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Flowering Time in Watermelon Is Associated with a Major Quantitative Trait Locus on Chromosome 3

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Abstract. **U.S. watermelon (*Citrullus lanatus*) production is worth ≈$0.5 billion annually to growers and nearly all of them are dependent on reliable synchronized flowering time of triploid cultivars and diploid pollenizers in their production fields. One aspect of this synchronization is time to flowering, the change from the vegetative to reproductive phase of a plant. Flowering time has emerged as one of the key traits in horticultural and agronomic crops to breed for escape from biotic and abiotic stresses. However, very little is known about the control of flowering time in watermelon. The number of genes involved, mode of inheritance, heritability, and the possible candidate genes are all unknown. In this study, quantitative trait loci (QTL) associated with days to first male flower (DMF), days to first female flower (DFF), and the female-male flower interval (FMI) were identified in a 'Klondike Black Seeded' × 'New Hampshire Midget' recombinant inbred line population over 2 years. Heritability for DMF, DFF, and FMI were 0.43, 0.23, and 0.10, respectively. Control of flowering time was oligogenic with a major, stable, colocalized QTL on chromosome 3 responsible for ≈50% of the phenotypic variation observed for DMF and DFF. This region of the draft genome sequence contains 172 genes, including homologs of the *flowering locus T* (*Cla009504)* and *tempranillo 1* (*Cla000855)* genes associated with flowering time in other species. *Cla009504* and *Cla000855* represent excellent candidate genes toward the development of a functional marker for marker-assisted selection of flowering time in watermelon. In addition to the major QTL on chromosome 3, two other QTL were identified for DMF (chromosomes 2 and 3) and DFF (chromosomes 3 and 11) and one for FMI on chromosome 2. Understanding the genes involved in this trait and the ability to select efficiently for flowering time phenotypes is expected to accelerate the development of new watermelon cultivars in changing environmental conditions.**

The change from the vegetative to the reproductive phase of a plant is an important aspect in most commercial agronomic and horticultural crops. A shorter production cycle often means lower input costs for the producer and less environmental impact through energy-saving and reduced pesticide use. A short production cycle also allows for escape from pathogens by harvesting crops before environmental conditions are favorable for high disease pressure (Poland et al., 2009). Flowering time is thus often used to avoid biotic and abiotic stresses. The time to first male and female flower and the interval between the appearance of male and female flowers in monoecious plants have also emerged as key traits used to breed for increased yield under drought conditions (Bolaños and Edmeades, 1993; Chapman and Edmeades, 1999; Richards, 2006; Siddique et al., 1990). The association of drought quantitative trait loci and flowering time loci (Ducrocq et al., 2008) and the realization that selection for specific flowering phenotypes increases yield under drought conditions have contributed to flowering time traits emerging as key breeding priorities for the future (Jung and Müller, 2009).

Flowering traits are complex and it is anticipated that climate change will greatly influence flowering (Craufurd and Wheeler, 2009). As can be expected for such an important trait, a large amount of research has been carried out and the genetic architecture and molecular pathways for flowering time are well described for model systems such as *Arabidopsis thaliana* and are becoming clearer for important agronomic crops (for recent reviews, see Buckler et al., 2009; Jackson, 2009; Matsoukas et al., 2012; Turck et al., 2008). The picture that is emerging from *A. thaliana* shows that the molecular pathways that control flowering include a large number of genes representing photoperiod (light signaling and circadian clock), vernalization, autonomous signals, and gibberellin biosynthesis. Very briefly, in the leaf *constans* [*CO* (Valverde et al., 2004)] transcription is up-regulated in response to signals received from the photoperiodic induction pathway. The accumulation of *CO* protein activates *flowering locus T* [*FT* (Kardailsky et al., 1999; Kobayashi et al., 1999; Valverde et al., 2004)], which is a floral inducer. *FT* can also be induced through a *CO*- independent pathway where *FT* suppressors are down-regulated. After moving to the meristem, the *FT* protein promotes other pathway integrator genes (Lee et al., 2008; Liu et al., 2008; Yoo et al., 2005), which affect floral meristem identity genes, leading to flowering (Abe et al., 2005; Lee et al., 2008; Melzer et al., 2008; Wigge et al., 2005).

