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Genetic Control of Photoperiod Sensitivity in Maize Revealed by Joint Multiple Population Analysis

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ABSTRACT

Variation in maize for response to photoperiod is related to geographical adaptation in the species. Maize possesses homologs of many genes identified as regulators of flowering time in other species, but their relation to the natural variation for photoperiod response in maize is unknown. Candidate gene sequences were mapped in four populations created by crossing two temperate inbred lines to two photoperiod-sensitive tropical inbreds. Whole-genome scans were conducted by high-density genotyping of the populations, which were phenotyped over 3 years in both short- and long-day environments. Joint multiple population analysis identified genomic regions controlling photoperiod responses in flowering time, plant height, and total leaf number. Four key genome regions controlling photoperiod response across populations were identified, referred to as *ZmPR*1–4. Functional allelic differences within these regions among phenotypically similar founders suggest distinct evolutionary trajectories for photoperiod adaptation in maize. These regions encompass candidate genes *CCA/LHY*, *CONZ1*, *CRY2*, *ELF4*, *GHD7*, *VGT1*, *HY1/SE5*, *TOC1/PRR7/PPD-1*, *PIF3*, *ZCN8*, and *ZCN19*.

MAIZE (*Zea mays* L. subsp. *mays*) was domesticated in southern Mexico and its center of diversity is in tropical Latin America (Goodman 1999; Matsuoka *et al.* 2002), where precipitation rates and day lengths cycle annually. The presumed ancestor of maize, teosinte (*Zea mays* L. subsp. *parviglumis*), likely evolved photoperiod sensitivity to synchronize its reproductive phases to the wetter, short-day growing season (Ribaut *et al.* 1996; Campos *et al.* 2006). A critical event in the postdomestication evolution of maize was its spread from tropical to temperate regions of the Americas (Goodman 1988), requiring adaptation to longer day lengths. The result of this adaptation process is manifested today as a major genetic differentiation between temperate and tropical maize (Liu *et al.* 2003) and substantially reduced photoperiod sensitivity of temperate maize (Gouesnard *et al.* 2002). Tropical maize exhibits delayed flowering time, increased plant height, and a greater total leaf number when grown in temperate latitudes with daily dark periods <11 hr (Allison and Daynard 1979; Warrington and Kanemasu 1983a,b). Identifying the genes underlying maize photoperiod sensitivity will provide insight into the postdomestication evolution of maize and may reduce barriers to the use of diverse tropical germplasm resources for improving temperate maize production (Holland and Goodman 1995; Liu *et al.* 2003; Ducrocq *et al.* 2009).

Natural variation at key genes in flowering time pathways is related to adaptation and evolution of diverse plant species (Caicedo *et al.* 2004; Shindo *et al.* 2005; Turner *et al.* 2005; Cockram *et al.* 2007; Izawa 2007; Slotte *et al.* 2007). Identification of some of the genes controlling adaptation in numerous plant species relied on regulatory pathways elucidated in Arabidopsis (Simpson and Dean 2002). Many key genes in the Arabidopsis flowering time regulatory pathways are conserved across diverse plant species (Kojima *et al.* 2002; Hecht *et al.* 2007; Kwak *et al.* 2008), but their functions have diverged, resulting in unique regulatory pathways in some phylogenetic groups (Colasanti and Coneva 2009). For example, *FRI* and *FLC* control most natural variation for vernalization response in Arabidopsis (Caicedo *et al.* 2004; Shindo *et al.* 2005), but wheat and barley appear to lack homologs of these genes

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and regulate vernalization response with different genes (Yan *et al.* 2004).

Maize exhibits tremendous natural variation for flowering time (Gouesnard *et al.* 2002; Camus-Kulandaivelu *et al.* 2006), for which numerous QTL have been identified (Chardon *et al.* 2004). In contrast, only a few flowering time mutants are known and only a handful of flowering time genes, including *DWARF8* (*D8*), *DELAYED FLOWERING1* (*DLF1*), *VEGETATIVE TO GENERATIVE TRANSITION1* (*VGT1*), and *INDETERMINATE GROWTH1* (*ID1*), have been cloned in maize (Thornsberry *et al.* 2001; Colasanti *et al.* 2006; Muszynski *et al.* 2006; Salvi *et al.* 2007; Colasanti and Coneva 2009). Variation at or near *D8* and *VGT1* is related to latitudinal adaptation, but these genes do not appear to regulate photoperiod responses and account for only a limited proportion of the standing flowering time variation in maize (Camus-Kulandaivelu *et al.* 2006, 2008; Ducrocq *et al.* 2008; Buckler *et al.* 2009).

