Genetic and molecular bases of photoperiod responses of flowering in soybean

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Flowering is one of the most important processes involved in crop adaptation and productivity. A number of major genes and quantitative trait loci (QTLs) for flowering have been reported in soybean (Glycine max). These genes and QTLs interact with one another and with the environment to greatly influence not only flowering and maturity but also plant morphology, final yield, and stress tolerance. The information available on the soybean genome sequence and on the molecular bases of flowering in Arabidopsis will undoubtedly facilitate the molecular dissection of flowering in soybean. Here, we review the present status of our understanding of the genetic and molecular mechanisms of flowering in soybean. We also discuss our identification of orthologs of Arabidopsis flowering genes from among the 46,367 genes annotated in the publicly available soybean genome database Phytozome Glyma 1.0. We emphasize the usefulness of a combined approach including QTL analysis, fine mapping, and use of candidate gene information from model plant species in genetic and molecular studies of soybean flowering.

Key Words: soybean, flowering, photoperiod sensitivity, maturity gene.

Introduction

Soybean (Glycine max (L.) Merr.) is grown over a wide range of latitudes, from equatorial to at least 50 degrees north and 35 degrees south. However, the cultivation area of each cultivar is restricted to a very 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. At present, nine major genes have been reported to control time to flowering and maturity in soybean: E1 and E2 (Bernard 1971), E3 (Buzzell 1971), E4 (Buzzell and Voldeng 1980), E5 (McBlain and Bernard 1987), E6 (Bonato and Vello 1999), E7 (Cober and Voldeng 2001a), E8 (Cober et al. 2010), and J (Ray et al. 1995).

Linkage analyses have located these genes to molecular linkage groups (MLGs) 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 (Akkaya et al. 1995, Cregan et al. 1999). At all of the loci except for E6 and J, dominant alleles delay time to flowering to different extents, interacting with the environment and with genotypes at other loci. The recessive alleles e6 and j were identified in crosses with late-flowering cultivars carrying a long-juvenile trait to condition later flowering (Bonato and Vello 1999, Ray et al. 1995). In addition to these major genes, many QTLs controlling time to flowering have been reported (Chapman et al. 2003, Cheng et al. 2011, Funatsuki et al. 2005, Githiri et al. 2007, Keim et al. 1990, Khan et al. 2008, Komatsu et al. 2007, Lee et al. 1996, Liu et al. 2007, 2011, Liu and Abe 2010, Mansur et al. 1993, Orf et al. 1999, Poopronpan et al. 2006, Tasma et al. 2001, Wang et al. 2004, Watanabe et al. 2004, Yamanaka et al. 2001, Zhang et al. 2004). 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, Watanabe et al. 2004, Yamanaka et al. 2005). Some of these QTLs are described in the Soybase database (http://soybase.org/). The major genes and QTLs for flowering often influence agronomic traits other than flowering and maturity, such as plant height and yield (Chapman et al. 2003, Cober and Morrison 2010, Lee et al. 1996, Mansur et al. 1993, Wang et al. 2004, Zhang et al. 2004), degree of cleistogamy (Khan et al. 2008, Takahashi and Abe 1994), and seed coat pigmentation and cracking caused by chilling stress (Githiri et al. 2007, Takahashi and Abe 1999). Understanding of their molecular bases and their interactions with the environment may therefore be necessary to determine genotypic combinations that will lead to a higher or more stable yield in the cropping season of a particular region. In this review, we summarize the results obtained...
from previous studies of major genes and QTLs for flowering and those from recent molecular dissections of the maturity genes E2, E3 and E4 and of soybean orthologs of the Arabidopsis FLOWERING LOCUS T gene. We also describe soybean orthologs for Arabidopsis flowering genes deposited in the Williams 82 genome database, and we discuss the resolution of QTL mapping and the positioning of these orthologs on genetic and physical maps. The information on soybean orthologs of Arabidopsis flowering genes should be helpful in the search for candidate genes for targeted major loci and QTLs for flowering in soybean, and in the development of functional DNA markers for use in breeding programs.

**Genetic bases for responses of flowering to artificially induced long daylength**

Most soybean cultivars have a short-daylength (SD) requirement for floral induction. Flowering is usually suppressed under long-daylength (LD) conditions but induced when the daylength is shorter than a critical length. This sensitivity to photoperiod varies among cultivars: in particular, it is weak or absent in soybean cultivars adapted to high latitudes. Four major genes (E1, E3, E4 and E7) have been well characterized for their responses to LD artificially induced by fluorescent and incandescent lamps with different red to far-red quantum (R:FR) ratios (Buzzell 1971, Buzzell and Voldeng 1980, Cober et al. 1996a, 1996b, 2001, Cober and Voldeng 2001a, 2001b, Kilen and Hartwig 1971, Saindon et al. 1989a, 1989b). The E3 locus was first identified by extending natural daylength to 20 h with the use of cool-white fluorescent lamps with a high R:FR ratio; the e3e3 recessive homozygote alone can initiate flowering under fluorescence-induced LD (FLD) (Buzzell 1971, Kilen and Hartwig 1971). The E4 locus was identified by extending the natural daylength to 20 h with incandescent lamps with a low R:FR ratio (Buzzell and Voldeng 1980). A homozygous recessive e4e4 genotype is necessary for plants homozygous for the e3 allele to flower under incandescence-induced LD (ILD) without any marked delay in flowering (Buzzell and Voldeng 1980, Saindon et al. 1989a). However, the e4e4 genotype cannot on its own confer insensitivity to FLD. E3 and E4 most likely control flowering under LD conditions with a wide range of R:FR ratios in a non-additive manner.

