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Mapping loci controlling flowering time in *Brassica oleracea*

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Abstract The timing of the transition from vegetative to reproductive phase is a major determinant of the morphology and value of *Brassica oleracea* crops. Quantitative trait loci (QTLs) controlling flowering time in *B. oleracea* were mapped using restriction fragment length polymorphism (RFLP) loci and flowering data of F_3 families derived from a cabbage by broccoli cross. Plants were grown in the field, and a total of 15 surveys were made throughout the experiment at 5–15 day intervals, in which plants were inspected for the presence of flower buds or open flowers. The flowering traits used for data analysis were the proportion of annual plants (PF) within each F_3 family at the end of the experiment, and a flowering-time index (FT) that combined both qualitative (annual/biennial) and quantitative (days to flowering) information. Two QTLs on different linkage groups were found associated with both PF and FT and one additional QTL was found associated only with FT. When combined in a multi-locus model, all three QTLs explained 54.1% of the phenotypic variation in FT. Epistasis was found between two genomic regions associated with FT. Comparisons of map positions of QTLs in *B. oleracea* with those in *B. napus* and *B. rapa* provided no evidence for conservation of genomic regions associated with flowering time between these species.

Key words *Brassica oleracea* · Restriction fragment length polymorphism · Quantitative trait loci · Flowering time

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Introduction

Brassica oleracea L. (n=9) comprises many horticultural types with widely different morphologies (e.g., cabbage, broccoli, cauliflower, kale, Brussels sprouts, and kohlrabi). Among these types, two flowering habits can be readily distinguished. Some types, such as cabbage and kohlrabi, are biennials and require exposure to low temperatures for flower initiation (vernalization), which is accomplished by overwintering in the field. Other types, such as broccoli and cauliflower, are annuals and will flower during a single growing season. Information on the genetic control of flowering could be useful in breeding programs. For instance, the development of biennial varieties with strong vernalization requirements (bolting resistance) is a major goal for regions where plants are overwintered in the field for harvesting vegetative parts during early spring (Yarnell 1956; Reid 1976; Mero and Honma 1985; Palada et al. 1987). On the other hand, cultivars with weak or no vernalization requirements are needed in tropical and subtropical regions for seed production (AVRDC 1993).

Hybrids between different horticultural types are readily obtained and have been used to study the genetic control of flowering. Segregating F_2 populations from crosses of annual and biennial types usually show continuous variation for time to flower, including plants that do not flower during the course of the experiment. In some *B. oleracea* crosses, the ratio of annual/biennial types in segregating F_2 populations has been reported to approximate that expected for a single gene (Detjen 1926; Horovitz and Perlasca 1954; Wellensieck 1960; Walkoff 1963; Landry et al. 1992) whereas in others the ratios suggest an oligogenic control both for this trait and for time to flower (Baggett and Wahlert 1975; Pelofske and Baggett 1979; Sachan and Singh 1987; Baggett and Kean 1989). Recently, RFLP markers were used to study the genetic control of flowering in single plants of an F_2 population derived from a cabbage by broccoli cross (Kennard et al. 1994). Four genomic regions were found associated with the annual/biennial habit and flowering time, and digenic epistasis

was detected between two regions controlling flowering time.

In the present experiment, the results from RFLP mapping of quantitative trait loci (QTLs) controlling flowering time in a cabbage by broccoli cross are also reported. However, F_3 families were used, which allowed for the replication of genotypes to evaluate phenotypes. Also, because this map shares a set of common marker loci with maps of *B. napus* (Ferreira et al. 1994) and *B. rapa* (Teutonico and Osborn 1994), it was possible to compare genomic regions associated with flowering time between these species.

Materials and methods

Plant materials

The inbred cabbage line Badger Inbred-16 (BI-16) was crossed as the female parent to the inbred broccoli line OSU Cr-7. A single F_1 plant was bud self-pollinated after vernalization for 8 weeks at 4°C. A total of 124 randomly selected F_2 plants were used for RFLP genotyping and the construction of a linkage map (Camargo 1994). F_2 plants were bud self-pollinated after vernalization, generating seeds of F_3 families. A subset of 92 F_3 families, self-pollinated progenies of the parents, the F_1 hybrid population, and progeny from backcrossing the F_1 to the broccoli parent (BCB population) were each evaluated for flowering time.