Quantitative trait loci (QTL) mapping was a key first step to identifying the genes underlying natural variation for flowering time in Arabidopsis (Koornneef *et al.* 2004). Photoperiodic QTL have been mapped previously in individual biparental maize mapping populations (Koester *et al.* 1993; Moutiq *et al.* 2002; Wang *et al.* 2008; Ducrocq *et al.* 2009). Such studies are informative with respect to the parents from which the populations were derived, but often do not reflect the genetic heterogeneity of broader genetic reference populations (Holland 2007).

Association mapping (Thornsberry *et al.* 2001; Ersoz *et al.* 2007) and combined analysis of multiple biparental crosses (Rebaï *et al.* 1997; Rebaï and Goffinet 2000; Blanc *et al.* 2006; Verhoeven *et al.* 2006; Yu *et al.* 2008) represent alternative approaches to understanding the variation in genetic control for complex traits among diverse germplasm. Association mapping has limited power to identify genes that affect traits closely associated with population structure, such as flowering time in maize (Camus-Kulandaivelu *et al.* 2006; Ersoz *et al.* 2007). In contrast, joint QTL analysis of multiple populations is not hindered by the associations between causal genes and population structure. Combined QTL analysis of multiple mapping populations provides improved power to detect QTL, more precise estimation of their effects and positions, and better understanding of their functional allelic variation and distribution across more diverse germplasm compared to single-population mapping (Rebaï *et al.* 1997; Wu and Jannink 2004; Jourjon *et al.* 2005; Blanc *et al.* 2006; Verhoeven *et al.* 2006; Yu *et al.* 2008; Buckler *et al.* 2009). Joint analysis also provides a direct test of the importance of higher-order epistatic interactions between founder alleles at individual loci with genetic backgrounds (Jannink and Jansen 2001; Blanc *et al.* 2006). In this study, joint analysis of multiple populations was used to test directly the hypothesis that diverse tropical maize lines carry functionally similar alleles at key photoperiod loci, which would imply genetic homogeneity for a common set of mutations and a shared evolutionary pathway for photoperiod insensitivity.

The objective of this study was to integrate candidate gene analyses with photoperiod QTL mapping across multiple maize populations. We tested candidate floral regulators known from other species for associations with natural variation for photoperiod response in maize. We analyzed flowering time in four interrelated recombinant inbred line (RIL) populations, each derived from crosses between temperate and tropical maize parents (Figure 1), in both long- and short-day environments to characterize their responses to distinct photoperiods. Joint population analysis provided high resolution of many QTL positions, permitting robust testing of underlying candidate genes. We directly and indirectly mapped homologs of flowering time candidates genes from Arabidopsis, rice, and barley on a dense consensus genetic map of these four populations, permitting identification of homologs that colocalize with genome regions associated with variation for photoperiod response. These mapping families are being integrated into the maize nested association mapping (NAM) population (Buckler *et al.* 2009; McMullen *et al.* 2009) because they were genotyped with the maize NAM map SNP markers, they involve the common parent B73, and their seed and genotypic information (File S1 cont.) are publicly available. Their availability further expands the genetic diversity represented by the maize NAM population and enhances this valuable public community resource.

MATERIALS AND METHODS

Plant materials for recombinant inbred line populations: We studied maize inbred lines B73, B97, CML254, and Ki14 and recombinant inbred lines derived from crosses among them. Inbred parents for this study were chosen as a sample of maize germplasm diversity from both tropical and temperate groups and on the basis of previously observed photoperiodic responses in summer *vs.* winter nurseries (http://www.panzea.org). B73 and B97 were both developed at Iowa State University (Russell 1972; Hallauer *et al.* 1994) and represent two distinct maize germplasm groups for U. S. Corn Belt Dent maize: Stiff Stalk temperate (B73), and non-Stiff Stalk temperate (B97; Liu *et al.* 2003). CML254 was developed by the International Maize and Wheat Improvement Center (CIMMYT) in Mexico (Srinivasan 2001) and Ki14 by Kasetsart University in Thailand (Chutkaew *et al.* 1997). CML254 and Ki14 are both tropical, but they represent distinct subgroups of tropical germplasm (Liu *et al.* 2003).