The known flowering loci, E1, E7 and E8, are also involved in the control of sensitivity to ILD, particularly in the double-recessive e3e3e4e4 genotype background (Cober et al. 1996b, 2001, 2010, Cober and Voldeng 2001a, 2001b). E1 has the largest effect on flowering (Bernard 1971, McBlain et al. 1987, Upadhyay et al. 1994). However, a near-isogenic line (NIL) of cv. Harosoy homozygous for E1, e3 and e4 (OT93-28) initiated flowering at the same time as the NIL homozygous for e1, e3 and e4 (OT85-9) under FLD, suggesting that E1 does not influence time to flowering under LD with a high R:FR ratio (Cober et al. 1996b). In contrast, E1 exhibits a marked inhibitory effect on flowering under ILD with a R:FR ratio of less than 1.0 (Cober et al. 1996b, Thakare et al. 2010). A homozygous recessive e7e7 genotype further weakens the response of plants homozygous for e1, e3 and e4 to ILD (Cober and Voldeng 2001a, Cober et al. 2001). However, the e7e7 genotype does not confer a complete loss of photoperiod sensitivity (Cober et al. 2001). Another recessive allele, e8, is involved in the genetic difference in flowering time observed between breeding lines of genotype e1e1e3e3e4e4e7e7 (Cober et al. 2010).

In addition to the double-recessive genotype at E3 and E4 (e3e3e4e4), another genetic mechanism is also involved in the control of ILD insensitivity. Abe et al. (2003) found that a Japanese early-maturing cultivar, Sakamotowase, had a genetic system for ILD insensitivity different from that of the Japanese early-maturing cultivar Miharudaizu (e3e3e4e4). Mapping analysis indicated that both cultivars differed in their genotypes at the E1 and E4 loci. The genotype at E3 was assumed to be e3e3 in both cultivars because of their insensitivity to FLD; this was confirmed in a later study with the use of functional DNA markers (Liu and Abe 2010). Testcrosses with a Harosoy NIL for e3 (e1e1e3e3e4e4) further revealed that Sakamotowase has a novel gene for ILD insensitivity at, or tightly linked to, the E1 locus (Liu and Abe 2010). Therefore, at least two different systems are involved in the genetic control of ILD insensitivity in soybean.

**Interaction between major genes and QTLs for flowering**

Major genes and QTLs for flowering often interact with one another to determine time to flowering. For example, the effects of some major genes such as E2 (qFT2) and E3 (qFT3) are weakened or masked in early-flowering genetic backgrounds, such as those conditioned by a recessive allele at the E1 locus (Upadhyay et al. 1994, Watanabe et al. 2004, Yamanaka et al. 2001). The two QTLs qFT2 and qFT3, detected in a cross between a Japanese cultivar, Misuzudaizu, and a Chinese forage soybean line, Moshido Gong 503, exhibited only a small allelic effect on flowering time under an early-maturing background conditioned by the recessive allele at qFT1 (e1e1), but the allelic effects became marked in a late-maturing background (E1E1) (Yamanaka et al. 2001). Similarly, using cv. Clark NILs for the E1, E2, and E3 loci, Upadhyay et al. (1994) found no effect of allelic substitutions at either E2 or E3 in an e1e1 background, 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 a combination of E4 with later-maturing genetic backgrounds (Saindon et al. 1989b). A marked allelic effect at E4 was observed in a segregating family with the E1E1 genotype (Abe et al. 2003). Accordingly, the E1 gene appears to control time to flowering epistatically over the other E genes.
E3 and E4 encode phytochrome A proteins

The different responses of E genes to LD conditions with different R : FR ratios have suggested that some of these genes are involved in phytochrome A (phyA)-regulated floral induction in soybean (Cober et al. 1996b, 2001). Liu et al. (2008) analyzed the sequence variation in a phyA homolog (GmphyA2) between NILs that were photoperiod sensitive and insensitive for E4. They found that a Ty1/copia-like retrotransposon designated SORE-1 was inserted in the first exon of the GmphyA2 gene of photoperiod-insensitive lines carrying the recessive e4 allele (Kanazawa et al. 2009, Liu et al. 2008). This insertion resulted in a premature stop codon causing a truncated and dysfunctional protein. Genetic mapping analysis confirmed that GmphyA2 cosegregated with E4 on MLG I (Gm20) (Abe et al. 2003, Liu et al. 2008). Furthermore, the NIL for e4 showed an impaired de-etiolation (greening) response under continuous FR-light conditions, as found in phyA null mutants of Arabidopsis (Neff and Chory 1998), rice (Takano et al. 2001, 2005), and pea (Weller et al. 1997, 2001). Taking these findings together, Liu et al. (2008) concluded 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. 2008). The function of GmphyA1 remains undetermined, because no genetic variant is available yet at this locus. However, two findings may indicate that GmphyA1, like E4, is involved in both de-etiolation response and flowering under FR-enriched LD conditions. First, the phyA function of the e4 allele in the de-etiolation response was not completely lost, whereas the phyA null mutants of Arabidopsis, pea, and rice all showed a complete loss of the de-etiolation response under continuous FR light (Neff and Chory 1998, Takano et al. 2001, 2005, Weller et al. 1997, 2001), suggesting that another phyA copy has a redundant function to E4. Second, a Harosoy NIL for double-recessive alleles at E3 and E4 (e3e3e4e4) did not respond to LD with a relatively high R : FR ratio (1.0–5.0) but showed delayed flowering under LD with a low R : FR ratio (<1.0) (Cober et al. 1996b, 2001). These redundant functions for de-etiolation and flowering suggest that GmphyA1 itself functions redundantly with E4 in both de-etiolation responses and photoperiod responses under FR-enriched light. However, sequence analyses of both homoeologs in wild (G. soja) and cultivated soybeans revealed that the nucleotide diversity at non-synonymous sites was lower in GmphyA1 than in GmphyA2, although the diversity at synonymous sites and non-coding regions was almost the same in the two loci, suggesting that GmphyA1 has been subject to more intense purifying selection than GmphyA2 (our unpublished data). Some degree of subfunctionalization may thus have occurred between the two phyA homoeologs. Further studies using dysfunctional mutants will be needed to determine the function of GmphyA1 in photoperiodic responses of flowering.

