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GENETIC AND MOLECULAR CONTROL OF THE FLOWERING TIME IN SOYBEAN (*Glycine max* (L.) Merrill)

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Photoperiod response to flowering is one of the most vital factors that affect in regional adaptation and yield in soybean. Soybean adaption at high latitude areas (long-day) requires early flowering and low photoperiod sensitive cultivars; adaptation to low latitudes (short-day) areas needs delayed flowering cultivars, which maximize vegetative growth and seed yield. This paper represents a genetic and molecular regulation of flowering time in soybean, which will help broad adaptability across latitudes. It is revealed that one to eleven main genes control the flowering time in soybean. The FT family of flowering integrators plays a central role in controlling the flowering time. The juvenile growth phase (JGP) determines the development rate for flowering; a long JGP results in the lengthening of the vegetative period and increases the soybean production in low latitude areas. This review outlines the JGP-related gene in soybean. We emphasize the interaction between major genes and QTLs for flowering in soybean. Several major genes and quantitative trait loci (QTLs) for flowering interact with one another including the environment to greatly influence flowering time. The molecular ground information of the flowering in Arabidopsis will help to understand the molecular dissection of flowering in soybean. This information could be used for breeding of high-yielding soybean cultivars in different latitudinal areas.

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INTRODUCTION

Garner and Allard (1920) recognized the importance of photoperiodic research in plants long decay ago. To date, it is also a priority topic in plant science. The evolution of flowering in soybean is the main factor of adaptation to the new environment (Fuller, 2007). Soybean can be grown from low to high latitude areas. The cultivation area of each cultivar is limited to a narrow range of latitudes. The wide adaptability of soybean has been created by natural variation in the major genes and quantitative trait loci (QTLs) controlling flowering. The information of flowering time controlling genes and quantitative trait loci (QTLs) could be helpful for wide adaptability in soybean. For instance, the introduction of delayed flowering genes-related genotypes may facilitate to produce new genotypes that lead to a longer vegetative growth period for cultivation in tropical areas. Similarly, early flowering genes-related genotypes are desirable where soybean is grown as a short-season crop. Therefore, it is rather important to provide distinct information about the flowering time-controlling genes of soybean to adapt to a diverse environment.

Flowering times were well guarded by a major gene in soybean. To date, 10 major genes have been introduced as E1 to E9 and J ((Bernard, 1971; Buzzell, 1971; Buzzell and Voldeng, 1980; McBlain and Bernard, 1987; Ray et al., 1995; Bonato and Vello, 1999; Cober and Voldeng, 2001; Cober, et al., 2010; Kong et al., 2014). These genes have different criteria under different photoperiodic conditions. However, the recessive alleles e6 and j were responsible for the long-juvenile traits to the condition later flowering (Bonato and Vello, 1999; Ray et al., 1995). Linkage analyses showed that the molecular linkage groups C1 (Gm04) for E8 (Cober et al., 2010), C2 (Gm06) for E1 and E7 (Cober and Voldeng, 2001a; Molnar et al., 2003), I (Gm20) for E4 (Abe et al., 2003; Molnar et al., 2003), L (Gm19) for E3 (Molnar et al., 2003) and O (Gm10) for E2 (Cregan et al., 1999). Furthermore, many QTLs controlling time to flowering have been stated (Chapman et al., 2003; Cheng et al., 2011, Funatsuki et al., 2005; Githiri et al., 2007; Komatsu et al., 2007; Lee et al., 1996; Liu et aI., 2007; Poopronpan et al., 2006). Some of these QTLs most likely correspond to one of the known major genes, such as E1, E2, E3, E4, or E8 (Cheng et al., 2011; Funatsuki et al., 2005; Githiri et al., 2007; Khan et al., 2008; Liu and Abe, 2010).