Recombinant inbred line population development: We developed four populations of maize RILs by making all possible crosses between temperate (B73 or B97) and tropical (CML254 or Ki14) parental lines (B73 × CML254, CML254 × B97, Ki14 × B73, and B97 × Ki14; Figure 1). The Ki14 × B73 population was developed at The Ohio State University, whereas the other three were developed at North Carolina State University. From F_2 progeny of each cross, single seed descent was employed to produce RILs at either the $F_{5:6}$ or $F_{6:7}$

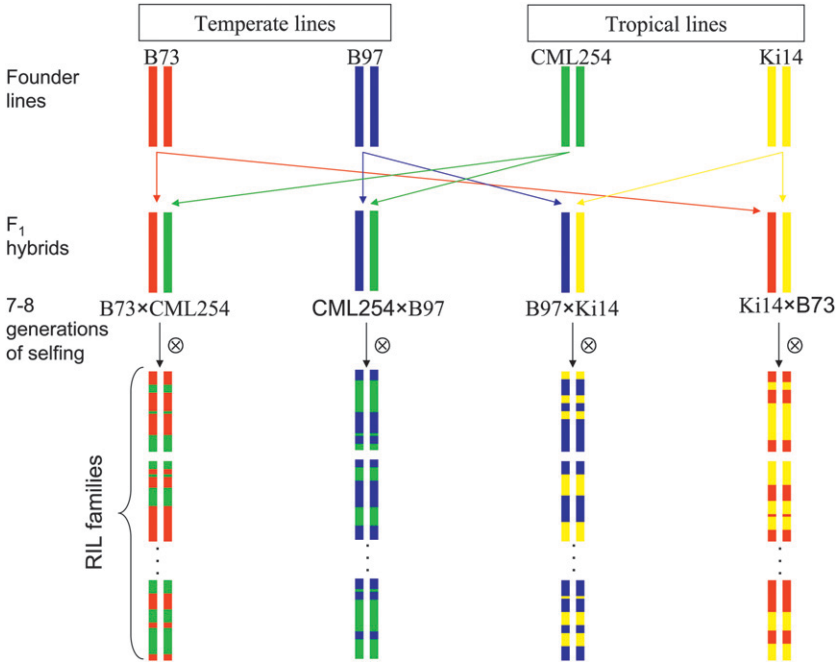

Figure 1.—Factorial mating of two temperate (B73 and B97) and two tropical (CML254 and Ki14) inbred maize lines to create four related recombinant inbred line mapping populations.

generations. Selfing generations alternated between long-day summer nurseries in Clayton, NC or Wooster, OH and short-day winter nurseries in Homestead, FL or Puerto Rico. Substantial losses of lines due to large anthesis–silking intervals (ASI), male and female sterility, and overall poor vigor were observed in all populations, which limited sample sizes of RILs in later generations. RIL seed was increased via full-sib mating and bulking of seed from up to 20 plants per line. In total, after eliminating several lines in each population that carried nonparental marker alleles, we studied 120, 126, 214, and 109 RILs from the B73 × CML254, CML254 × B97, B97 × Ki14, and Ki14 × B73 populations, respectively. Small seed lots of RILs are freely available from J. B. Holland upon request.

RIL experimental design and phenotyping: Phenotypes were measured under long-day conditions during four summer seasons from 2004 to 2007 at Clayton, NC (latitude 35.7° N, average day length from May 1 to July 31—the typical period from planting to flowering—is 14 hr 10 min from sunrise to sunset). The number of replications per environment is explained in supporting information, Table S1. In all years, locations, and populations, we employed an augmented alpha lattice design with an average of 9% of plots planted to repeated parental checks, which permitted the adjustment of phenotypic data for incomplete block effects (Wolfinger *et al.* 1997), even for the environment with only one complete replication. An additional long-day measurement of days to anthesis (DTA) was taken in 2006 at Andrews, NC—a location with a similar latitude and day length as Clayton, but at a higher elevation (latitude 35.2° N, 518 *vs.* 134 meters above sea level). Short-day phenotyping was carried out during three winter seasons from 2005 to 2007 at Homestead, FL (25.4° N, average day length from October 1 to December 31—the typical period from planting to seed filling—is 11 hr and 9 min from sunrise to sunset).