The E3 gene was also identified as a phyA homolog by fine-mapping around a QTL for flowering time (qFT3) (Watanabe et al. 2009). qFT3 is one of three major QTLs detected in a cross between Misuzudaizu and Moshido Gong 503, and on the basis of map position it has been suggested as a candidate for the maturity gene E3 in MLG L (Gm19) (Watanabe et al. 2004). Fine-mapping by using a residual heterozygous line (RHL) derived from this cross delineated qFT3 within a 93-kb region of a single TAC clone in which a phyA homolog, GmphyA3, was located. Sequence analyses of GmphyA3 revealed one amino acid (AA) substitution between the parental lines: the early-flowering allele from Moshido Gong 503 possesses an AA substitution from glycine to arginine at an AA site of phyA that is conserved across diverse plant species. Furthermore, an NIL of Harosoy homozygous for e3 contained a truncated protein caused by deletion of a segment covering a genomic region 13 kb long, beginning in the fourth exon and extending downstream. The identity between E3 and GmphyA3 was confirmed by using an artificially induced mutant lacking a 40-bp segment in the first exon; this mutation was detected by TILLING (Targeting Induced Local Lesions In Genomes). The mutant allele encoded a truncated protein and flowered earlier than the parental variety Bay under FLD (Watanabe et al. 2009). The control of photoperiodic response of flowering to FLD by e3 is therefore attributed to a dysfunctional GmphyA3 allele. Unlike the E4 locus, however, the E3 locus on its own is not involved in the control of de-etiolation response under continuous R or FR light (Liu et al. 2008).

As in the case of the homoeologs GmphyA1 and GmphyA2, soybean possesses a homoeolog of GmphyA3, namely GmphyA4, in MLG N (Gm03) (Watanabe et al. 2009). However, the GmphyA4 sequence of G. Williams 82, a cultivar used for whole-genome sequencing, is most likely dysfunctional because of a deletion in the third exon (Watanabe et al. 2009). Furthermore, neither a major gene nor a QTL controlling flowering time has so far been reported near the genomic position of GmphyA4.

The phyA protein is an effective FR sensor that is involved, directly and/or via interactions with other photoreceptors, in various developmental processes such as seed germination, de-etiolation, and phototropic responses in etiolated seedlings; it is also involved in early neighbor detection, shade perception, resetting of circadian rhythms, and flowering in light-grown plants (reviewed by Casal et al. 1997). In addition, Franklin et al. (2007) and Franklin and Whitelam (2007) revealed that phyA also functions as an R-light photoreceptor, particularly in R light with high photon irradiance. The different responses of E3 and E4 to LD conditions with different R : FR ratios suggest that the two genes participate in different aspects of the phyA functions controlled by the Arabidopsis phyA gene.

The possible roles of the other photoreceptors, such as phytochrome B (phyB) and cryptochrome (CRY), in the photoperiodic pathway of flowering have not been fully
addressed in soybean. Zhang et al. (2008) revealed that a soybean 
CRY1 ortholog, GmCRY1a, rescued the Arabidopsis 
late-flowering cry2 mutant in ectopic expression analysis 
with a CaMV35S::GFP-GmCRY1a construct, suggesting that 
the GmCRY1a protein promotes floral initiation. 
Furthermore, the GmCRY1a protein exhibited a pattern of 
photoperiod-dependent rhythmic expression that was cor-
related with the photoperiodic flowering and latitudinal dis-
tributioncline of soybean cultivars. However, the genetic var-
iation affecting the circadian expression pattern remains 
unknown and is suggested to reside outside GmCRY1a itself 
(Zhang et al. 2008). Recently, Cheng et al. (2011) found a 
QTL near the region of MLG C1 (Gm04) in which E8 and 
GmCRY1a are located (Cober et al. 2010, Matsumura et al. 
2009). It is thus necessary to determine whether the natural 
variation in GmCRY1a expression is the cause of differences 
in flowering time.

