. Several *Phaseolus* genomes are available for downloading, sequence searching, and browsing at both Phytozome (https://phytozome.jgi.doe.gov) and Legume Information System (https://legumeinfo.org) databases. Genetic characterization through high-throughput sequencing of common bean collections and segregant populations is increasing last years, examples are the genomic studies carried out from two panels: the Middle American Diversity Panel, which was developed by the USDA-funded Common Bean Coordinated Agricultural Project (BeanCAP), with 280 modern bean genotypes (Moghaddam et al., 2016); and the Andean Diversity Panel, with 396 accessions (Cichy et al., 2015; Oladzad et al., 2019) carried out genotyping by sequencing for the Bean Abiotic Stress Evaluation panels, with data to identify markers associated with yield under both heat- and drought-stress environments.

1.5. Photoperiod pathway

In plant life cycles, the time of the transition to flowering is critical to reproductive success and is regulated by external environmental factors (such as light, temperature) and endogenous signals such as age and developmental state. Seasonal changes in day length (photoperiod) play an important role in the regulation of flowering through the photoperiod pathway (Cerdán & Chory, 2003). The plants co-ordinate their flowering by utilizing a reliable indicator of environmental changes, such as changes in day length that allows plants to adjust for flowering time. Flowering in short-day (SD) plants occurs upon day length shortening, whereas, in long-day (LD) plants, flowering occurs with the increase in day length, and in day-neutral (DN) plants flowering occurs irrespective of day length variations (Lu et al., 2020; Yu et al., 2008). Moreover, the plants are categorized as obligate and facultative within the day length responses. Absolute inductive photoperiods are mandatory for obligate plants and such plants remain in a vegetative state without such requirement. In contrast, facultative plants show accelerated flowering under inductive conditions and undergo normal flowering even in non- inductive photoperiod.

In principle, photoperiodic flowering mechanisms can be divided into three parts: light input, circadian clock, and output. Phytochromes and cryptochromes, two essential types of photoreceptors in higher plants, play important role in flower induction. The photoperiod pathway begins with the perception of light signals by photoreceptors in leaves (Tripathi et al., 2019).

Phytochromes perceive far-red and red light, whereas cryptochromes perceive UVA and blue light. After sensing the photoperiod, photoreceptors transmit the signal to the circadian clock, defined as the internal timer synchronized with solar time that oscillates with a stable phase of approximately 24 h. The core clockwork of the 'circadian' timing system operates at the level of single cells. Arabidopsis clock design acts as a reference clock for other plants (McClung, 2013). Components of the circadian clock are encoded by regulatory genes that are activated at specific time points, such as morning-phased genes at the beginning of the light period or evening-phased genes at the beginning of the dark period (Lin, 2000). In plants responding to day length, the endogenous rhythm changes through the periodicity changes of the light/dark cycles lead to the flowering induction through the photoperiodic pathway. Day length and clock signals are integrated by the *GIGANTEA* (*GI*) and *CONSTANS* (*CO*) genes. The regulation of daytime *CO* expression is the primary process of time measurement in the photoperiodic flowering pathway, while GI proteins positively regulate *CO* transcription (Imaizumi et al., 2003)**.**

1.6. Flowering in response to changing day length: the long-day plant *Arabidopsis thaliana as a model.*

Arabidopsis thaliana is a facultative LD plant (~16 h of light and 8 h of dark). In the current model of the Arabidopsis circadian clock, most components function as repressors. At dawn, two MYB transcription factors, *CIRCADIAN CLOCK ASSOCIATED1* (*CCA1*) and *LATE ELONGATED HYPOCOTYL* (*LHY*), repress evening-phased genes (Kamioka et al., 2016; Nagel et al., 2015). Genetic results showed that *CCA1* and *LHY* directly act as transcriptional activators for the morning-phased genes *PSEUDO RESPONSE REGULATOR9* (*PRR9*) and *PRR7* (Farre´ et al., 2010).

From early in the morning to the first-half part of the night, *PRR9*, *PRR7*, and *PRR5* redundantly repress the transcription of *CCA1* and *LHY,* which allows the induction of the evening-phased genes *EARLY FLOWERING3* (*ELF3*), *ELF4*, and *LUX ARRYTHMO* (*LUX*) transcription factor (Liu et al., 2016). *LUX, ELF3*, and *ELF4* form the Evening Complex that represses *PRR9* (Herrero et al., 2012). The Evening Complex interacts with other clock and with red-light signaling components (such as phytochromes, and *COP1*, etc.) (Huang et al., 2016).