Watermelon production is responsible for ≈7% of world vegetable production acreage (Food and Agriculture Organization of the United Nations, 2011). However, very little is

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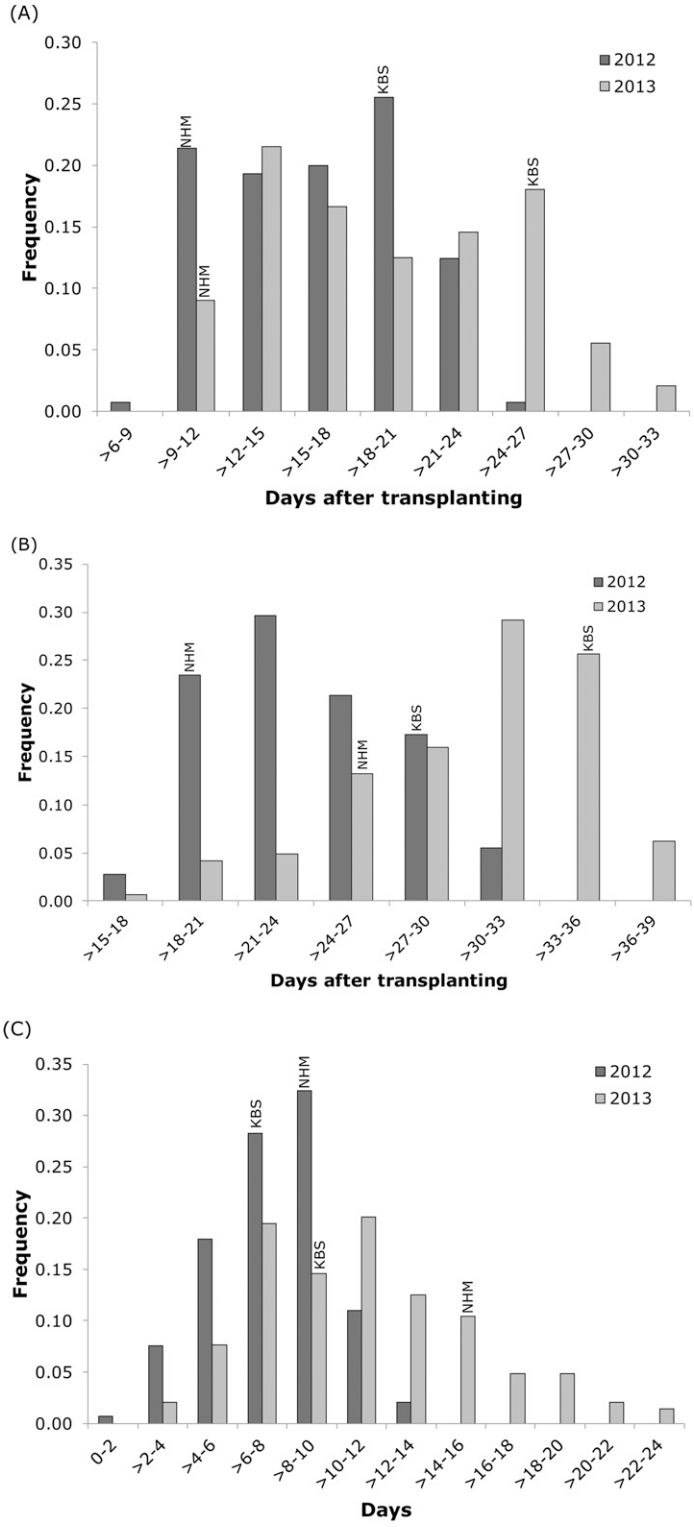

Fig. 1. Frequency distribution for (**A**) days to first open male flower, (**B**) days to first open female flower, and (**C**) female–male interval for 2012 (n = 145) and 2013 (n = 144) in the 'Klondike Black Seeded' (KBS) × 'New Hampshire Midget' (NHM) watermelon recombinant inbred line population as well the parental phenotypes.

known about the control of flowering time in this monoecious crop. Commercial cultivars are day-neutral (George, 2009) and male flowers usually open first, followed by female flowers at a ratio of roughly 7:1 (Wehner, 2008). The interval between the opening of the first male flower and first female flower is dependent on the cultivar and environmental conditions.