**E2** is a soybean ortholog of the Arabidopsis 
GIGANTEA gene

A candidate gene for E2 was identified through map-based 
cloning of qFT2, a QTL for flowering detected in a region of 
MLG O (Gm10) where E2 was previously mapped (Akkaya 
et al. 1995, Cregan et al. 1999), in a cross between 
Misuzudaizu and Moshido Gong 503 (Watanabe et al. 
2004). By fine-mapping of the progeny of an RHL derived 
from this cross, Watanabe et al. (2011) successfully mapped 
quartet2 within a 94-Kbp region in a single BAC clone contain-
ing a Williams 82 genomic region in which nine annotated 
genes were predicted. One of the genes, Glyma10g36600, 
showed a high degree of similarity to the Arabidopsis 
GIGANTEA (GI) gene. Sequence analyses revealed that the 
Glyma10g36600 sequences in Misuzudaizu, the donor par-
ent for the early-flowering allele of qFT2, and cv. Harosoy, 
which carries a recessive e2 allele, contained a premature 
stop codon caused by a single nucleotide substitution in 
exon 10 and would therefore produce a truncated and dys-
functional GI-like protein; in contrast, the sequences in 
Moshido Gong 503, the donor for the late-flowering allele of 
quartet2, and a Harosoy NIL for E2 did not contain the pre-
mature stop codon. These results suggested that quartet2 (E2) 
encodes a soybean GI ortholog. This hypothesis was further 
supported by the analysis of a GI mutant detected by TILLING 
from an EMS-mutagenesis population of cv. Bay. The 
mutant line, which harbored a premature stop codon in 
exon 10, flowered earlier than Bay (E2/E2) (Watanabe et al. 
2011).

GI encodes a nuclear-localized membrane protein that 
functions upstream of CONSTANS (CO) and FLOWERING 
LOCUS T (FT) in Arabidopsis (Fowler et al. 1999, Hug et al. 
2000, Koornneef et al. 1998, Mizoguchi et al. 2005). GI 
coupled with a blue-light receptor protein (FLAVIN 
BINDING, KELCH REPEAT, F-BOX 1 [FKF1]) forms a 
blue-light-dependent complex that degrades a repressor 
protein (CYCLING DOF FACTOR 1 [CDF1]) that binds the 

promoter region of CO; degradation of the repressor protein 
thereby induces CO expression (Imaizumi et al. 2003, 2005, 
Nelson et al. 2000, Sawa et al. 2007). Another function of 
GI is the regulation of a CO-independent pathway that coop-
erates with other transcriptional factors such as TARGET OF 
EGRI PROTEIN 1 (TOE1) to control FT expression via 
microRNAs (Jung et al. 2007). Furthermore, GI also directly 
controls the expression of FT in Arabidopsis (Sawa and Kay 
2011). As in other plant species, it is reasonable to assume 
that GI-regulated pathways, which may be either CO-
dependent or CO-independent, are involved in control of 
photoperiodic flowering in soybean as well.

**Soybean FLOWERING LOCUS T orthologs**

One of the striking findings obtained from the extensive mo-
lecular dissections of flowering in Arabidopsis and rice is 
that the product of FT, FT protein, is a florigen that moves 
through the phloem to the shoot apex (Corbesier et al. 2007, 
Jaeger and Wigge 2007, Mathieu et al. 2007, Notaguchi et al. 
2008, Tamaki et al. 2007), and its function is highly con-
served across unrelated species (Böhlenius et al. 2006, 
Hayama et al. 2007, Hsu et al. 2006, Izawa et al. 2002, 
Kojima et al. 2002, Lifschitz et al. 2006, Yan et al. 2006). 
Kong et al. (2010) found that soybean possesses at least ten 
FT homologs, which consist of five sets of tandemly linked 
gene pairs. These pairs are separated into three clades, each 
corresponding to one of three clades of pea (Pisum sativum) 
FT genes, PsFTa, PsFTb and PsFTc (Hecht et al. 2011).

Expression analyses of cv. Harosoy and its NILs grown 
in SD and LD conditions have indicated that two of the ten 
FT homologs, GmFT2a (Glyma16g26660) and GmFT5a 
(Glyma16g04830), showed highly upregulated expression 
under SD (inductive conditions for flowering), but highly 
suppressed expression under LD (non-inductive conditions) 
(Kong et al. 2010, Thakare et al. 2010). Ectopic expression 
analyses of GmFT2a and GmFT5a driven by the CaMV35S 
promoter showed that these genes can promote floral ini-
tiation in Arabidopsis ecotype Colombia (Col-0) and comple-
mence the function of FT mutants ft-1 and ft-3, providing 
additional evidence that the GmFT2a and GmFT5a gene 
products function as florigens in Arabidopsis (Kong et al. 
2010, Thakare et al. 2011). Similarly, Arabidopsis FT ecot-
ically expressed in soybean by using the Apple latent 
spherical virus vector can promote flowering in both in-
determinate and determinate soybean cultivars under non-
inductive conditions (Yamagishi and Yoshikawa 2010). 
These results indicate that FT is a key player in floral ini-
tiation in soybean as well.

Expression of GmFT2a and GmFT5a is under the control of 
phyA homologs E3 and E4 (Kong et al. 2010). An NIL of 
cv. Harosoy homozygous for phyA mutants e3 and e4 
showed a high level of expression of both GmFT2a and 
GmFT5a under LD, whereas expression of both genes was 
highly suppressed in the photoperiod-sensitive cv. Harosoy 
(E3E3E4E4). In Arabidopsis, the combination of phyA and
CRY2 promotes flowering through stabilization of the CO protein (Valverde et al. 2004). This promotive function of phytochrome A in flowering is also observed in pea (an LD plant) and rice (an SD plant); phyA mutants in both species delayed flowering under inductive light conditions (Takano et al. 2005, Weller et al. 2001). This is in contrast to the soybean e3 and e4 mutant alleles, which cause no flowering delay under inductive (SD) conditions (Cober et al. 1996b, Cober and Voldeng 2001b). Furthermore, night-break experiments in rice demonstrate that transcription of Hd3a (a rice FT ortholog) is determined mainly by light-signal transduction dependent on PHYB, not PHYA (Ishikawa et al. 2005, 2009). The relative roles of photoreceptors in photoperiodic flowering may therefore vary among plant species. The genetic variation in photoperiodic expression of the soybean FT homologs is most likely attributable to allelic variation of each of the two phyA homologs.