Evaluation of flowering

Seeds were planted in the greenhouse on April 29, 1993, and transplanted to the field at the West Madison Agricultural Research Station of the University of Wisconsin on June 10, 1993. Plots consisting of 12 plants from each F_3 family, parents, F_1 hybrid and BCB were arranged in rows, and plants were spaced 1 m apart both within and between rows. The experiment consisted of two complete randomized blocks. Standard cultural practices were used for insect and weed control. For the evaluation of flowering, a total of 15 surveys were made throughout the growing season at 5–15 day intervals, from July 15 until October 16, in which individual plants were inspected for the presence of flower buds or open flowers. Two quantitative traits related to flowering time were used for statistical and QTL analysis: (1) the proportion of flowering or budding plants within each plot at the end of the experiment (127 days after transplanting), referred to as PF, and (2) a flowering-time index (FT) defined as:

$$FT = \sum_{i=1}^{16} [X_{(i)} - X_{(i-1)}] \times T_{(i-1)}$$

where $X_{(i)}$ is the proportion of flowering or budding plants at time (days) after transplant $T_{(i)}$ determined at each survey (i). In order to include plants that did not bud at the end of the experiment in the calculation, $X_{(i)}$ at a hypothetical $T_{(16)}$ was assumed to be 1.0. PF is a qualitative evaluation of the annual/biennial habit of F_3 families while FT approximates the time when 50% of the plants within an F_3 family started to flower (FT_{50}). However, in cases where the proportion of flowering plants did not reach 1.0 at the end of the experiment, FT underestimates FT_{50} since an equal weight is assigned to all plants that did not flower during the course of the experiment. Therefore, FT artificially reduces the phenotypic variance of the population and could decrease the ability to detect QTLs with small phenotypic effects. However, the calculation of FT for F_3 families is straight forward, involves minimal data transformation, and combines both qualitative (annual/biennial) and quantitative (days to flower) parameters associated with flowering time.

Analyses of variance were performed separately for PF and FT data in order to detect any family or block effects. Data for each family were pooled across blocks, and PF and FT were recalculated for use in QTL analysis. The normality of the phenotypic distributions were tested by the Shapiro-Wilk correlation test (Minitab Inc. 1991) prior to QTL analysis.

QTL analysis

Information from a previously described RFLP linkage map developed for this population (Camargo 1994) was used for mapping QTLs associated with flowering time. The map contained 112 marker loci covering 1002 cM with an average marker interval of 9.9 cM. Each locus was named after the probe used for detection: *wg* and *tg* loci were detected with annonymous genomic DNA clones and *ec* loci were detected with annonymous cDNA clones. A letter (a or b) at the end of the locus name designates multiple segegating loci that were detected with the same clone. QTLs were mapped using an interval mapping method (Lander and Botstein 1989) with the aid of the computer program MAPMAKER/QTL 1.1 (Lincoln et al. 1992). A LOD score ($\log_{10}$ of the likelihood odds ratio that a QTL is present versus absent) greater than 2.5 was used to declare the presence of a QTL within a marker interval. The possible modes of gene action were determined using MAPMAKER/QTL 1.1 as described by Paterson et al. (1991). Briefly, the 'try' command of MAPMAKER/QTL was used to calculate the LOD scores of constrained (fixed) genetic models in which a particular type of gene action (additive, dominant, or recessive in the case of an F_2 population) is assumed for the QTL. The LOD score of the constrained model was then compared to the LOD of the unconstrained (free) model where no assumptions are made regarding the mode of gene action. If the LOD of the constrained model was at least 1.0 lower than the unconstrained model ($\Delta LOD \leq -1.0$), then the mode of gene action specified by the constrained model was declared unlikely. Significant QTL effects were included in a multilocus model as described by Paterson et al. (1991) in order to determine the percentage variation explained by all the QTLs detected.

Significant associations between specific markers and flowering traits detected by MAPMAKER/QTL were confirmed by a single-factor analysis of variance of the trait means for the three marker genotypic classes at the marker locus closest to the peak LOD using Minitab's GLM procedure. Digenic epistatic interactions between pairs of selected markers were investigated by a two-factor analysis of variance as described by Edwards et al. (1987).