At night, *TIMING OF CAB EXPRESSION1 (TOC1;* also known as *PRR1*) contributes to the repression of *CCA1* and *LHY* transcription (Huang, 2012). In addition, *TOC1* interacts with *PHYTOCHROME INTERACTING FACTOR3* (*PIF3*) to repress transcription of their co-target genes (Soy et al., 2016). In addition to these repressors, other genes such *LIGHT REGULATED WD1* (*LWD1*) and *LWD2*, act as activators of *PRR9*, *PRR5*, and *TOC1* (Wang et al., 2011).

Transcriptional and posttranslational regulation of *CO* is important for incorporating day-length information into the flowering mechanism. In the morning, *CO* transcription is repressed by the *CYCLING DOF FACTOR* (*CDF*) family (Fornara et al., 2009). Transcription of *CDFs* is induced in the morning by *CCA1* and *LHY* (Niwa et al., 2007), and repressed by *PRR9*, *PRR7*, and *PRR5* in the afternoon (Nakamichi et al., 2012). The photoreceptor *FLAVIN-BINDING, KELCH REPEAT, F-BOX 1 (FKF1)* removes *CDF*-dependent repression of *CO* transcription in the LD afternoon (Fornara et al., 2009). *FKF1* also forms a complex with *GI*, the *FKF1-GI* complex is involved in the degradation of *CDF1*. This temporal degradation in LD is achieved by the coincidence of the circadian clock-controlled timing of *FKF1* and *GI* expression with perception of light by *FKF1* (Kay, 2007). Once *CDF* is removed by the *FKF1-GI* complex from the *CO* promoter, the activators *FLOWERING BHLH* family bind to *CO* and activate its transcription (Ito et al., 2012). *CO* transcript is highly expressed from the late afternoon to the dawn, but CO protein only accumulates in the late afternoon in LD photoperiods. Moreover, to set a narrow time window for CO protein stabilization, plants utilize multiple photoreceptors. Blue-light photoreceptors, *CRY1* and *CRY2*, stabilize *CO* in a light-dependent manner by attenuating *COP1-SUPPRESSOR OF PHYA-105 1* (*SPA1*) activity throughout the day (Zuo et al., 2011). Two phytochromes, *PHYA* and *PHYB*, act antagonistically on CO protein stability regulation. CO protein is destabilized by red light through *PHYB*, but stabilized by far-red light through *PHYA* (Valverde et al., 2004).

The small globular protein *FLOWERING LOCUS T* (*FT*) has originally been described as a key regulator of the photoperiod pathway, *FT* gene constitutes a central integrator of diverse endogenous and environmental signals (reviewed in Song et al., 2015; Srikanth & Schmid, 2011). FT protein is produced in the phloem companion cells (PCC) in the leaf vasculature and is subsequently transported through vasculature to the vegetative shoot apical meristem (SAM), where it interacts with 14-3-3 proteins and the bZIP transcription factor *FD*. This flower-promoting complex directly binds to the promoters of flowering time and floral homeotic genes to convert the vegetative meristem into a reproductive inflorescence meristem (Abe et al., 2005; Collani et al., 2019; Kawamoto et al., 2015). Therefore, *FT* functions as the key floral promoter. *Gibberellic acid* (*GA*) is required for proper induction of flowering through *FT* in LD (Porri et al., 2012), while *DELLA* proteins act as negative regulators of *FT* expression in vascular tissues (Galvão et al., 2012). Other transcription factors, such as *CIBs* redundantly activate *FT* expression (Liu et al., 2013).

1.7. Photoperiod response-related genes in legumes

Control of flowering time in legumes is an important factor in adaptation and crop production. Several works have begun to shed light on genes and mechanisms involved in control of flowering by environmental factors. While the basic genes and gene families central to pathways controlling flowering time in Arabidopsis appear to be largely conserved in legumes, there are numerous examples of gene duplication and loss.