An SD-to-LD transfer experiment further demonstrated the difference in response to photoperiod between GmFT2a and GmFT5a. Expression of GmFT2a was strictly regulated by photoperiodic changes from SD to LD, whereas the response of GmFT5a to photoperiodic changes was gradual, and its expression was retained at low levels even after the plants were transferred to LD (Kong et al. 2010). These findings suggest that, in addition to the phyA-mediated photoperiod response, a second regulatory mechanism may also be involved in the differences in expression pattern between GmFT2a and GmFT5a. Under the phyA-mediated photoperiodic regulation system, GmFT2a and GmFT5a may redundantly and strongly induce flowering under shorter daylengths, but under longer daylengths GmFT5a alone may promote flowering in a photoperiod-independent manner. These two FT homologs may therefore coordinate control flowering in soybean.

In addition to E3 and E4, E2 influences the mRNA abundance of FT homologs. Watanabe et al. (2011) found a clear association between flowering time and the GmFT2a expression in two sets of NILs for the E2 locus; dysfunctional e2 alleles promoted GmFT2a expression and conditioned earlier flowering. However, they could not observe significant differences in the GmFT5a expression between the NILs. These results suggest that the E2 gene (GmGla) mainly controls flowering time through the regulation of GmFT2a (Watanabe et al. 2011). The different responses to photoperiodic changes observed between GmFT2a and GmFT5a (Kong et al. 2010) may thus be caused by involvement of the Gl (E2)-regulated pathway in GmFT2a expression, but not in GmFT5a expression. More detailed studies are needed to test this hypothesis. On the other hand, Thakare et al. (2010) found no difference in the expression of several orthologs of Arabidopsis flowering-time genes, including FT, CO, GI, and TIMING OF CAB EXPRESSION 1 (TOC1), between genotypes E1E1 and e1e1 (both in an e3e3e4e4 genetic background) in young seedlings 8 days after planting under ILD. However, differences in the expression of GmFT2a and GmFT5a between the E1E1 and e1e1 genotypes became marked 10 days after planting under these conditions: the E1 allele inhibited the expression of both FT homologs compared with the e1 allele (Thakare et al. 2011).

**Soybean orthologs of Arabidopsis flowering genes**

Extensive molecular dissections of flowering by using artificially induced mutants in Arabidopsis have revealed that at least 100 genes are involved (Ehrenreich et al. 2009, Hetch et al. 2005, Quecini et al. 2007). Natural variation in flowering time in major crops such as rice, wheat, and pea has been often reported to result from the variation in orthologs of Arabidopsis flowering genes. Examples include Hdl1 (CO) and Hd3a (FT) in rice (Kojima et al. 2002, Yano et al. 2000), Vrn1 (APETALA1) and Vrn3 (FT) in wheat (Yan et al. 2003, 2006), and LATE FLOWERING (TERMINAL FLOWER 1; TFL1), LATE BLOOMER1 (GI) and GIGAS (FT) in pea (Foucher et al. 2003, Hecht et al. 2007, 2011). Genomic information on soybean orthologs of Arabidopsis flowering genes, such as the number of orthologs and their genomic positions, may therefore provide useful clues for dissecting the molecular bases of flowering in soybean. Several studies have already identified and characterized the soybean orthologs of Arabidopsis photoreceptors, clock-associated genes, and flower-identity genes as flowering genes (Kong et al. 2010, Liu et al. 2007, 2008, 2010, Matsumura et al. 2009, Tasma and Shoemaker 2003, Thakare et al. 2010, 2011, Tian et al. 2010, Watanabe et al. 2009, 2011, Xue et al. 2011, Zhang et al. 2008).

We extracted the orthologs of 109 non-overlapping Arabidopsis flowering genes (cited by Ehrenreich et al. 2009, Hetch et al. 2005, Quecini et al. 2007) from the Williams 82 genome database (Phytozome Glyma 1.0; http://www.phytozome.net/). We detected a total of 333 orthologs of 92 Arabidopsis genes from among a total of 46,367 annotated genes (Table 1, Supplemental Table 1 and Supplemental Fig. 1). This survey indicated that soybean possesses orthologs for most of the Arabidopsis flowering genes. It also highlights 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 flowering genes. Furthermore, relatively large syntenic blocks exist in the homoeologous regions of three pairs of chromosomes, Gm04 (MLG C1) and Gm 06 (MLG C2), which contain two sets of blocks of 6 and 8 orthologs each Gm03 (MLG N) and Gm19 (MLG L), which contain blocks of 12 orthologs each and Gm10 (MLG G) and Gm20 (MLG I), which contain blocks of 5 orthologs each (Fig. 1). The functions of these multiple orthologs in the control of soybean flowering should be clarified in further studies. As suggested by functional analyses of the multiple homologs of phyA (Liu et al. 2008, Watanabe et al. 2009), FT (Kong et al. 2010) and TFL1 (Liu et al. 2010, Tian et al. 2010), it is reasonable to speculate that, within each set of duplicated genes, each gene has a function...
either redundant to, or differentiated from, the others, thus generating more diverse and more complex flowering behaviors in soybean.