We measured five traits in each plot, including DTA, days to silking (DTS), plant height (PH), ear height (EH), and total leaf number (TLN). We defined DTA and DTS as the number of days between planting and when 50% of the plants in a plot were shedding pollen or exerting silks, respectively. Because of the strong influence of temperature on DTA and DTS, flowering time measurements were converted to growing degree days (GDD) following McMaster and Wilhelm (1997), with 10° as T_{BASE} and 30° as T_{max}. GDDTA and GDDTS represent the cumulative average daily heat units that a row of plants received from the time that seeds were sown in the field until anthesis or silking occurred, respectively. In replications where both GDDTA and GDDTS were evaluated, the anthesis–silking interval was also calculated as the difference in GDD between DTA and DTS (GDDASI). PH and EH were measured in centimeters as the distance between the ground and the last leaf node or the primary ear branch, respectively. The earliest emerging leaves naturally senesce before flowering in maize, which prevents measuring total leaf number (TLN) by simply counting visible leaves at the end of the growing season. Therefore, we marked fifth, tenth, and occasionally fifteenth leaves of each measured plant soon after they emerged. The marked tenth leaf was almost always identifiable at the end of the growing season, permitting counts of the total number of leaves on that same plant at the end of the growing season. We measured PH, EH, and TLN on two plants per plot in summer 2006, and on three plants per plot in all subsequent replications.

Phenotypic data analysis: Data from the RIL populations were analyzed using SAS version 9.1 Proc Mixed (SAS Institute, 2002–2004). Data from summer long-day environments were analyzed separately from data from winter short-day environments. Parents were considered fixed genotypes and RILs were considered random effects, permitting estimation of best linear unbiased predictors (BLUPs) for each RIL, following Piepho *et al.* (2006). Complete replications, incomplete blocks, environments, and year-by-genotype interactions were also considered random effects. Columns and rows representing the physical layouts of the summer environments were also included as random effects to account for spatial variation. Each combination of the six measured characters and environmental day length (short- or long-day length) was considered a distinct trait for genetic analysis. We also estimated the photoperiodic response of each trait by subtracting the BLUPs for the trait measured in short-day environments from the BLUPs for the trait measured in long-day environments for each RIL within each year and analyzing the response across years. Thus, for each measured

characteristic we obtained three distinct BLUPs, representing the genotypic value in short-day environments, in long-day environments, and for the photoperiod response. In total, BLUPs for 18 traits were obtained for each mapping line.

Genotypic data: Genomic DNA was extracted from the bulked leaf tissue of 10 plants representing each of the RILs using the Invitrogen Charge Switch Genomic DNA extraction kit (Invitrogen, Carlsbad, CA). We used simple sequence repeat (SSR) markers from the maize genetic database (http://www.maizegdb.org) and SNP markers from the Panzea project (http://www.panzea.org) to define linkage groups. SSR markers were genotyped using gel electrophoresis on SFR agarose (Amresco, Solon, OH). SNP markers were genotyped using the Illumina Golden Gate SNP genotyping assay (Fan *et al.* 2003) with a 1536-locus array. The context sequences for the successful assays from this array can be obtained from http://www.panzea.org/lit/data_sets.html#SNPs, file NAM_snp-080715.xls. This same set of SNP markers was used to create the maize NAM map (www.maizegdb.org; McMullen *et al.* 2009). Thus, these populations can be incorporated into the overall NAM platform in future genetic analyses to expand the genetic diversity sampled in that mapping platform.