On the other hand, flowering locus T (FT) is a vital integrator whose functions are preserved in the crop species. Few studies have focused on GmFT2a and GmFT5a as floral integrators in the case of soybean (Kong et al., 2010; Sun et al., 2011; Watanabe et al., 2011; Xia et al., 2012; Nan et al., 2014; Xu et al., 2015), because their expression patterns related with photoperiod (Kong et al., 2010), and their overexpression stimulates flowering even in noninductive conditions (Sun et al., 2011; Nan et al., 2014). Induction of GmFT2a and GmFT5a expression is regulated by two PHYA genes E3 and E4; expression is inhibited under long day conditions, but this inhibition is eliminated in a double recessive homozygote, e3/e3 e4/e4 (Kong et al., 2010; Xu et al., 2015). This PHYA-dependent regulation is mediated by E1 and E1L genes, repressors of GmFT2a and GmFT5a expression (Xia et al., 2012; Xu et al., 2015). E1 and E1L genes hinder flowering by down-regulating soybean orthologues of Arabidopsis FLOWERING LOCUS T (FT) genes, GmFT2a and GmFT5a, under long day (LD) conditions, even though the effects of E1L genes on flowering are weaker than that of E1 (Xu et al., 2015). In this study, we will provide enough information about major genes and QTLs for flowering that will absolutely increase the geographical adaptation of soybean.

E1 and its identities

E1 is the first identified gene trace back as early as the 1920s when photoperiodism was discovered (Owen, 1927). This gene has large effects on flowering and maturation and important rule in photoperiod sensitivity (Upadhyay et al., 1994; Xu et al., 2015; Han et al., 2019). The report showed E1 alleles displayed an early flowering time phenotype, without considering of the genetic background at other E loci or daylength conditions (Xia et al., 2012). E1 has two homologs in soybean, E1La, and E1Lb (Xia et al., 2012; Xu et al., 2015), with expression patterns similar to that of E1 under both LD and short day (SD). Both genes function as inhibitors of flowering, like E1, as revealed by virus-induced gene silencing (Xu et al., 2015). Furthermore, a single-base deletion in the E1Lb coding sequence confers earlier flowering under both red (R) light and far-red (FR) light-enriched LD, independently of E1 (Zhu et al., 2019). Furthermore, the E1 in soybean represses the expression of orthologs of the florigen gene FLOWERING LOCUS T (FT) and inhibits flowering (Xia et al., 2012; Zhang et al., 2016).

E2 and its identities

E2 encodes a soybean ortholog of Arabidopsis GIGANTEA (GmGIa) (Watanabe et al., 2011). This gene effects on soybean flowering. When upregulated regarding the Cauliflower mosaic virus (CaMV) 35S promoter as a control, E2 could not show the delayed flowering phenotype of the Arabidopsis mutant, and it increased the flowering time of wild-type (Col-0) Arabidopsis plants, whereas the e2 allele partially rescued the phenotype but there was no effect on the flowering of Col-0 (Wang et al., 2016b). These results showed that the functions of E2 varied from those of GI in Arabidopsis. Furthermore, Li et al., 2013 reported that circadian regulatory systems are controlled by the E2 gene.

E3 and its identities

E3 homologs encode the Arabidopsis photoreceptor phytochrome A (phyA) i.e., GmphyA3 (Liu et al., 2008a; Watanabe et al., 2009). E3 is responsible for regulating photoperiodic flowering under both natural and artificially induced LD conditions (Cober et al., 1996a). The E3 was initially characterized in experiments examining flowering in response to artificial LD, where natural daylength was increased up to 20 h using light sources enriched in R or FR (Cober et al., 1996b). The response to R-enriched LD was influenced only by E3. Therefore, the phyA (GmphyA3) proteins confer sensitivity to LD, particularly to FR-enriched LD (Cober et al., 1996b). E3 has great effects on flowering with the natural conditions in a wide range of latitudes (Lu et al., 2015). The function of E3 in mediating the flowering response to a wide range of R:FR ratios contrasts with phyA in Arabidopsis, which is mainly occurred for flowering responses under FR-rich day extensions (Johnson et al., 1994; Song et al., 2018). There is also reported that e3 affect by LD, particularly under FR-rich day extensions and in the presence of functional E1 (Cober et al., 1996a, 1996b; Cober and Voldeng, 2001a), resulting in contributions from other phytochrome photoreceptors.