Information on the physical position of orthologs to known *Arabidopsis* genes (Supplemental Table 1 and Supplemental Fig. 1) may help to identify candidate genes for targeted major loci and QTLs. Fig. 2 is an example showing the usefulness of physical map information in identifying candidate genes responsible for three flowering QTLs detected in a cross between Misuzudaizu and Moshiro Gong 503 (Watanabe et al. 2004, 2009, 2011; Yamanaka et al. 2001, 2005). The positions of DNA markers tagging the three QTLs, which were originally detected in an RIL population derived from these two parents, delineated their genomic positions in specific regions of Gm06 (MLG C2), Gm10 (MLG O) and Gm19 (MLG L). Fine-mapping and QTL analysis detected two DNA markers separated by a genetic distance of 2 cM, Satt365 and Satt489, for *qFT1* (Yamanaka et al. 2005). The region flanked by the two markers corresponds to a physical distance of approximately 3 Mbp in a pericentromeric region where repetitive sequences are very rich and recombination is severely inhibited (Cannon and Shoemaker 2012; Schmutz et al. 2010). The genome sequence information predicted only one ortholog of an *Arabidopsis* flowering gene, REPRESSOR OF GA1-3 (Glyma06g23940) in the region (Fig. 2). Considering the involvement of *qFT1* (*E1*) in photoperiod sensitivity, however, this ortholog is not likely to be the responsible gene, although further studies are needed to confirm its identity. Similarly, QTL mapping placed *qFT2* (*E2*) and *qFT3* (*E3*) in regions on Gm10 (MLG O) and Gm19 (MLG L), respectively; each QTL is flanked by two SSR markers, which are separated by ca. 11 cM and 15 cM, respectively (Watanabe et al. 2004). These regions contain one and three orthologs for *qFT2* and *qFT3*, respectively, although the physical distances between the markers are still over 1.0 Mbp (Fig. 1). Fine-mapping studies further narrowed these regions into regions of less than 100 Kbp within single genomic DNA clones, and finally a single ortholog could be evaluated and identified as a candidate gene for each *qFT* (Watanabe et al. 2009, 2011). Hence, fine-mapping subsequent to QTL analysis, together with a candidate gene approach based on the

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**Fig. 1.** Syntenic blocks containing soybean orthologs of *Arabidopsis* flowering genes in homoeologous regions of different chromosomes. The orthologs, represented by *Arabidopsis* gene symbols, are shown in their positions on the soybean physical maps. The orthologs within each set of syntenic blocks are arranged in the same order, but the blocks are sometimes inverted relative to one another. st and en indicate start and end of chromosome, respectively.
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Concluding remarks

It will probably not be so easy to identify the molecular bases of the major genes and QTLs for flowering in soybean, although novel genes that have no corresponding *Arabidopsis* flowering gene should not be excluded from consideration as candidate genes.