The major crop legumes fall within two sister clades, galegoid and phaseoloid clades (Collani et al., 2019). In general, species within the galegoid clade (e.g., pea, lentil, chickpea, faba bean) are from temperate regions and with respect to flowering time control are vernalization-responsive LD plants, whereas those in the phaseoloid clade (e.g., soybean, cowpea, pigeonpea, common bean) generally originate from lower latitudes and are SD plants (Summerfield & Roberts, 1985).

The orthologs of *PHYA* and *GI* are important regulators of photoperiodic flowering in several legumes such as pea and soybean, functional variation in these orthologs is clearly associated with differences in the expression of *FT* genes (Hecht et al., 2007; Liu et al., 2008; Watanabe et al., 2011). There are three distinct phytochromes in legumes (*PHYA*, *PHYB*, and *PHYE*), and lacks a representative of the ancient *PHYC* clade, although the *PHYA* lineage has undergone a more recent duplication in the phaseoloid clade (Liu et al., 2008). The cryptochrome gene *CRY1* has also been duplicated in the phaseoloid legumes, while an older duplication of the *CRY2* gene is common to all legumes (Platten et al., 2005). The galegoid clade appears to have only a single gene orthologous to the circadian-clock related factor genes *CCA1* and *LHY,* whereas the *TOC1*, *GI*, and *ELF3* genes have variously undergone duplication in both legume groups, galegoid and phaseoloid clades (Hecht et al., 2007). The CO protein is represented by two co-orthologs clades in the SD legumes, but only one in the LD legumes (COLa) (Wong et al., 2014). Another feature of legumes is the expansion of the *FT* gene family. Legumes have three distinct subclades of *FT* genes; *FTa*, *FTb*, and *FTc* (Hecht et al., 2011). Legumes have additional *SVP* and *SOC1* genes (Jaudal et al., 2014).

A transcription factor unique to legumes, named as *E1*, seems to be vital in regulating photoperiodic flowering in soybean (Cao et al., 2017; Xia et al., 2012). In wild soybean, *E1* inhibits flowering (Cao et al., 2017; Xia et al., 2012). The molecular mechanism of *E1* has been well studied in soybean, with genes acting upstream of *E1* (such as *PHYAs*, *LHYs*, *Tofs*) (Lu et al., 2017, 2020; Xu et al., 2013) and genes acting downstream of *E1* (such as *FTs*) reported (Kong et al., 2010; Watanabe et al., 2011).

1.8 Flowering time in common bean

Flowering time is a key trait determining the seed yield in many crops such as common bean, so its manipulation is a relevant plant breeding target to produce varieties that are better adapted to changing climatic conditions (Jung & Müller, 2009). Thus, early flowering can be exploited to escape stressful conditions (e.g., drought and heat) and/or pathogen attacks that can both negatively affect the production. On the other hand, late flowering means a long vegetative phase and higher yields because it provides a photosynthate accumulation increased. A flowering time well-synchronized with target environmental conditions would achieve better crop yields. Moreover, the genetic manipulation of the time-to-flower trait is one of the major targets in plant breeding programs, so a wide geographical range of cultivation presents a major challenge.

The common bean is a facultative SD plant (GArner & Allard, 1920). Wild bean accessions and most Andean cultivars are mainly photoperiod sensitive, whereas Mesoamerican cultivars are mostly less sensitive to photoperiod or DN (White & Laing, 1989). The prevalence of photoperiod insensitivity among cultivated beans indicates that day-neutrality in beans is a recently acquired trait as the result of selection pressure applied during domestication and more recent breeding efforts. White & Laing (1989) identified eight photoperiod response classes (Classes 1–8) in this species: Class 1 displayed 0–3 d delays, while Class 8 displayed over 100 d delays. Bean cultivars belonging to all these classes are cultivated in a variety of conditions around the world (Beebe, 2012).

In common bean, several Quantitative Trait Loci (QTL) mapping and association studies have detected some genomic regions associated with flowering (Blair et al., 2006; González et al., 2016; González et al., 2021a; Koinange et al., 1996; Pérez-Vega et al., 2010; Raggi et al., 2014; Samira Mafi Moghaddam, 2016; Yuste-Lisbona et al., 2014). However, the majority of the loci were detected as QTL, and probably, different works have detected the same loci; however, the lack of common markers among different mapping studies makes difficult to determine whether or not they are the same locus.