Four of the SNP markers were developed from sequences identical or homologous to flowering time or morphology genes known from maize: *D8*, *ZFL2*, *FEA2*, and *HD1*. We also developed several markers from maize DNA sequences with high homology to photoperiodic and flowering time genes of Arabidopsis and rice (DNA sequences for these genes from B73 and the other 25 founders of the maize NAM population obtained from Edward Buckler, USDA-ARS), including *CHLOROPHYLL A/B BINDING PROTEIN* (*CAB*), *CIRCADIAN CLOCK ASSOCIATED 1* (*CCA1*), *CONSTANS-LIKE* (*CO*), *CRYPTOCHROME 2* (*CRY2*), *HEADING DATE3A/FLOWERING LOCUS T* (*HD3A*), *INDETERMINATE-RELATED PROTEIN 7* (*ID7*), *ZEA MAYS FLORICAULA1* (*LEAFY*), and *PHYTOCHROME C1* (*PHYC*). Sequences were aligned and indels and SNPs called. PCR primer pairs were designed to flank targeted indels or SNPs (Table S3). SNPs were assayed as cleaved amplified polymorphic sequences (CAPS) or derived cleaved amplified polymorphic sequences (dCAPS; Neff *et al.* 1998). Because the sequencing panel did not include CML254 or Ki14, several CAPS and dCAPS markers were developed for each gene and screened on the founders of our populations to identify polymorphic sequences. In addition, we sequenced alleles of two *LATE ELONGATED HYPOCOTYL* homologs (*LHY* and *LHYC8*) from the four founder lines of the populations studied here and developed CAPS or dCAPS markers for these genes.

All RILs were genotyped at polymorphic SSR and candidate gene sequences, and all RILs in the B73 × CML254, CML254 × B97, and Ki14 × B73 populations were also genotyped for all 1536 SNP markers. Because of limited resources, only a subset consisting of the 15 earliest, 15 latest, and a random sample of 98 RILs out of the remaining 184 total RILs from the B97 × Ki14 population were genotyped with SNPs.

A combined genetic map with the data from the four RIL populations was created. Preliminary genetic order of all loci was established with JoinMap 3.0 (Van Ooijen and Voorrips 2001). The COMPARE feature of Mapmaker/exp 3.0 (Lincoln *et al.* 1992) was then used to clarify regions where the JoinMap order differed greatly from the order of either the maize NAM or intermated B73 × Mo17 (IBM2) 2008 neighbors maps (http://www.panzea.org; http://www.maizegdb.org). Using Mapmaker, a combined map of the four RIL mapping populations was produced with 1339 (1088 SNP, 241 SSR, and 10 candidate gene) markers in the revised marker order. Individual maps for each of the four populations were then produced utilizing a similar method. A total of 866 (767 SNP, 97 SSR, and 2 candidate gene), 546 (459 SNP, 83 SSR, 4 candidate gene), 561 (476 SNP, 79 SSR, and 4 candidate gene), and 839 (765 SNP and 74 SSR) markers were placed on the genetic maps of B73 × CML254, CML254 × B97, B97 × Ki14, and Ki14 × B73, respectively. Seventy-three markers were mapped on all four populations, and each pair of populations had 221–315 common polymorphic markers.

QTL mapping: QTL mapping in individual populations was undertaken with MCQTL 4.0 software (Jourjon *et al.* 2005) on the basis of the RIL BLUPs. Permutation analysis (Churchill and Doerge 1994), based on 1000 permutations for each trait, was used to estimate empirically the genomewide $\alpha = 0.05$ LOD threshold rates for each trait in each of the RIL populations. The automated iterative QTL mapping (iQTLm) procedure of Charcosset *et al.* (2000) was used to search for QTL for each trait. In each population, cofactors were selected using 0.9 times the LOD threshold estimated for each specific combination of model and trait as recommended by Delannoy *et al.* (2006). Significant QTL were declared when LOD scores exceeded the genomewide $\alpha = 0.05$ threshold.

Two combined population QTL mapping models (connected and disconnected models) were tested for each trait with MCQTL. The connected analysis assumes that the founder parental allele effects are consistent across populations, so that four allele effects were estimated (with three degrees of freedom) at each QTL, whereas the disconnected analysis assumes that founder parent allele effects vary across populations, resulting in eight allele-by-population effect estimates (with four degrees of freedom) at each QTL (Blanc *et al.* 2006; Mangin *et al.* 2007). Permutation analyses and iQTLm procedures were used to search for QTL for each trait under both connected and disconnected models in the same way as for individual populations. The final connected and disconnected models for each trait were compared using Schwarz's Bayesian information criterion (BIC), and the model with the better BIC value was selected. QTL effects and 2-LOD support intervals were estimated from the final model with best BIC for each trait. Allelic effects at each locus were compared with approximate *t*-tests ($\alpha = 0.05$).