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| Gene         | Abbreviation | Gene function                                                                 | Soybean homologous genes       | Characterized genes in soybean |
|--------------|--------------|--------------------------------------------------------------------------------|--------------------------------|-------------------------------|
| AT1G8090     |              | 5′-3′ exonuclease family protein                                                | Glyma07g11320                  |                               |
| AT2G25920    |              | 3′-5′ exonuclease domain-containing protein/K homology domain-containing protein | AT2G25910.2                    |                               |
| AT5G62640    |              | proline-rich family protein                                                     | Glyma05g1510, Glyma7g10370     |                               |
| AT5G62310    | ADO3, FKF1   | flavin-binding, kelch repeat, F box 1                                           |                               |                               |
| AT4G19960    |              | K-box region and MADS-box transcription factor family protein                  | Glyma05g29590, Glyma05g12730, Glyma13g29510, Glyma15g09500 |                               |
| AT3G61120    | AGL13        | AGAMOUS-like 13                                                                 |                               |                               |
| AT4G1880     | AGL14        | AGAMOUS-like 14                                                                 |                               |                               |
| AT3G57230    | AGL16        | AGAMOUS-like 16                                                                 |                               |                               |
| AT2G26360    | AGL17        | AGAMOUS-like 17                                                                 |                               |                               |
| AT4G2950     | AGL19, GL19  | AGAMOUS-like 19                                                                 |                               |                               |
| AT2G45650    | AGL21        | AGAMOUS-like 21                                                                 |                               |                               |
| AT4G37940    | AGL22        | AGAMOUS-like 22                                                                 |                               |                               |
| AT2G45650    | AGL6         | AGAMOUS-like 6                                                                  |                               |                               |
| AT5G69110    | AGL8, FUL    | AGAMOUS-like 8                                                                  |                               |                               |
| AT3G4210     | ANR1, AGL44  | AGAMOUS-like 44                                                                 |                               |                               |
| AT1G69120    | APL1, AGL7   | K-box region and MADS-box transcription factor family protein                  | Glyma01g38180, Glyma05g31810, Glyma05g07380, Glyma06g22650, Glyma08g27680, Glyma7g08890, Glyma18g50910 |                               |
| AT4G0920     | AP2, FLO2, FLI | Integrase-type DNA-binding superfamily protein                                   |                               |                               |
| AT3G5430     | AP3, ATAP3   | K-box region and MADS-box transcription factor family protein                  | Glyma01g38180, Glyma05g31810, Glyma05g07380, Glyma06g22650, Glyma08g27680, Glyma7g08890, Glyma18g50910 |                               |
| AT5G24470    | APRR5, PRR5  | pseudo-response regulator 5                                                     |                               |                               |
| AT2G46790    | APRR9, PRR9, TLJ | pseudo-response regulator 9                                                   |                               |                               |
| AT2G27550    | ATC         | centroradialis                                                                 | G lam a10g08340, G lam a2g30940, G lam a13g22030, G lam a13g39360 |                               |
| AT5G2430     | ATCOL4, COL4 | CONSTANS-like 4                                                                 | G lam a04g06240, G lam a06g06300, G lam a07g08920, G lam a08g24550, G lam a12g0320, G lam a4g21260, G lam a18g11180, G lam a18g11400 |                               |
| AT5G7660     | ATCOL5, COL5 | CONSTANS-like 5                                                                 | G lam a3g01290, G lam a7g07420 |                               |
| AT5G3510     | ATGD1A, GD1A | alpha/beta-Hydrolases superfamily protein                                       | G lam a01g3010, G lam a03g30460, G lam a10g02790 |                               |
| AT5G3010     | ATGD1B, GD1B | alpha/beta-Hydrolases superfamily protein                                       | G lam a01g3010, G lam a03g30460, G lam a10g02790 |                               |
| AT5G3270     | ATGD1C, GD1C | alpha/beta-Hydrolases superfamily protein                                       | G lam a01g3010, G lam a03g30460, G lam a10g02790 |                               |
| AT2G17770    | BZIP27      | basic region/leucine zipper motif 27                                            | G lam a1g36810                 |                               |
| AT2G46830    | CCA1        | circadian clock associated 1                                                   | G lam a07g05410                 |                               |
| AT5G62430    | CDF         | cycling DOF factor 1                                                           |                               |                               |
| AT5G1580     | CO, FG      | B-box type zinc finger protein with CTT domain                                   |                               |                               |
| AT5G1580     | COL1, ATCOL1 | CONSTANS-like 1                                                                |                               |                               |
| AT3G02380    | COL2, ATCOL2 | CONSTANS-like 2                                                                |                               |                               |
| AT2G24790    | COL3, ATCOL3 | CONSTANS-like 3                                                                |                               |                               |
| AT4G0920     | CR1, BL1, HY4, OOP2, ATCRY1 | cryptochrome 1                                                               |                               |                               |
| AT1G04400    | CR2, PPA, AT-PHH1, PHH1, ATCRY2 | cryptochrome 2                                                              |                               |                               |
| AT1G18100    | E12A11, MFT | PEBP (phosphatidylethanolamine-binding protein) family protein               | G lam a5g34030, G lam a08g05650 |                               |
| Gene   | Abbreviation | Gene function                                                                 | Soybean homologous genes | Characterized genes in soybean |
|--------|--------------|--------------------------------------------------------------------------------|--------------------------|--------------------------------|
| AT1G2140 | EBS          | PHD finger family protein/bromo-adjacent homology (BAH) domain-containing protein | Glyma06g12850, Glyma12g20980, Glyma12g35680, Glyma13g347400, Glyma19g23530 | Glyma19g23530 |
| AT2G20930 | ELF3, PYK20 | Hydroxyproline-rich glycoprotein family protein                               | Glyma04g32020, Glyma07g01600, Glyma08g21110, Glyma14g10530, Glyma17g4980 | Glyma17g4980 |
| AT2G40080 | ELF4       | Protein of unknown function (DUF1313)                                          | Glyma11g3270, Glyma14g06480, Glyma18g03130 | Glyma11g3270 |
| AT5G07930 | ELF6       | Zn finger (C2H2 type) family protein/translation factor jumonji (Jmj) family protein | Glyma10g35350, Glyma20g32160 | Glyma10g35350 |
| AT1G79370 | ELF7       | Hydroxyproline-rich glycoprotein family protein                               | Glyma07g1830, Glyma08g21490 | Glyma07g1830 |
| AT2G06210 | ELF8, VIP6 | binding                                                                       | Glyma05g24180, Glyma09g07980, Glyma15g19450 | Glyma05g24180 |
| AT5G1530  | EMF1       | Embryonic flower 1 (EMF1)                                                     | Glyma04g08680, Glyma06g08790 | Glyma04g08680 |
| AT5G51230 | EMF2, VEF2, CYR1, AtEMF2 | VES-F-box of polycomb protein                                                  | Glyma10g23370, Glyma10g23420, Glyma11g03950, Glyma20g16680 | Glyma10g23370 |
| AT4G15880 | ESD4, ATESD4 | Cysteine proteases superfamily protein                                         | Glyma06g17320, Glyma07g37640, Glyma09g04970, Glyma15g15890, Glyma17g34530 | Glyma06g17320 |
| AT4G16280 | FCA         | RNA binding/abscisic acid binding                                              | Glyma09g13020, Glyma09g04970 | Glyma09g13020 |
| AT4G35900 | FD, FD-1, atflc14 | Basic-leucine zipper (bZIP) transcription factor family protein               | Glyma03g31080, Glyma03g31110, Glyma19g33950, Glyma19g33950 | Glyma03g31080 |
| AT2G33835 | FES1       | Zinc finger C-x8-C-x5-C-x3-H type family protein                              | Glyma09g07120, Glyma10g07120, Glyma13g07120, Glyma13g07120 | Glyma09g07120 |
| AT5G10140 | FLC, FLEF, AGL25 | K-box region and MADS-box transcription factor family protein               | Glyma02g07650, Glyma08g28470, Glyma08g47810, Glyma08g47820, Glyma16g04830, Glyma16g04840, Glyma16g04850, Glyma19g28400 | Glyma02g07650 |
| AT3G01950 | FPA         | RNA binding                                                                    | Glyma07g37640, Glyma10g04970, Glyma15g15890, Glyma17g34530 | Glyma07g37640 |
| AT5G24860 | FPF1, ATRF1 | Flowering promoting factor 1                                                   | Glyma04g14070, Glyma04g14070, Glyma04g14070, Glyma04g14070 | Glyma04g14070 |
| AT4G09650 | FRL1, FRA | FRIGIDA-like protein                                                           | Glyma04g14070, Glyma04g14070, Glyma04g14070, Glyma04g14070 | Glyma04g14070 |
| AT5G61840 | FRL2       | FRIGIDA-like 2                                                                 | Glyma04g14070, Glyma04g14070, Glyma04g14070, Glyma04g14070 | Glyma04g14070 |
| AT1G65480 | FT          | PEBP@phosphatidyethanolamine-binding protein)family protein                   | Glyma02g07650, Glyma03g31080, Glyma03g31110, Glyma19g28400 | Glyma02g07650 |
| AT2G19520 | FVE, AGC1, MS4, NAC4, NAC94, ATMS4 | Transducin family protein/WD-40 repeat family protein            | Glyma02g07650, Glyma03g31080, Glyma06g17320, Glyma15g18450 | Glyma02g07650 |
| AT1G34840 | FYO        | Transducin/WD40 repeat-like superfamily protein                               | Glyma02g07650, Glyma03g31080, Glyma06g17320, Glyma15g18450 | Glyma02g07650 |
| AT4G02780 | GA1, ABC31, ATCPS1, CPS, CPSI | Terpenoid cyclases/Pretein prenyltransferases superfamily protein | Glyma03g31080, Glyma04g14070, Glyma04g14070, Glyma19g28400 | Glyma03g31080 |
| AT1G4920 | GAI, RG142 | GRAS family transcription factor protein                                        | Glyma02g08240, Glyma05g03020, Glyma05g27190, Glyma08g10140, Glyma20g34260 | Glyma02g08240 |
| AT1G2270 | GI, FB      | Gigantea protein (GI)                                                          | Glyma09g07240, Glyma09g07240, Glyma20g39080 | Glyma09g07240 |
| AT2G39810 | HOS1       | Ubiquitatin protein ligases                                                     | Glyma04g14070, Glyma10g03840 | Glyma04g14070 |
| AT5G23150 | HUA2       | Tudor/PWWP/MBT domain-containing protein                                       | Glyma11g03070, Glyma14g02890 | Glyma11g03070 |
| AT4G02560 | LD         | Homeodomain-like superfamily protein                                           | Glyma03g31080, Glyma04g14070, Glyma05g03020 | Glyma03g31080 |
| AT5G61850 | LFY, LFY3  | Floral meristem identity control protein LEAFY (LFY)                          | Glyma04g14070, Glyma04g14070, Glyma04g14070, Glyma20g19600 | Glyma04g14070 |
| AT1G1060 | LH1, LH51  | Homeodomain-like superfamily protein                                           | Glyma03g31080, Glyma06g19380, Glyma09g45030 | Glyma03g31080 |
| AT2G8915 | LKP2, ADO2 | LOV KELCH protein 2                                                           | Glyma04g15150, Glyma3g30403, Glyma20g11040 | Glyma04g15150 |
| AT2G61100 | MBP3, ATMBP3 | myb-domain protein 33                                                          | Glyma03g31080, Glyma06g19380, Glyma09g45030 | Glyma03g31080 |
| AT3G46640 | PCLI       | Homeodomain-like superfamily protein                                           | Glyma03g31080, Glyma06g19380, Glyma09g45030 | Glyma03g31080 |
| AT1G25540 | PFT1       | Phloem tissues and flowering time regulatory protein (PFT1)                   | Glyma04g14070, Glyma04g14070, Glyma04g14070, Glyma20g19600 | Glyma04g14070 |
Table 1. (continued)