In the last years, two genetic components of the day-length sensing and response mechanism have been identified in common bean, orthologs of *PHYA3* and *COL2*-like genes. Previous studies had identified a strong dominant photoperiod sensitive gene, named as *Ppd*, that regulates flowering time sensitivity in beans (Gu et al., 1998; Kornegay et al., 1993; Kwak et al., 2008; Wallace et al., 1991; White et al., 1996; White & Laing, 1989). More recently, the red/far-red photoreceptor gene *PHYA3* was identified as the *Ppd* gene on chromosome 01 (Weller et al., 2019). Later, (González et al., 2021b) showed that allelic variation for a *CONSTANS-like* gene,

COL2, underlies a second locus that regulates daylength-insensitive early flowering confer early flowering under LD conditions. Interestingly, the analysis of 40 haplotypes among diverse wild, landrace and domesticated accessions showed that recessive *col2* alleles confer early flowering under LD conditions and that arose independently in both gene pools, demonstrating a replicated evolution of daylength insensitivity in bean through mutation of *COL2*. Investigation of the molecular processes that act downstream or in parallel of *COL2* and *PHYA3* is therefore likely to provide further insights into the genetic control of flowering, such outcomes may be useful in securing common bean as a crop for future climates and to higher latitudes.

2. Aims and scope of the study.

Preliminary mapping results of Devoleg Group revealed a QTL for flowering time, named as DTF-9.4, which was mapped on chromosome 09 and explained more than 30% phenotypic variance. By phenotyping and genotyping recombinant lines for the mapped QTL interval its region narrowed to 200 kb, with only two candidate gene annotated, *PvFUL* and *PvE1*. The purpose of the present study was validating the effect of DTF-9.4 in LD and to analyze the influence of this QTL on other related-traits using near-isogenic lines (NILs) developed through marker-assisted selection. Thus, two pairs of contrasting NILs, dtf-9.4 line (*col2, e1, ful1*) and DTF-9.4 line (*col2, E1, FUL1*), were used to confirm the effect of the QTL in a *col2* mutated background.

3. Material and methods

3.1. Materials and growth conditions for flowering time

Background: A population of 185 RILs ($F_{2:7}$) (BN population), derived from a cross between a photoperiod-insensitive and early flowering cultivar from Spain (Bolita, PHA0595) and a late flowering photoperiod-responsive landrace from Bolivia (PHA1037) had been used previously for linkage map construction and QTL analysis of flowering time (González et al., 2021a). Bolita is a large white seeded cultivar from Spain with a type II indeterminate growth habit, and PHA1037 is a large seeded red nuña accession from Bolivia, with a type IV indeterminate climbing growth habit. A QTL named as DTF9.4 in Chr.09 was identified in various environments, explaining between 2-32% of the phenotypic variation. Individuals carrying residual heterozygosity for the QTL DTF9.4 region were identified in progeny of a single RIL from this population (RHL26). These NILs were developed with a *col2* mutated genetic background, since the *COL2* WT does not reveal the effect of other genes involved in the photoperiod pathway as are masked by the strong effect of this gene. Finally, two near-isogenic segregating populations: NILs 26-48 (dtf-9.4 line: *col2*, *e1*, *ful1*) and NIL 26-65 (DTF-9.4 line: *col2, E1, FUL1*) were developed for fine-mapping and expression analysis.

Material of this study: NILs (200 seeds of each one), and parents (PHA0595 and PHA1037, 10 seeds of each one) were grown under LD (natural light was supplemented with artificial light) in a greenhouse trial at Pontevedra, Spain (latitude 42º 24′ 17.99″ N, longitude 8º 38′ 38.2″ W, altitude 40 m above sea level) (14h light, 20–25ºC night–day regime, relative humidity 50%–70%). These were sown in 28 cm pots prepared with a 1:1 gravel: vermiculite mixture. A randomized complete block design with two replications was employed. Date of sowing was 12/11/2021. All plant material was supplied with sufficient water and nutrients.

Flowering traits: Days to flowering (DTF) was recorded as the number of days between seedling emergence and the day of opening of the first flower. Node of flowering initiation (NFI) as the number of nodes on the main stem to the first flower. Days to fully expanded immature pod (IP), days to physiological maturity pod (MP), with fully developed seed (yellowish pod), and days to dry pod (harvest maturity) (DP).