We tested for QTL × QTL epistasis using the epistasy function of MCQTL, which searches for any genome positions that interact with the QTL previously declared with significant effects. When epistatic interactions were detected, the BIC of the QTL models with and without epistasis were compared to judge their significance.

Inferring candidate gene locations: Candidate gene positions were inferred on the combined map if they could not be mapped directly due to lack of a polymorphic gene marker. First, a list of the key candidate photoperiod/flowering genes from Arabidopsis, rice, maize, and barley was created (Table S4). For genes previously identified in other species, we searched for their maize homologs using BLAST-X at the National Center for Biotechnology Information Web site (http://www.ncbi.nlm.nih.gov/). DNA sequences originating from maize were considered to be homologous to candidate genes from other plant species if their BLAST-X homologies were smaller than $E = 1.0 \times e^{-15}$. If no homolog was identified with the BLAST-X search, then a second search was conducted with BLAST-N directly on the MaizeGDB.org database utilizing the maize reference BAC library. In addition to BLAST searches, predicted genes homologous to a subset of Arabidopsis and rice genes were identified by searching the Gramene.org database for the Arabidopsis or rice gene, then using the "gene trees" tool to identify predicted orthologs in the maize reference genome sequence (Liang *et al.* 2007). Candidate genes and candidate gene homologs were positioned on our map using the maize genome browser at MaizeGDB.org to identify their location on the physical map

TABLE 1

Parental mean phenotypic values from long- and short-day environments and for photoperiod response (long-day−short-day means)

	GDDTA	GDDTS	GDDASI	PH	EH	TLN
Inbred line	Growing-degree days (GDD)			cm		No. of leaves
			Short-day environments			
B73	873 (31)	881 (36)	9 (6.8)	142 (12.3)	63 (5.0)	18 (0.37)
B97	809 (38)	841 (43)	31 (9.2)	120 (14.0)	50 (6.8)	15 (0.53)
CML254	1003 (35)	1005 (39)	1 (8.0)	126 (13.4)	71 (6.3)	20 (0.45)
Ki14	936 (36)	994 (40)	58 (8.4)	109 (13.1)	63 (6.1)	19 (0.45)
			Long-day environments			
B73	879 (19)	902 (24)	18 (5.8)	173 (7.2)	76 (3.0)	20 (0.26)
B97	867 (21)	910 (28)	40 (6.6)	159 (7.7)	74 (3.6)	19 (0.34)
CML254	1377 (26)	1440 (40)	58 (9.9)	162 (9.2)	99 (5.0)	29 (0.37)
Ki14	1107 (23)	1302 (29)	194 (7.1)	164 (8.1)	91 (4.0)	24 (0.39)
			Photoperiodic responses (long-day minus short-day responses)			
B73	5	22	9	31*	12*	2***
B97	58	69	9	38*	23**	3***
CML254	373***	433***	57***	37*	28**	8***
Ki14	171***	308***	136***	55**	29***	4***

Values in parentheses represent the standard error of each estimate. *Significantly different from zero at $0.05 < P < 0.01$. **Significantly different from zero at $0.01 < P < 0.001$. ***Significantly different from zero at $P < 0.0001$.

of sequenced and ordered BAC clones (obtained from MaizeGDB, September 2009). The SNP markers forming the backbone of the genetic map also have known BAC and contig addresses (Table S4). Mapped SNP loci flanking the candidate gene-containing BACs defined map intervals containing the candidate gene. In cases where local physical sequence order disagreed with map order, we extended the candidate gene interval to flanking markers that displayed ordering consistent with the physical map to reflect the uncertainty of these positions.