Results

Population phenotypes

During the course of the experiment, none of the selfed plants of the cabbage parent showed any signs of flower initiation. BI-16 has a strong vernalization requirement, usually 8 weeks of cold treatment at 4°C, with flower initiation occurring approximately 1 month later. Flowering has never been observed in non-vernalized plants grown in the greenhouse for periods exceeding 2 years. In contrast, all selfed plants of the broccoli parent flowered by 66 days after transplanting (Fig. 1A). Similarly, all F_1 hybrid plants had flower buds by the end of the experiment but flowering was markedly delayed in relation to Cr-7 plants (Fig. 1A). F_1 plants were tall and vigorous and had small broccoli-like heads. The flowering time of BCB plants was intermediate between that of Cr-7 and the F_1 plants (Fig. 1A).

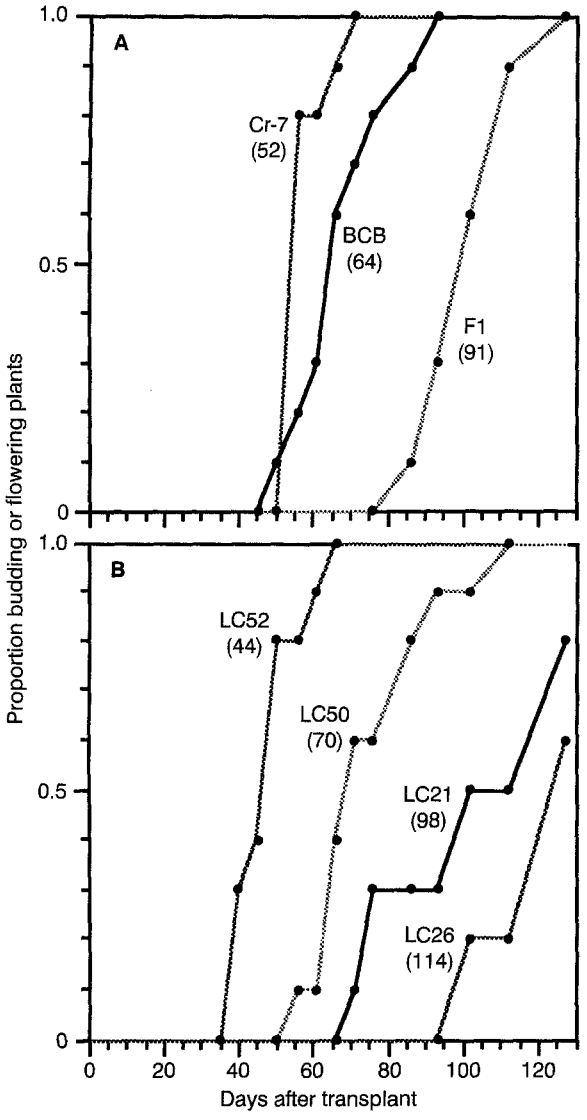

Fig. 1 Proportion of budding or flowering plants versus days after transplanting to the field for the broccoli parent (*Cr-7*), the F_1 hybrid (*F1*), and the F_1 backcrossed to the broccoli parent (*BCB*) (**A**); and for selected F_3 families (**B**). The flowering-time index of each line is in *parentheses*