The percentage of watermelon production in the United States devoted to seedless fruit has increased dramatically from 51% in 2003 to reach 85% in 2009 (U.S. Department of Agriculture, 2011). The seedless fruit is produced on triploid plants, but because pollination is required for fruit set and these plants produce negligible amounts of viable pollen, diploid pollen sources (pollenizers) are required (Boyhan et al., 2000; Maynard, 1992; Maynard and Elmstrom, 1992). As a result of this local preference for seedless fruit, U.S. watermelon production is dependent on synchronized flowering of diploid pollenizers and triploid watermelon cultivars for fruit production. However, the number of genes involved, mode of inheritance, heritability, and the possible candidate genes are all unknown for this crop. These factors are critical impediments to efficient breeding of watermelon cultivars in a changing environment, and especially for the United States where fruit production is dependent on synchronized flowering between two cultivars (a triploid and a pollenizer).

Recently, molecular tools have become available for watermelon that can now be used to advance breeding efforts. We recently produced the first single nucleotide polymorphism (SNP) maps for watermelon (Sandlin et al., 2012) and mapped the first QTL in the species (Prothro et al., 2012a, 2012b, 2013; Sandlin et al., 2012). In 2012, the draft watermelon genome sequence (Guo et al., 2013) became available and here we describe the use of these resources to elucidate the control of flowering time in watermelon.

Materials and Methods

Plant materials and genetic map. The 'Klondike Black Seeded' (KBS) × 'New Hampshire Midget' (NHM) recombinant inbred line (RIL) population developed previously to map QTL associated with fruit and seed traits (Prothro et al., 2012a; Sandlin et al., 2012) was advanced in the greenhouse (Jan. to Apr. 2012) through single seed descent (SSD) from F_7 to F_8 to generate seed for the current experiment.

Trait phenotyping. During Summer 2012 and 2013, 150 RILs and parental cultivars were sown in seedling trays and transplanted ≈2 weeks later on 23 May 2012 and 22 May 2013 at the Durham Horticulture Farm, in Watkinsville, GA. One plant per RIL/parental cultivar was planted per block in a completely randomized bock design with 10 blocks/replications. Plants were grown according to University of Georgia Cooperative Extension Service recommendations

on plastic mulch with between-row spacing of 1.83 m and in-row spacing of 0.9 m. In 2012, the vines were turned to make data collection easier, but, in 2013, high rainfall limited entry into the field to only days essential for data collection.

Data were collected three times per week for days to the opening of the first male flower, days to the opening of the first female flower, and subsequently calculated for female–male interval. Bisexual flowers were scored as female. Pearson correlations were calculated using JMP 9.0.2 (SAS Institute, Cary, NC).

Heritability on family-mean base was calculated as $h^2 = \sigma^2_G / \{[\sigma^2_G + (\sigma^2_{G*Y}/e) + (\sigma^2_e/er)]\}$ for the combined environments (Holland et al., 2003; Nyquist and Baker, 1991), where σ^2_G equaled genetic variance among the entries, σ^2_{G*Y} the variance of genetic × years interaction, σ^2_e the variance of experimental error, e the number of years, and r the number of replications. Because the data were unbalanced, e and r were computed as harmonic mean of years and harmonic mean of total replications across all years, respectively (Holland et al., 2003).