RESULTS

Phenotypic variation under short- and long-day lengths: Tropical inbred parent lines Ki14 and CML254 had significant photoperiod responses for all traits measured, with increased time to flower, height, and total leaf number in long-day environments (Table 1). Temperate parents B73 and B97 had significant but smaller photoperiod responses for height and leaf number and no significant photoperiod responses for flowering time (Table 1). These results are congruent with a phytotron study of inbred responses to different photoperiods where other environmental conditions were maintained constant (File S1; Table S2; Figure S1; Figure S4), demonstrating that the phenotypic differences between long- and short-day length field environments primarily represent photoperiodic responses.

Trait heritabilities ranged from 42 to 96% within mapping families, and most traits had heritabilities >75% (Table S5), demonstrating the reliability of phenotypic data for mapping QTL. Under short day lengths, phenotypic variation was compressed and no genomic region was associated with more than one day difference in flowering time (Table 2). We focus here on the genomic regions associated with photoperiod response, which tended to be similar to those regions causing variation under long-day lengths (Table 2; Figure 2).

Single population and combined multiple population QTL mapping: Analysis of each population separately suggested that many QTL differed between populations, but rarely did we find QTL that were unique to a single mapping population (Figure S2). Joint population analyses had much lower permutation-based significance thresholds and much higher QTL LOD scores than individual population analyses (Figure 3; Figure S2). Furthermore, the combined connected population analysis increased the precision of QTL position estimates over those of individual population analyses (Figure 3). Specifically, the 2-LOD support intervals of QTL mapped with the connected population analysis were significantly smaller on average (24 cM) than those mapped in individual populations (35 cM; $P < 0.0001$). The increased resolution of the joint analysis can be illustrated at the QTL with largest effect on the photoperiod response, centered at position 60.1 cM on chromosome 10, which explains 39–40% of the phenotypic variation for the anthesis and silking date photoperiod responses in the combined analysis (Table 2). The 2-LOD support interval around this QTL (expected to contain the causal gene with good probability with large population sizes; Van Ooijen 1992) ranged in size from 5 to 29 cM in the individual population analyses, but was narrowed to 1 cM in the joint analysis. The high resolution of QTL positions in the joint analysis greatly reduces the genome space in

TABLE 2

Peak LOD score positions, positions representing endpoints of 2-LOD support interval, proportion of phenotypic variation explained (*r*2), and allelic effects of QTL detected with combined connected population analysis model