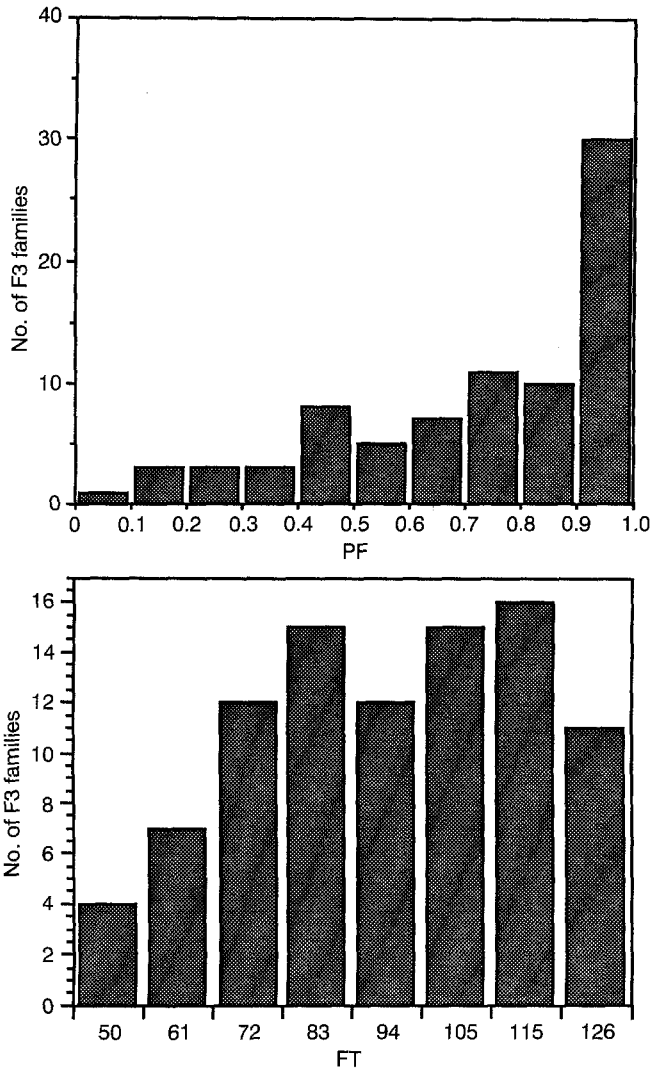

Fig. 2 Phenotypic distributions of F_3 families for the proportion of flowering plants at 127 days after transplanting (*PF*) and flowering time index (*FT*)

F_3 families varied widely for flowering time with some consisting entirely of early flowering plants and others having very late-flowering and non-flowering plants (Fig. 1B), but families consisting solely of broccoli or cabbage types were not observed. Based on an analysis of variance, family effects were significant ($P<0.05$) and block effects were non-significant ($P>0.05$) for both PF and FT. Data collected from the two blocks were pooled to obtain single PF and FT values for each family and these values were used for QTL analyses. None of the F_3 families were composed entirely of biennial plants and, therefore, a discrete classification of families into annuals or biennials was not possible. The F_3 families were not normally distributed for PF and FT ($P<0.05$; Fig. 2), and the distribution for PF was highly skewed towards the broccoli parent. A $(FT)^{1.5}$ transformation normalized the data, whereas a $(PF)^2$ reduced the skewness but did not normalize the distribution.

QTL analysis

Marker intervals containing putative QTLs for flowering traits were identified using both transformed and untransformed data (Table 1). Although the LOD values and the estimates of the percentage phenotypic variation explained by the QTLs for the two data sets were slightly different, all marker intervals with significant LOD values for untransformed data also had significant LOD values for transformed data, except for the interval in LG 2 for PF which was just below the LOD threshold. Also, the two intervals significantly associated with PF were significantly associated with FT. Therefore, the results presented hereafter