3.2. dCAPS genotyping

Genomic DNA was extracted from all individual plants of each genotype (Anex I). DNA concentrations were measured using the Nanodrop 2000 spectrophotometer (Figure 3A). The Group designed markers for the polymorphisms found in the genotype insensitive PHA0595 for *PvCOL2*, *PvE1*, *PvFUL1*, and *PvPHYA3* (Table 1). Programs PCRs were carried out in a final volume of 20 µl containing 100 ng genomic DNA, 1X PCR buffer, 2 mM dNTPs, 10 pmol of each primer and 1 U of Taq DNA polymerase (GoTaq Promega). Amplification was carried out in a Thermocycler Agilent Technologies (Figure 3B). Once the product was amplified, 10 µl were taken for digestion with the specific enzyme depending on the gene to be genotyped (Table 1). The digestion mix contained 7.8 µl of MQ water, 2 µl of buffer and 0.2 µl of enzyme. The digestion products obtained for were resolved on 2 % agarose gel by electrophoresis (Figure 3C). Most of the samples corresponded to their pre-established genotype (*NILcol2e1ful* or *NILcol2E1FUL*), only a few showed discordant results in their genotyping, which were eliminated for further analysis and their seed was not collected (Figure 3D). All individuals were genotyped with the four markers to ensure their belonging to the corresponding genotypic class.

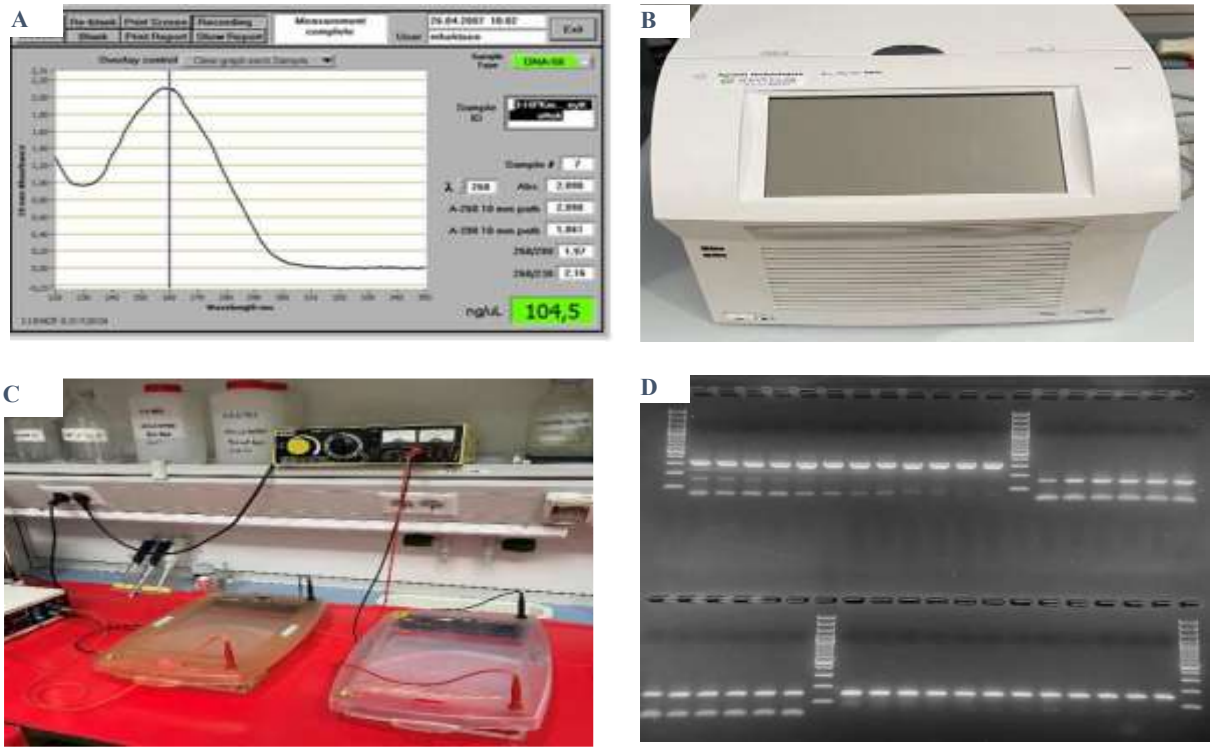


Figure 3. A. Screen of nanodrop showing the concentration and the ratio of DNA. B. Thermocycler Agilent Technologies. C. Electrophoresis equipment: sources and cuvettes. D. Agarose gel with the genotyped of NILs samples with *PvE1* marker (246 pb) and *PvCOL2* (125 pb).