QTL detection. Composite interval mapping was used to identify QTL associate with the three traits using Model 6, a walk speed of 2 cM, and a window size of 5 cM (Zeng, 1994; Zeng et al., 1999) with WinQTL Cartographer Version 2.5 (Wang et al., 2011). Data were analyzed separately for different years as well as jointly (averaged over years). Significance of the QTL was determined using 1000 permutations ($\alpha = 0.05$) (Churchill and Doerge, 1994; Doerge and Churchill, 1996)

Candidate genes. The sequences of the SNP markers (Sandlin et al., 2012) closest to the QTL (Table 2) were used to determine the approximate location of the stable QTL on chromosome 3 of the draft genome sequence (Guo et al., 2013). The predicted genes in that region were then compared with genes known be involved in flowering time in other crops (Blackman et al., 2011; Ehrenreich et al., 2009; Jung et al., 2012; Matsoukas et al., 2012).

Results and Discussion

The average DMF for NHM and KBS was 9.4 and 21 d, respectively, in 2012 and 11.7 and 25.8 d in 2013 (Fig. 1A). In 2012, the average DFF for NHM and KBS was 18.3 and 29.1 d and in 2013 it was 26.5 and 34.6 d (Fig. 1B). The FMI for the 2 years was 9.5 and 14.7 d for NHM and 7.1 and 8.5 d for KBS, respectively (Fig. 1C) with all traits showing some degree of transgressive segregation in the RIL population. There was a significant positive correlation between DMF and DFF within and across years and a significant negative correlation between DMF and MFI (Table 1). It appears that a larger MFI is associated with earlier male flowers rather than later female flowers, although there was also a significant negative correlation between MFI_{2013} and DFF_{2012} (but not DFF_{2013}).

Generally, plants flowered later in 2013 (DMF_{avg} = 19.2 d, DFF_{avg} = 30.3 d) than 2012 (DMF_{avg} = 16.1 d, DFF_{avg} = 23.9 d) (Fig. 1A–B), probably as a result of the unusually high amount of rainfall in 2013. The total rainfall for the duration of this experiment was 98.3 mm in 2012 (10 rain days) and 292.9 mm in 2013 (21 rain days), whereas the average for this period from 2002 to 2011 was 137.1 mm with 14.5 rain days. DFF was more affected than DMF, leading to a higher FMI in 2013 (11.1 d) than 2012 (7.7 d), probably as a result of the timing of the high rainfall in the period from 11 to 27 d after transplanting (69.3 mm in 2012 and 276.1 mm in 2013). Heritability for DMF, DFF, and MFI was 0.43 ± 0.035, 0.23 ± 0.030, and 0.10 ± 0.022, respectively. This is much lower than what has been observed for days to male flowering ($h^2 = 0.84$), days to female flowering ($h^2 = 0.83$), and anthesis-silking interval ($h^2 = 0.68$) in the highly replicated maize (*Zea maize*) populations described by Buckler et al. (2009). In melon (*Cucumis melo*), heritability of days to anthesis (DA) of 0.64 (Zalapa et al., 2008) has been reported. However, it should be noted that in the latter study DA was defined as the time from transplanting to the time when 50% of plants were flowering rather than the individual plant basis of the current study.

Table 1. Pearson correlations for days to first male flower (DMF), days to first female flower (DFF) and male–female interval (FMI) for 2012 and 2013 in the 'Klondike Black Seeded' × 'New Hampshire Midget' watermelon recombinant inbred line population.

	2012 DMF	2012 DFF	2012 FMI	2013 DMF	2013 DFF
2012 DFF	0.79**[z]				
2012 FMI	–0.51**	0.12			
2013 DMF	0.79**	0.74**	–0.24*		
2013 DFF	0.57**	0.68**	0.05	0.67**	
2013 FMI	–0.47**	–0.28*	0.38**	–0.65**	0.131

[z]**, * Significant correlations at $P < 0.0001$ and $P < 0.01$, respectively.