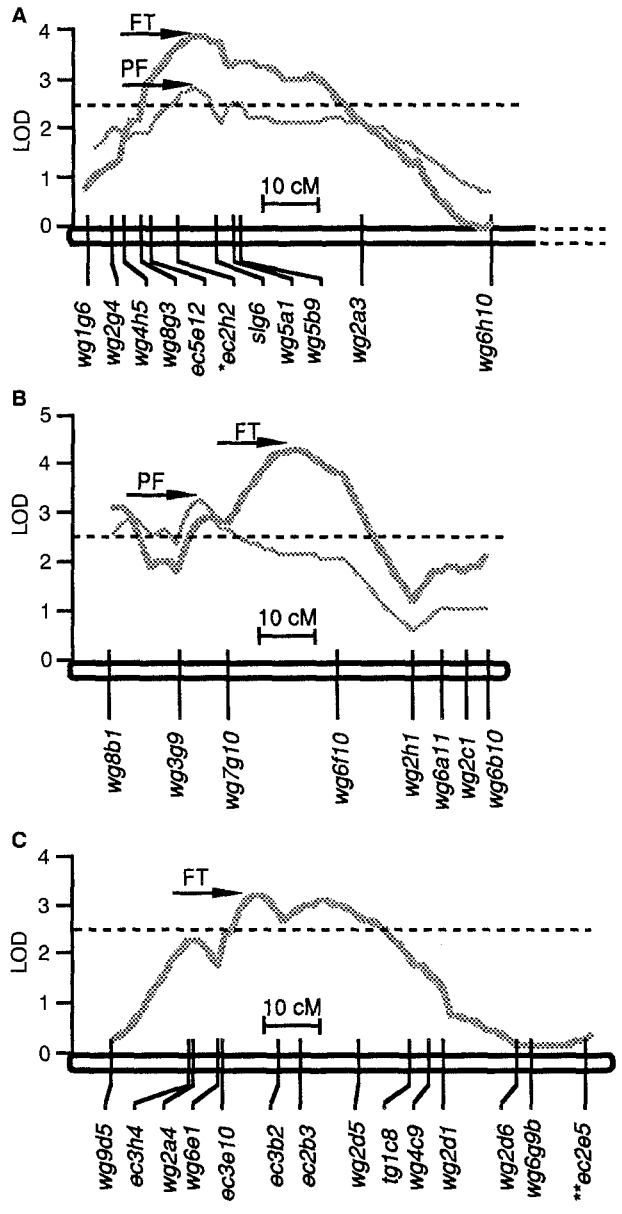

Fig. 3 LOD scores for flowering-time index (*FT*) and the proportion of flowering plants (*PF*) on linkage groups 2 (**A**), 6 (**B**), and 8 (**C**). Peak LOD scores for each trait are indicated by *arrows*. Marker loci are indicated on the x-axes. * and ** indicate marker loci with significant deviation from expected segregation ratios at $P<0.05$ and 0.01, respectively. Only a portion of linkage group 2 is shown

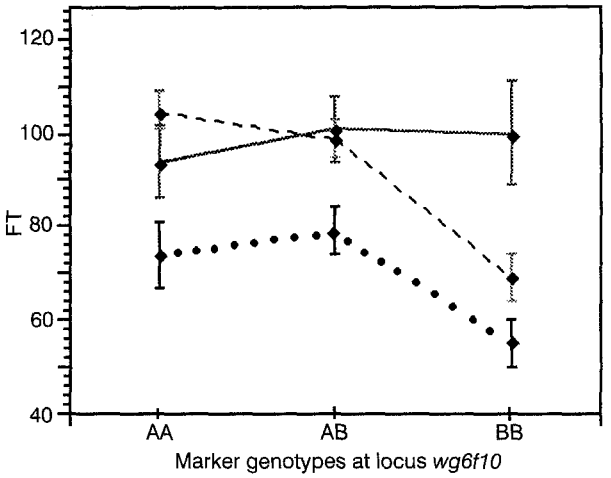

Fig. 4 Illustration of epistasis between genomic regions controlling flowering-time index (*FT*) for marker locus *wg6f10* on linkage group 8 (*A*=cabbage alleles, *B*=broccoli alleles) and marker locus *ec3b2* on linkage group 6 (*solid line* AA, *dashed line* AB, and *dotted line* BB genotypes). Means and standard errors of the nine possible two-locus marker genotypic classes are shown

focus on putative QTLs detected by the analysis of untransformed FT data.

Three regions on linkage groups (LGs) 2, 6, and 8 (Table 1; Fig. 3) were associated with FT. The locus on LG 6 explained 29.9% of the variation in FT and can be regarded as a major locus. Dominance or additivity of cabbage alleles at this locus was likely. Families homozygous for cabbage alleles at the marker locus *wg6f10* flanking this QTL had a mean FT=103 whereas families homozygous for broccoli alleles had a mean FT=76. The two QTLs detected on LGs 2 and 8 accounted for smaller portions of the phenotypic variation (Table 1). Recessive or additive gene action of cabbage alleles was likely at the locus on LG 2, whereas dominant or additive gene action was likely at the locus on LG 8.

A multi-locus model including the peak effects of the three putative QTLs explained 54.1% of the variation for FT, with cabbage alleles contributing towards higher FT values in all cases. No additional QTLs were detected with this model. The significance of marker-locus trait associations detected by interval mapping was confirmed by single-factor ANOVA for all three putative QTLs (data not shown). The codominant marker loci used for the analyses of variance were *wg5a1* on LG 2 (LOD=3.3), *wg6f10* on LG 6 (LOD=3.8), and *ec3b2* on LG 8 (LOD=3.2).