E4 and its identities

Liu et al. (2008a) stated the photoreceptor phytochrome is GmphyA2 between NILs that were photoperiod sensitive and insensitive for E4. GmphyA2 co-segregated with E4 on MLG I (Gm20) by the concrete genetic mapping (Abe et al., 2003; Liu et al., 2008a). In addition, the NIL for e4 showed an impaired de-etiolation (greening) response under continuous FR-light conditions using Arabidopsis (Neff and Chory, 1998). Liu et al. (2008a) reported that the E4 gene encodes the GmphyA2 protein and that the recessive e4 allele is a loss-of-function allele. Soybean possesses a homoeologous copy of GmphyA2, namely GmphyA1, in MLG O (Gm10) (Choi et al., 2007; Liu et al., 2008a). The function of GmphyA1 remains undetermined because no genetic variant is available yet at this locus. However, two findings may indicate that E4 is responsible for both de-etiolation response and flowering under FR-enriched LD conditions.

E5 and its identities

McBlain and Bernard (1987) first identified the new locus E5 and stated the genetic effect of E5 on time to flowering and maturity. Auchithya et al. (2016) looked at E series gene assigned to molecular linkage groups (MLGs) without E5. He conducted an experiment using F2 populations expected to segregate for E5. Finally, results showed that there was no candidate QTL for E5 was found. Therefore, a unique E5 gene may not exist.

E6 and its identities

Recessive e6 is responsible for late flowering under short period and prolongs both vegetative and reproductive growth (Ray et al., 1995; Bonato and Vello, 1999). The maximum effect of e6 was observed under 12 h (Cober, 2011). The molecular parameter of E6 has not yet been determined, although genetic analysis indicated that E6 is closely linked to J (Li et al., 2017).

E7 and its identities

Genetic analysis showed that the E7 is responsible for early flowering (Cober and Voldeng, 2001b; Cober et al., 2010). The recessive allele of this loci grants with earlier flowering and maturity under FR-enriched LD or natural daylengths (45.42°N). E7 is situated on the chromosome (Chr) 6 (Cober and Voldeng, 2001a; Molnar et al., 2003). It is also stated that the allelic effects of the E7 loci are not only relevant in early flowering but also contribute to the control of flowering time and maturity in the merger with various maturity genotypes (Kong et al., 2018).

E8 and its identities

The E8 loci were identified as an early-flowering character (Cober and Voldeng, 2001b; Cober et al., 2010). It is reported that the E8 is located on Chr4 (Cober et al., 2010). The allelic effects of the E8 loci showed a similar charter-like E7.

E9 and its identities

E9 has been identified as an early flowering character by the molecular dissection of a QTL from a wild soybean accession (Kong et al., 2014; Liu et al., 2007). Zhao et al. (2016) reported that E9 is FT2a, an ortholog of Arabidopsis FLOWERING LOCUS T. without considering of daylength conditions, the e9 recessive allele was transcribed at a very low level in comparison which delays flowering.

E10 and its identities

GmFT4 is expressed in Arabidopsis, which is delayed flowering (Zhai et al., 2014). Similarly, Samanfar et al. (2017) reported that GmFT4 may be responsible for E10, which distinctly delays flowering.

E11 and its identities

E11 is located on Chr7 which affects flowering time and maturity (Wang et al., 2019). A mapping analysis revealed that the most likely candidate gene for E11 (Glyma.07G48500) is one of the four soybean homologs of Arabidopsis CIRCADIAN CLOCK ASSOCIATED 1 (CCA1) and LATE ELONGATED HYPOCOTYL (LHY) (Wang et al., 2019).