Three QTL were associated with DMF in 2012 and one in 2013, whereas two QTL were identified for DFF and one for MFI in the 2 years (Table 2; Fig. 2). A major QTL for DMF (*Qdmf3-1*) and DFF (*Qdff3-1*) located on chromosome 3 explained ≈50% of the phenotypic variance observed in the population and was stable across the 2 years (Table 2; Fig. 2). In 2013 a QTL for FMI (*Qfmi3*) was also detected in this region. Additional QTL for DMF (*Qdmf3-2*) and DFF (*Qdff3-2*) were identified on chromosome 3 in 2012 but were not colocalized. QTL for DMF (*Qdmf2*) and MFI (*Qmfi2*) in 2012 were identified at a similar position on chromosome 2, but were not detected in 2013, whereas a QTL for DFF (*Qdff11*) was detected on chromosome 11 in 2013 but not in 2012. Joint analysis (averaged over years) detected the colocalized QTL on chromosomes 2 (*Qdmf2* and *Qfmi2*) and 3 (*Qdmf3-1*, *Qdff3-1*, and *Qfmi3*).

Co-localization for QTL for flowering traits is common and has been observed in other species (Buckler et al., 2009). QTL mapping in other crops suggested that a small number of genes with large effects are associated with flowering time in self-pollinating crops (Cockram et al., 2007; Izawa et al., 2003; Wills and Burke, 2007), whereas in out-crossing crops like maize, flowering time is controlled by a large number of QTL with small additive effects (Buckler et al., 2009). Despite being an out-crossing crop, our results indicate oligogenic control of flowering time in domesticated watermelon. However, it should be noted that watermelon has high natural self-pollination rates, as reflected by the lack of inbreeding depression in the species (Kumar et al., 2013; Kumar and Wehner, 2010; Wehner, 2008). Major colocalized QTL were also found to be associated with days to male and female flower development in *Cucurbita pepo* (Esteras et al., 2012). It remains to be seen whether oligogenic control of flowering time holds true for wild relatives of these cultivated crops.

Favorable alleles (early flowering) at the major QTL (*Qdmf3-1*, *Qdff3-1*) are contributed by the early flowering parent NHM (Table 2). However, the favorable allele at *Qdmf2* is contributed by the late flowering KBS parent. This is not unexpected, because antagonistic additive effects are expected

Table 2. Genomic regions associated with quantitative trait loci (QTL) for days to first male flower (DMF), days to first female flower (DFF), and male–female interval (FMI) for 2012 (n = 145) and 2013 (n = 144) in the 'Klondike Black Seeded' × 'New Hampshire Midget' watermelon recombinant inbred line population.

Trait	Suggested name	Yr	Chr (LG)[z]	Position (cM)	LOD[y]	R^2 (%)[x]	Additive effect[w]	LOD-1 support interval (cM)[v]	LOD-1 support interval (cM)[v]
DMF	*Qdmf2*	2012	2 (lg9)	75.71	3.4	4.0	–0.86	72.7	78.8
DMF	*Qdmf3-1*	2012	3 (lg11)	8.21	25.7	47.5	2.93	8.1	9.6
DMF	*Qdmf3-2*	2012	3 (lg11)	65.61	3.1	3.8	0.81	56.1	66.5
DMF	*Qdmf3-1*	2013	3 (lg11)	9.21	33.2	61.8	4.51	8.2	9.6
DMF	*Qdmf2*	Joint	2 (lg9)	76.71	5.8	6.1	–1.21	72.5	79.5
DMF	*Qdmf3-1*	Joint	3 (lg11)	8.21	35.4	61.0	3.74	8.0	9.2
DFF	*Qdff3-1*	2012	3 (lg11)	9.21	24.7	44.6	2.45	8.2	10.0
DFF	*Qdff3-2*	2012	3 (lg11)	79.91	4.7	5.8	0.87	78.2	84.7
DFF	*Qdff3-1*	2013	3 (lg11)	9.21	17.5	39.1	2.75	8.1	10.7
DFF	*Qdff11*	2013	11 (lg3)	106.21	4.0	6.9	–1.15	103.7	113.5
DFF	*Qdff3-1*	Joint	3 (lg11)	9.21	22.3	44.7	2.53	8.1	10.4
FMI	*Qfmi2*	2012	2 (lg9)	75.71	4.3	10.7	0.84	66.5	73.6
FMI	*Qfmi3*	2013	3 (lg11)	8.21	6.6	16.2	–1.74	5.7	13.6
FMI	*Qfmi2*	Joint	2 (lg9)	7.57	3.8	8.0	0.88	72.4	80.7
FMI	*Qfmi3*	Joint	3 (lg11)	8.21	7.8	17.8	–1.24	2.1	10.8