Digenic epistasis

Two-way interactions between pairs of marker loci associated with FT indicated significant ($P<0.005$) digenic epistasis between the genomic regions on LGs 6 and 8. The epistatic effect between these regions can be illustrated by plotting the mean FT of all nine possible two-locus marker genotypic classes for the markers closest to the LOD peaks (Fig. 4). The phenotype of F_3 families homozygous for cabbage alleles at the marker locus *ec3b2* on LG 8 (AA plants, solid line in Fig. 4) was not affected by their genotype at the marker locus *wg6f10* on LG 6, whereas families homozygous for broccoli alleles or heterozygous (BB or AB plants; dotted or traced lines in Fig. 4, respectively), had a significant decrease ($P<0.05$) in FT when two cabbage alleles were substituted by broccoli alleles at the locus on LG 6.

Table 1 Marker intervals significantly associated with flowering-time index (FT) and the proportion of flowering plants at 127 days after transplanting (PF)

Marker interval	Linkage group[a]	Peak LOD score	%Var[b]	Gene action[c]		
				a	d	Mode
FT						
ec2h2-slg6	2	3.9 (3.9)[d]	19.7 (20.6)	10.2	−11.4	A, R
wg6f10-wg7g10	6	4.3 (4.0)	29.9 (27.0)	15.6	7.2	A, D
ec3b2-ec3e10	8	3.2 (3.2)	19.2 (18.4)	13.7	6.5	A, D
PF						
ec2h2-slg6	2	2.9 (2.3)	16.1 (13.7)	0.1	−0.1	A, R
wg7g10-wg3g9a	6	3.4 (3.3)	20.6 (20.0)	0.1	0.2	A, D

[a] Linkage groups as described in Camargo (1994)
[b] Percentage of phenotypic variation explained by QTLs
[c] a=additive value of cabbage alleles, d=dominance value of cabbage alleles; possible modes of gene action of cabbage alleles (A=additive, D=dominance, and R=recessive) based on a comparison between LOD scores of constrained models and the unconstrained model
[d] Values in parenthesis refer to the analysis of transformed data

Discussion

Previous studies on the genetic control of flowering in *B. oleracea* used single F_2 plants as the experimental unit. In the present study, replicated F_3 families were used instead to provide a better estimate of the genotype effects of F_2 plants. The continuous distribution of F_3 families for FT suggested polygenic control of flowering time, in agreement with some of the previous studies on cabbage×broccoli crosses (Baggett and Wahlert 1975; Pelofske and Baggett 1979; Baggett and Kean 1989; Kennard et al. 1994). Based on the absence of completely biennial F_3 families, there was no evidence for a single dominant gene controlling annual habit, as reported by some authors (Detjen 1926; Horovitz and Perlasca 1954; Wellensieck 1960; Walkoff 1963; Landry et al. 1992). This could be due to the use of different genotypes, but the distinction between annual/biennial types is also dependent on the duration of the experiment. For example, plants containing alleles that extend the time to flower beyond the length of the experiment will be classified as biennials. Thus, monogenic ratios could be obtained depending on the growing conditions and the length of the experiment. It is worth noting that Landry et al. (1992) reported ratios consistent with a single dominant gene controlling annual habit in a cross between a cabbage-type breeding line and an annual rapid-cycling *B. oleracea*, but they were unable to map it in a relatively dense RFLP linkage map. The authors recognized the need for a quantitative approach since more than one locus could be involved.

Results of marker interval analysis confirmed that flowering time is under oligogenic control, with at least three putative loci involved. Two QTLs on different linkage groups were found associated with PF, a parameter that expresses the proportion of annual plants within an F_3 family. These regions were also found to be associated with FT, an index related to days to flower. The putative locus on LG 2 is linked to *slg6*, a gene that encodes an S-locus-specific glycoprotein involved in the self-incompatibility mechanism of *B. oleracea* (Nasrallah et al. 1985), while the putative locus on LG 6 is linked to a QTL that controls petiole length (Camargo et al. 1995). Linked regions controlling both growth habit and flowering time also were reported in another *B. oleracea* study (Kennard et al. 1994). A third region was associated with FT but not with PF.