J gene and its identities

The characteristics of recessive j alleles inhibit flowering and prolong both the vegetative and reproductive growth periods, this phenomenon is known as the “long-juvenile, long pre-inductive growth phase” which is an adaptive character in low latitudes areas (Ray et al., 1995; Bonato and Vello, 1999). The QTL mapping and map-based cloning showed that the J gene is a homolog of Arabidopsis EARLY FLOWERING 3 (Lu et al., 2017; Yue et al., 2017). Functional analysis of the J gene revealed that promoting flowering not only under SD but also under daylengths of 14 h using transgenic and conventional near-isogenic lines (Lu et al., 2017). The molecular basis of the J gene is closely linked to E6 (Li et al., 2017).

FT homologue

It is well known that soybean has 12 FT-like genes in six homeologous pairs: GmFT1a/b, GmFT2a/b, GmFT2c/d, GmFT3a/b, GmFT5a/b, and GmFT4/6. GmFT2b, GmFT4, GmFT5b, and GmFT6 are expressed at very low levels in trifoliate leaves under SD conditions (Kong et al., 2010). GmFT2a and GmFT5a seem to be a major part of the FT family (Kong et al., 2010) due to early flowering (Guo et al., 2015) and delayed flowering when downregulated by RNA interference (RNAi) (Guo et al., 2015). On the other hand, GmFT1a and GmFT4 are inhibitors of flowering (Zhai et al., 2014; Liu et al., 2018a). GmFT1b is also responsible for delayed flowering (Liu et al., 2018a). GmFT6 did not affect flowering time regarding ectopically expressed in Arabidopsis (Fan et al., 2014). However, GmFT6 inhibits flowing considering Arabidopsis TERMINAL FLOWER1 (TFL1) promoter (Wang et al., 2015).

Responsible gene for high latitude

Photoperiod is longer in high latitude areas, the cultivars whose have early flower and mature for adaptive in these areas. E1, E3, and E4 are the major loci for the photoperiod sensitivity and adaptation to high latitudes areas (Cober et al., 1996a; Abe et al., 2003; Liu and Abe, 2010; Xu et al., 2013). Soybean insensitive cultivars are also important cultivars also another option to increase adaption in high latitude areas. The most common genotype in photoperiod-insensitive cultivars is the double recessive e3 e4 genotype (Xu et al., 2013).

Responsible gene for low latitude

Brazil is the pioneer of soybean production in low latitude areas (Neumaier and James, 1993). Brazil introduces long juvenile traits in low latitude targeted areas (Carpentieri-Pípolo et al., 2002). The long juvenile cultivars produce enough vegetative growth periods under SD, resulting in a larger grain yield (Carpentieri-Pípolo et al., 2002). Ray et al. (1995) reported that the long juvenile characteristic is controlled by a single recessive gene. The Soybean Genetic Committee approved the symbol J/j is responsible for the long JGP. It is also stated that the recessive e6 alleles inhibit flowering and prolong both the vegetative and reproductive growth periods at low latitudes areas (Bonato and Vello, 1999).

High priority gene for photoperiod response

Major gene is the focus of study in a plant. In soybean, most of the priority has been given to the functional importance of the E1/E1L genes. Genetical evidence showed that the E1 immediately upstream of FT genes as a direct transcriptional regulator but downstream of most other flowering time loci. Multiple photoreceptors for photoperiodic flowering have been caught by light signals (Liu et al., 2008a; Zhang et al., 2008; Watanabe et al., 2009). The phytochrome A proteins (including E3 and E4) are activated by light signals at LDs and upregulate E1 transcription. The activities of circadian clock genes (morning phased genes: GmPRR3-GmLHY/ CCA1) and evening genes: J and GmLUX) are genetically dependent on E1. The effects of these genes on flowering could not affect by the absence of e1-nl background (Lu et al., 2017, 2020), suggesting that E1 is the main of these clock genes, a concept consistent with their roles in regulating E1 expression. Furthermore, it is also stated that soybean COL genes could function as an initiator of E1 expression, a better future for soybean research (Zhang et al., 2020b). Thus, E1 may play a main rule that integrating light and circadian clock signals and transferring these signals to FT orthologs as output, and E1 has become a high priority for future studies in soybean research.