[z]Chromosome (Guo et al., 2013; Ren et al., 2012) and linkage group (Sandlin et al., 2012).
[y]Log_{10} likelihood ratio.
[x]Phenotypic variation explained.
[w]Negative values indicate that the effect is contributed by the allele from male parent.
[v]Genomic region that includes QTL and flanking regions with LOD values larger than the QTL LOD minus 1.

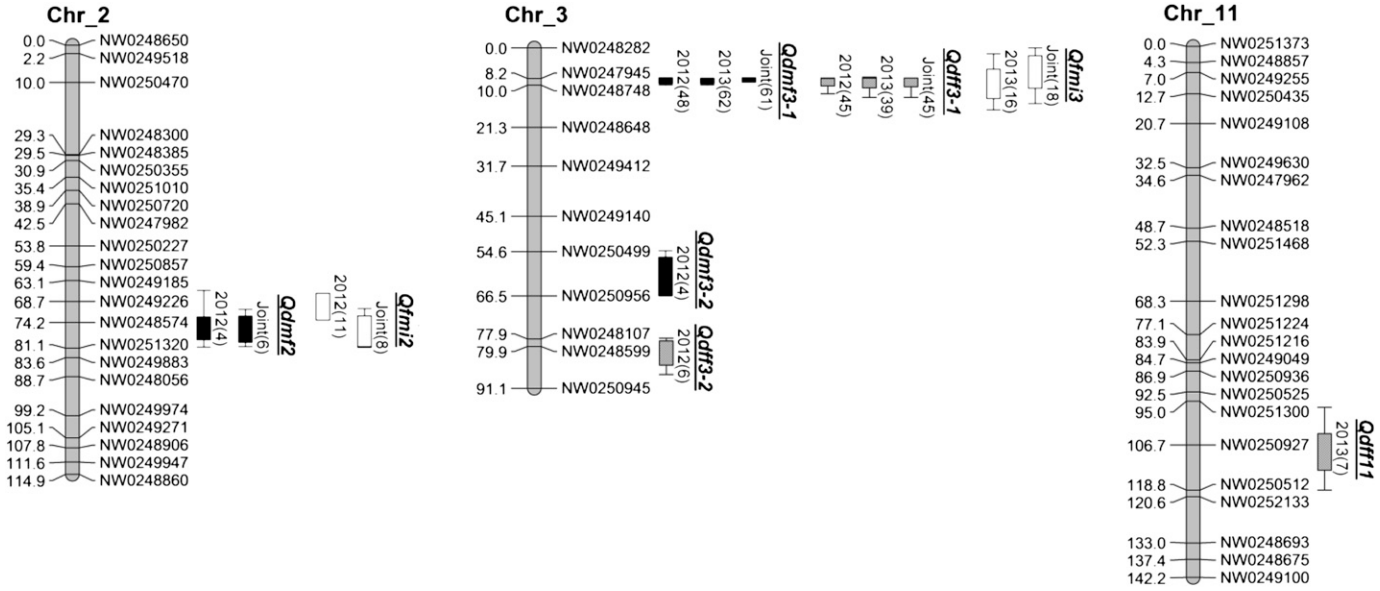

Fig. 2. Quantitative trait loci (QTL) identified for days to first open male flower (black box), days to first open female flower (gray box), and female-male interval (white box) for 2012, 2013, and joint data in the 'Klondike Black Seeded' × 'New Hampshire Midget' watermelon recombinant inbred line population. CentiMorgans are given on the left of the chromosomes (Chr) and the length of the box and whiskers represent the LOD-1 and LOD-2 support interval for the QTL, respectively. The suggested name for each QTL is underlined, whereas the number in parentheses is the approximate percentage of phenotypic variance explained by the particular QTL. The figure was produced using MapChart Version 2.1 (Voorrips, 2002).