Broccoli alleles at all three putative loci contributed towards a shorter flowering time. The one F_3 family that was homozygous for broccoli alleles at flanking markers for all three QTLs (progeny LC52 in Fig. 1) had the lowest FT value of all progenies. No inferences could be made about the phenotypic effects of having cabbage alleles at all three QTLs, since no such F_2 plant was recovered. However, no F_3 families comprised only of biennial types were observed in this study. Thus, it is possible that genotypes homozygous for cabbage alleles would resemble the cabbage parent in that vernalization would be required for flower initiation. Genotyping of biennial plants from specific F_3 families should add important information to this hypothesis. Late annual F_3 plants forming cabbage heads were recovered within one F_3 family (progeny LC26 in Fig. 1), with flower stalks developing from small heads lateral to the main central head. This family originated from an F_2 plant homozygous for cabbage alleles at the marker loci flanking the QTLs on LGs 2 and 8 but heterozygous at the marker loci flanking the QTL on LG 6 and it could be used as a genetic source of annual cabbage types.

Definitive conclusions about the modes of gene action were hindered because the means of F_3 families were used rather than the phenotypic value of the F_2 plants. As pointed out by Paterson et al. (1991), these values underestimate the dominance gene effects due to an increase in homozygosity with an additional generation of selfing. Epistasis was detected between two genomic regions controlling flowering time on LGs 6 and 8. Epistasis for genes controlling flowering has been observed previously for *B. oleracea* (Kennard et al. 1994) and *B. juncea* (Sachan and

Singh 1987) but not for *B. napus* (Thurling and Vijendra Das 1979; Ferreira et al. 1995).

The three putative loci detected by marker analysis explained a relatively large portion of the phenotypic variation. Kennard et al. (1994) also found three chromosomal regions with large phenotypic effects on flowering but they also reported additional regions with smaller effects and no such regions were found in our study. This could be due to the use of different parental genotypes, experimental conditions, and/or phenotypic scoring methods. However, we used a much higher threshold for declaring significant QTLs than was used by Kennard et al. The positions of QTLs reported in our study and in Kennard et al. can not be compared because different probes were used for mapping in the two studies.

The results of the present study are based on a single population evaluated in one environment, and therefore we do not know if the same QTL would have significant effects in other crosses and/or environments. However, our preliminary results based on backcrossing the late-flowering phenotype from BI-16 into a rapid cycling stock (CrGC3-1 from the Crucifer Genetic Cooperative, University of Wisconsin, Madison, Wis., USA) suggest that cabbage alleles at two of the loci are effective in that genetic background. After four generations of backcrossing with selection in backcross generations based only on flowering time of greenhouse- or growth chamber-grown plants, cabbage alleles were still segregating at *wg6f10* in LG 6 and *wg2d5* in LG 8 (unpublished data). Plants heterozygous for one or the other of these marker loci have been selected and are being further backcrossed to more precisely define the effects of these alleles. Cabbage alleles at RFLP loci near the QTL on LG 2 were not detected; however, cabbage alleles at this QTL were recessive in our cabbage broccoli population and may not have conferred a phenotype in backcross generations.

The map positions of flowering-time QTLs were reported previously for *B. napus* (Ferreira et al. 1995) and *B. rapa* (Teutonico and Osborn 1995) using RFLP linkage maps that had marker loci in common with our *B. oleracea* map. Although there was evidence for conservation of chromosomal segments between *B. oleracea* and *B. rapa* (Teutonico and Osborn 1994) and between *B. oleracea* and *B. napus* (Camargo 1994), there was no evidence for conservation of flowering-time genes between *B. oleracea* and these species. None of the *B. oleracea* LGs containing flowering-time QTLs had more than one marker locus in common with LGs containing flowering-time QTLs in *B. rapa* or *B. napus*. One probe (WG6B10) detected an RFLP locus in common between LG 9 of *B. napus*, which contained a QTL having a major effect, and LG 6 in *B. oleracea*. However, this locus mapped right at the peak LOD score for the QTL in *B. napus*, whereas in *B. oleracea* it mapped about 45 cM from the peak LOD score. Although we found no evidence for homology between the flowering-time genes identified in *B. oleracea* and those identified in *B. napus* and *B. rapa*, this hypothesis should be tested further by fine-structure mapping of additional marker loci linked to flowering-time genes in the three species.

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