Soybean orthologs of Arabidopsis flowering genes

Molecular studies of flowering reported that at least 100 genes are responsible by using artificially induced mutants in Arabidopsis (Ehrenreich et al., 2009, Hetch et al., 2005, Quecini et al., 2007). Many studies have identified and characterized the soybean orthologs of Arabidopsis photoreceptors, clock-associated, and flower-identity genes as flowering genes (Liu et al., 2007, 2008, 2010; Matsumura et al., 2009; Tasma and Shoemaker, 2003; Thakare et al., 2010). 333 orthologs of 92 Arabidopsis genes have been detected from among a total of 46,367 annotated genes (Watanabe et al., 2012). This author also stated that soybean possesses orthologs for most of the Arabidopsis flowering genes. It also recognized that a striking but expected feature resulting from the paleopolyploidy of the soybean genome (Cannon and Shoemaker, 2012; Schmutz et al., 2010): soybean clearly has multiple copies of most of the Arabidopsis gene related to flowering. Furthermore, QTL analysis through fine-mapping subsequent may help to identification and characterization of molecular ideas of major genes along with a candidate gene approach by the physical positions of Arabidopsis orthologs and QTLs for flowering in soybean.

Interaction between major genes and QTLs for flowering in soybean

The major genes and QTLs interact with one another during flowering in soybean e.g., the effects of E2 (qFT2) and E3 (qFT3) are weakened or masked in early-flowering genetic backgrounds by the presence of recessive allele at the E1 locus (Watanabe et al., 2004; Yamanaka et al., 2001). Yamanaka et al., 2001 reported that the two QTLs qFT2 and qFT3 identified in a cross between the Misuzudaizu, and Moshido Gong 503 cultivars exhibited only a small allelic effect on flowering time under an early-maturing background by the presence of recessive allele at qFT1 (e1e1), but the allelic effects became instinct in a late-maturing background (E1E1). Upadhyay et al. (1994) reported that there was no effect of allelic substitutions at either E2 or E3 in an e1e1 background in Clark NILs, whereas the effect of the E1 allele was marked and almost the same as that of the E2 and E3 alleles combined. Furthermore, the E2 and E3 alleles each interact positively with the E1 allele to enhance the photoperiod sensitivity (Upadhyay et al. 1994). A similar genetic interaction was observed in many researches (Saindon et al., 1989b; Abe et al., 2003).

CONCLUSION

- Photoperiodic research in flowering started since 1920 when Garner and Allard first identified this trait. To date, it is a demandable research idea to increase adaptability and increase the yield of crops.
- Over time, many researchers have characterized the genetic control of photoperiodic flowering genes and loci that contribute to increase the adaption of soybean.
- The molecular nature of different loci related to soybean flowering has been identified and outlined their various interactions and revealed how they combine in different ways to help soybean adapt to different latitudes.
- Many studies reported the central hub gene in the photoperiodic flowering in soybean.
- Recent studies solve the question about how phyA contributes to light sensing for the photoperiod response in soybean and how the E1 gene interacts in soybean flowering and the functional divergence of FT family genes.
- Most of the major genes and QTLs interact with one another as well as with the environments, which is a complex phenomenon.
- Ultimately, we are also got a clear idea about the molecular evolution of specific soybean flowering time alleles. This idea will facilitate to increase in the understanding of the genetic and molecular bases of flowering are expected to contribute to breeding to increase the adaptability of soybean.

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