for traits with transgressive segregation (deVicente and Tanksley, 1993; Rieseberg et al., 1999).

The LOD-1.5 support interval [≈95% confidence interval (Silva et al., 2012)] for the major QTL on chromosome 3 stretches from 8.2 to 12 cM, which corresponds to approximately the 12.0 to 17 Mbp region on chromosome 3 of the watermelon draft genome (Guo et al., 2013). This region contains 172 predicted genes, including *Cla009504*, a homolog of *FT* in squash [*Cucurbita moschata*, *Cm_FTL2* (Lin et al., 2007)] and rice [*Oryza sativa*, *Hd3a* (Kojima et al., 2002)] and *Cla000855*, an AP2/ERF and B3 domain-containing transcription factor with homology to *TEM1* in *A. thaliana* (Castillejo and Pelaz, 2008). Expression of *Cm_FTL2* and *Hd3a* in *A. thaliana* lead to earlier flowering (Kojima et al., 2002; Lin et al., 2007), whereas *TEM1* is a repressor of *FT* and thus up-regulation of *TEM1* leads to delayed flowering (Castillejo and Pelaz, 2008; Osnato et al., 2012). *TEM1* also regulates genes associated with gibberellin biosynthesis and thus connects the latter to the photoperiod

pathway (Osnato et al., 2012). *Cla009504* and *Cla000855* represent excellent candidate genes toward the development of functional markers (Andersen and Lübberstedt, 2003) for marker-assisted selection (MAS) for flowering time in watermelon. We are currently sequencing the *Cla009504* and *Cla000855* alleles in this population and examining gene expression in early and late flowering genotypes. Flowering time traits are the target for MAS in several economically important crops including maize (Ducrocq et al., 2009), canola [*Brassica napus* (Raman et al., 2013)], soybean [*Glycine max* (Zhang et al., 2013)], rice (Yano et al., 2001), and wheat [*Triticum aestivum* (Yan et al., 2006)]. Functional markers, where the genotypic sequence used for selection is the cause of the phenotype, is the preferred marker type because there is no recombination between the marker and the trait gene (Andersen and Lübberstedt, 2003).

To ensure the broad applicability of any developed markers, future research needs to validate the stability of the QTL in multiple environments. During the RIL population seed increase through SSD in the greenhouse, data were also collected for DMF and DFF. Although this was under artificial light (14 h light/10 h dark) in the greenhouse and each line was represented by only a single plant, the major QTL on chromosome 3 (*Qdmf3-1* and *Qdff3-1*) were associated with flowering time [DMF_{GH}-LOD = 26.1, DMF_{GH}-R^2 = 50%, DFF_{GH}-LOD = 14.0, DFF_{GH}-R^2 = 28% (data not shown)]. This suggests that this QTL will have broad applicability in MAS for flowering time in watermelon.

Other aspects that need to be addressed in future research are the duration and consistency of flowering. These are critical traits in breeding for synchronized flowering where consistent pollen availability from pollenizers at the time when female triploid flowers are receptive, is essential.

Seedless watermelon production has unique challenges that require innovative solutions that will move the science of watermelon breeding forward. We identified a major, stable QTL associated with flowering time in watermelon, which gives us insight into the genetic architecture of this economically important trait. In addition, we identified candidate genes for further study toward elucidation of flowering time pathways and MAS that will reduce the breeding cycle of watermelon cultivars.

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