Table 1. CAPs/dCAPs markers used to genotype the NILs segregating material of chromosome 9, the markers used for genotyping with the flowering genes *PvCOL2* and *PvPHYA3* are also shown.

Marker/Gen	**Pos. (Mb)**	**Primer-F**	**Primer-R**	**T[a]**	**Bands (parents PHA0595 / PHA1037)**	**Enzyme**
Phvul.009G203400 (*PvFUL1*)	30.86	CAACACTCTCGCAAAGAAGG	TCCATTTCATCAGCTTGTCG	60	111+62 / 174	VspI
Phvul.009G204600 (*PvE1*)	31.04	AGACTTCGTGCGAAGAAGAGA	AAGGATGTGGATGTGAAGCAC	63	246/284	CAP
Phvul.004G046601 (*PvCOL2*)	56.48	TGTGTGGGTGTGTGAAGGGT	GACCCAAGATGAGGAGAACG	60	125+30/155	HphI
Phvul.001G221100 (*PvPHYA3*)	47.64	TGCAACACAACTTTTCAAGGA	ATCACCATCACGTCCAAACA	60	164/101+63	MnlI

3.3. Statistical analyses

To evaluate the effect of the DTF9.4 region, differences among the four groups of NILs and the parents were evaluated together using ANOVA. In the ANOVA model, genotype was considered as fixed factors. All the analyses were carried out with was conducted using XLSTAT 2014 (http://www.xlstat.com). Statistical analyses were undertaken using *t*-tests to compare phenotypic variation in the NIL pairs.

4. Results and discussion

4.1. Genotyping and validation of NILs

To carry out the genotyping of the plants, the use of specific markers for each gene was essential to be able to obtain the complete genotyping of all the lines used in the study and can select the plants needed for the trial. Once we had reviewed the results of the genetic analysis, we merged them with the phenotyping results and began to consider all data together.

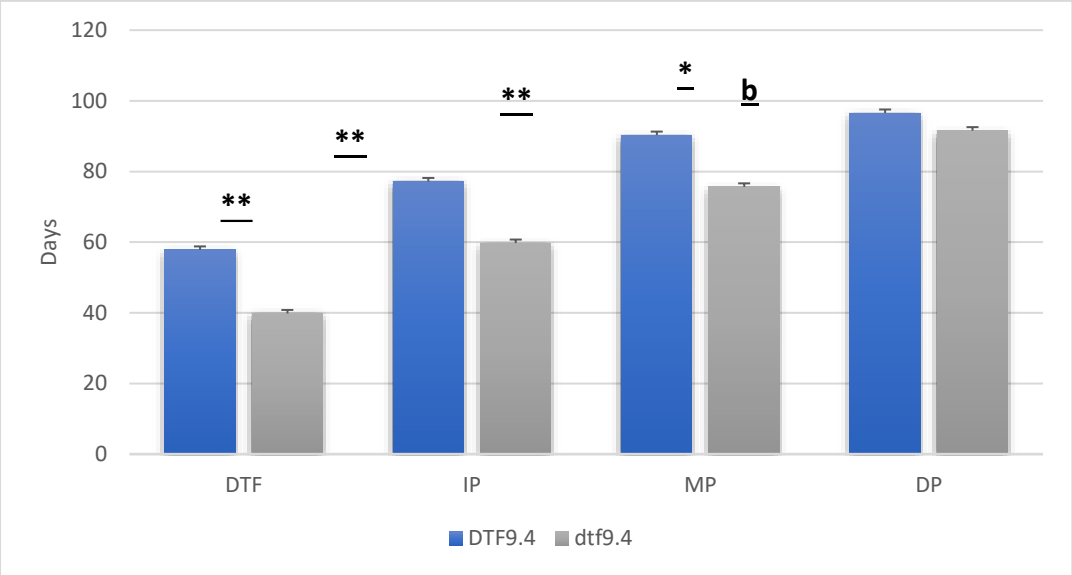
4.2. Agronomic performance of NILs in comparison with both parents.