| Gene Abbreviation | Gene function | Soybean homologous genes |
|-------------------|---------------|--------------------------|
| AT5G21390          |               |                          |
| AT5G21400          |               |                          |
| AT5G21410          |               |                          |
| AT5G21420          |               |                          |
| AT5G21430          |               |                          |
| AT5G21440          |               |                          |
| AT5G21450          |               |                          |
| AT5G21460          |               |                          |
| AT5G21470          |               |                          |
| AT5G21480          |               |                          |
| AT5G21490          |               |                          |
| AT5G21500          |               |                          |
| AT5G21510          |               |                          |
| AT5G21520          |               |                          |
| AT5G21530          |               |                          |
| AT5G21540          |               |                          |
| AT5G21550          |               |                          |
| AT5G21560          |               |                          |
| AT5G21570          |               |                          |
| AT5G21580          |               |                          |
| AT5G21590          |               |                          |
| AT5G21600          |               |                          |
| AT5G21610          |               |                          |
| AT5G21620          |               |                          |
| AT5G21630          |               |                          |
| AT5G21640          |               |                          |
| AT5G21650          |               |                          |
| AT5G21660          |               |                          |
| AT5G21670          |               |                          |
| AT5G21680          |               |                          |
| AT5G21690          |               |                          |
| AT5G21700          |               |                          |
| AT5G21710          |               |                          |
| AT5G21720          |               |                          |
| AT5G21730          |               |                          |
| AT5G21740          |               |                          |
| AT5G21750          |               |                          |
| AT5G21760          |               |                          |
| AT5G21770          |               |                          |
| AT5G21780          |               |                          |
| AT5G21790          |               |                          |
| AT5G21800          |               |                          |
| AT5G21810          |               |                          |
| AT5G21820          |               |                          |
| AT5G21830          |               |                          |
| AT5G21840          |               |                          |
| AT5G21850          |               |                          |
| AT5G21860          |               |                          |
| AT5G21870          |               |                          |
| AT5G21880          |               |                          |
| AT5G21890          |               |                          |
| AT5G21900          |               |                          |
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