To evaluate the genetic effects of DTF9.4 on reproductive traits, NIL26-48 (dtf-9.4 line) and NIL26-65 (DTF-9.4 line) were compared to identify delay in flowering time. The ANOVA indicated significant differences (*P<0.001*) between both groups of NILs for all traits but not between replications (Table 2, Figure 4). NIL dtf9.4, with *e1* mutated, flowered almost the same time as the insensitive parental PHA0595 (39 and 36 days, respectively). Flowering time of the NIL DTF9.4 was around 20 days later. The sensitive parent PHA1037, with *COL2* WT, did not flower. The difference in days to flowering between both classes continued until maturity and dry pod. A significant difference was also noted for node of flowering initiation, with a mean of 8 for *NILe1* class and 14 for the *NILE1* class (Table 2, Figure 4).

Table 2. Means ± standard error and ranges of flowering and fruit ripening traits of segregating classes from RHL26 with *col2* genetic background.

Genotype		**N**	**DTF-nasc (range)**	**NFI (range)**	**IP-nasc (range)**	**MP-nasc (range)**	**DP-nasc (range)**
col2/e1/ful1	PHA0595	10	36 ± 0.02 (34-37)	6	52 ± 0.02 (50-65)	71 ± 0.01 (69-72)	83 ± 0.01 (81-85)
col2/e1/ful1	NIL26-48	189	39 ± 0.19 (33-45)	8 ± 0.08 (5-10)	60 ± 0.20 (53-65)	76 ± 0.29 (41-85)	91 ± 0.40 (79-102)
col2/E1/FUL1	NIL26-65	177	58 ± 0.41 (53-65)	14 ± 0.19 (10-22)	77 ± 0.41 (66-95)	91 ± 0.21 (86-101)	97 ± 0.45 (87-120)
COL2/E1/FUL1	PHA1037	10	Not flowering				

DTF: days to flowering; NFI: node of flowering initiation; IP; days to immature pod; MP: days to mature pod; DP: days to dry pod.



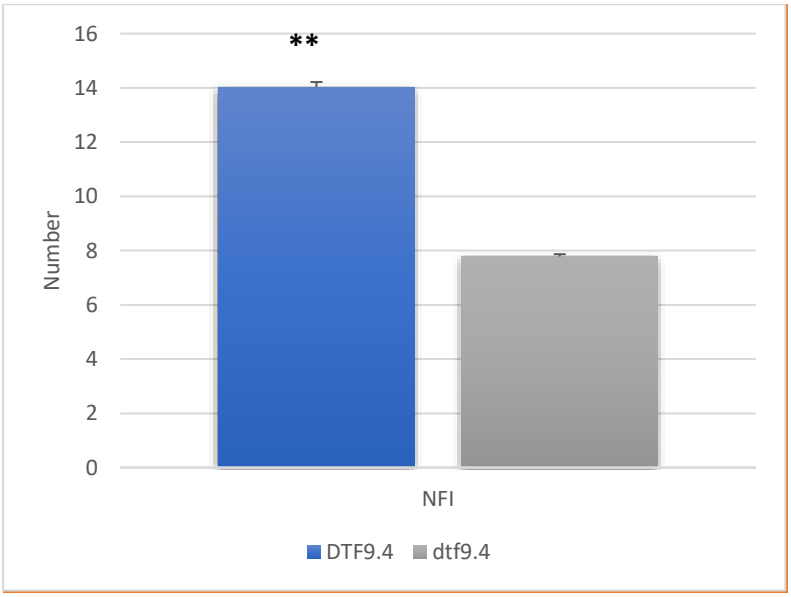


Figure 4. Differences in agronomic trait between the confirmed NILs dtf9.4/DTF9.4. Data represent mean ± SE with error bar on top. * Indicates significant difference at $P \leq 0.05$; ** indicates significant difference at $P \leq 0.01$. Statistics done using *t*-test.

These results indicate that the mutation in the candidate genes of the QTL was sufficient to induce early flowering under the LD condition. The phenotype detected from the two NILs revealed that dtf9.4 allele significantly promoted the flowering time and maturity under the LD conditions. It would be interesting to determine the effect of QTL on SD environment. Moreover, the QTL showed a pleiotropic effect in node of flowering initiation. Flowering represents the transition from the vegetative phase to the reproductive phase in plants. The formation or development of branch number mainly occurs during vegetative growth stage. Plants subsequently

shift to the reproductive phase when genes that control flowering are activated. Therefore, the expression of flowering time genes directly or indirectly can influence number of nodes of flowering initiation.

The main candidate gene of QTL DTF9.4 is the *E1* gene. In soybean, the expression levels of *E1* are regulated by daylength, presenting a rhythmic pattern with two peaks under LD conditions, and much lower expression levels under SD conditions (Xia et al. 2012; Xu et al. 2015; Zhai et al. 2015). Cober et al. (1996) also developed NILs *E1/e1* in soybean and found that *E1* allele delayed both flowering and maturity by 16 days under the natural day length compared with early-maturing alleles. However, under the 12 h SD condition, there are no differences in flowering and maturity between both NILs, indicating that *E1* inhibits flowering only under LD conditions. Our results in common bean agree with the effect of *E1* on LD. This leads us to think that it would be interesting to see the effect of DTF9.4 in SD and the *E1* expression patterns of both NILs in both photoperiods to see if it acts the same way.

The *e1* mutants in soybean exhibited significant changes in the architecture, including initiation of terminal flowering, formation of determinate stems, and decreased branch numbers (Wan et al., 2022).These data also agree with our results, in which the mutated NIL has a lower number of floral initiation nodes and strengthens the pleiotropic effect of the gene on plant architecture.

5. Conclusions

The NILs developed and validated in this study confirmed that DTF9.4, is a major locus responsible for flowering time under LD. Analysis of the markers and phenotype profiles of the NILs revealed that *E1* region was responsible for the photoperiodic response in the NILs developed in *col2* background. The confirmed NILs and identified candidate gene are valuable resources for future studies, although its phenotyping in SD environment, the study of the gene expression of the candidate gene and its validation in other germplasm will be necessary for a definitive proof of the role of the candidate gene in the common bean photoperiod pathway.

Annex 1

For PCR

SOLUTIONS

Extraction Buffer (EB): 250 ml

- 5 g CTAB
- 25 ml 0.2M EDTA
- 25 ml 1M TRIS-HCl pH
- 70 ml NaCl2
- pH 8.0 con 1 M TRIS-HCl 8.0
- No autoclave

Precipitation Buffer (PB)

- 50 mM Tris-HCl pH8
- 10 mM EDTA
- 1% w/v CTAB

Other solutions

•Chloroform-Isoamylic alcohol 24:1

- 1.5 M NaCl
- Rnase A (25mg/ml)
- Ethanol (EtOH) 70% and 100%

DNA Extraction Protocol

1. Collect a young leaf in aluminum envelope in liquid nitrogen and store at -80ºC. Pulverize the aluminum sachets. Divide in two tubes: (1) Eppendorf ¼ tissue, and (2) cold cryovial in liquid nitrogen and store at -80°C.
2. Add 600µl EB and agitate again in shaker mill for 1 min. Spin.
3. Incubate 30 min at 60ºC, occasionally mixing gently.

4. Extract TWICE with 500µl Chloroform-Isoamylic alcohol (24:1) -20ºC, mix, spin 10min 14000rpm, transfer the aqueous phase to a new Eppendorf tube.

5. Add 1ml of PB. Mix gently. A thread like precipitate forms at RT in 5-10 min (can leave longer at this step)

6. Centrifuge 10 min 14000 rpm and discard the supernatant

7. Dissolve the pellet in 300 µl of 1.5M NaCl containing 1µl RnaseA (25mg/ml).

8. Incubate 30mins or more at 50ºC

9. Add 600µl 100% EtOH -20ºC, mix gently and let it sit at room temperature for 30 mins (can be longer).

10. Centrifuge 10mins 14000rpm.

11. Carefully pour out EtOH and pat dry on paper towel

12. Wash the pellet with 200µl 70% EtOH -20ºC.

13. Centrifuge 5mins 14000rpm.

14. Carefully pour out EtOH and pat dry on paper towel.

15. Air dry (1hr) or Spin Vac (5min) the pellet.

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