Short-day QTL									
	QTL 2-LOD support interval and peak				Phenotypic	Additive effect			
Trait	Chr	Peak − 2 LOD	LOD Peak	Peak + 2 LOD	*r*2	B73	B97	CML254	Ki14
GDDTA	1	262	278	287	0.07	7.6a	−5.7b	−1.4bc	−0.5c
GDDTA	4	5	11	21	0.04	0.8a	1.7a	−5.4b	2.9a
GDDTA	5	46	52	133	0.05	−2.5a	−0.5a	5.8b	−2.9a
GDDTA	8	65	66	76	0.08	−3.5a	−0.9a	7.7b	−3.4a
GDDTA	9	99	103	147	0.06	4.3a	−7.2b	−0.5c	3.3ac
GDDTS	1	179	193	245	0.05	0.0ab	−5.6a	2.9b	2.8b
GDDTS	1	296	300	313	0.05	7.4a	−2.6b	−2.4b	−2.4b
GDDTS	5	48	54	60	0.06	−3.3a	−0.2a	7.8b	−4.3a
GDDTS	6	25	35	43	0.05	−1.1ab	−4.7a	1.1ab	4.6b
GDDTS	8	65	74	98	0.08	−4.5a	3.1b	8.3b	−6.9a
GDDTS	9	99	103	110	0.08	6.6a	−7.8b	−1.1c	2.4ac
GDDTS	10	124	136	179	0.05	1.5ab	−4.3a	−2.5a	5.4b
GDDASI	1	49	59	89	0.06	0.1ab	2.7b	−2.0a	−0.8a
GDDASI	2	104	108	125	0.08	−0.8ab	−2.6b	0.6ac	2.8c
GDDASI	3	72	93	102	0.06	−0.7a	3.2b	−2.3a	−0.3a
GDDASI	4	37	46	62	0.08	0.7ab	2.8b	−1.1ac	−2.5c
GDDASI	6	86	107	134	0.03	−0.8a	−0.8a	−0.8a	2.4b
GDDASI	8	61	67	93	0.13	−1.0a	5.1b	−1.7a	−2.4a
GDDASI	10	89	97	172	0.04	0.5a	0.3a	−3.2b	2.5a
PH	1	227	236	242	0.05	1.8a	−1.4b	−1.0bc	0.6ac
PH	3	89	96	113	0.08	0.7a	−2.3b	0.2a	1.4a
PH	8	46	55	61	0.15	1.1a	−3.6b	2.0a	0.5a
PH	10	142	158	168	0.05	0.2ab	1.5a	−1.4b	−0.3b
EH	1	256	276	293	0.07	1.6a	−1.5b	−0.9b	0.7a
EH	1	324	331	340	0.05	1.4a	0.2ab	−1.0b	−0.6b
EH	3	95	98	102	0.09	0.6a	−2.0b	0.6a	0.8a
EH	5	153	157	164	0.05	−0.2a	−0.9a	1.5b	−0.3a
EH	6	30	40	44	0.07	−2.0a	0.5bc	1.6b	−0.1c
EH	6	61	69	76	0.05	1.8a	−0.3b	−0.1b	−1.3b
EH	7	55	59	63	0.08	−0.5ab	1.4c	0.8ac	−1.6b
EH	8	56	59	64	0.10	0.8ab	−2.4c	2.1a	−0.4b
EH	8	117	123	128	0.07	−0.9a	−1.2a	1.5b	0.5ab
EH	10	48	60	66	0.06	−0.5ab	1.0ac	−1.8b	1.4c
TLN	1	115	134	153	0.05	−0.1a	−0.1a	0.0ab	0.2b
TLN	1	184	200	280	0.05	0.1a	−0.2b	0.0a	0.1a
TLN	2	80	87	125	0.10	0.2a	0.1a	−0.2b	0.0a
TLN	5	84	88	135	0.05	−0.2a	0.0ab	0.1b	0.0b
TLN	5	155	156	158	0.11	0.0a	−0.2b	0.2c	0.1ac
TLN	7	48	60	80	0.07	0.0ab	0.2a	−0.0b	−0.2b
TLN	8	124	130	133	0.08	−0.1ab	−0.2a	0.2c	0.0b
TLN	10	119	122	126	0.07	−0.2a	0.0b	0.2c	−0.1ab
Long-day QTL									
GDDTA	1	131	133	139	0.12	−8.4a	−5.1ab	11.3c	2.2b
GDDTA	2	180	184	187	0.09	−6.6a	−4.2ab	10.9c	−0.2bc
GDDTA	3	163	181	181	0.07	−8.0a	−2.2ab	6.0c	4.2bc
GDDTA	8	70	74	76	0.15	−7.4a	−6.2a	15.6b	−1.9a
GDDTA	9	106	115	120	0.09	−8.8a	−2.8ab	10.4c	1.2b
GDDTA	10	59	60	69	0.25	−6.6a	−14.2a	9.9b	11.0b
GDDTA	10	158	174	191	0.05	2.4a	−11.5b	6.4a	2.7a
GDDTS	1	138	144	146	0.08	−11.2a	−2.4b	9.5c	4.1bc
GDDTS	1	200	214	239	0.06	−3.7ab	−8.2a	10.2c	1.7c
GDDTS	2	180	183	185	0.09	−9.0a	−4.4a	13.5b	0.0a
GDDTS	3	159	171	181	0.05	−6.0ab	−5.7a	3.0bc	8.7c

(*continued*)

TABLE 2

(Continued)

Short-day QTL									
	QTL 2-LOD support interval and peak				Phenotypic	Additive effect			
Trait	Chr	Peak − 2 LOD	LOD Peak	Peak + 2 LOD	$r2$	B73	B97	CML254	Ki14
GDDTS	8	69	75	127	0.08	−10.4a	−0.4a	14.8b	−4.0a
GDDTS	9	103	107	124	0.07	−10.1a	−2.3ab	10.1c	2.3bc
GDDTS	10	59	60	63	0.28	−11.9a	−16.8a	9.7b	19.1b
GDDTS	10	135	166	190	0.05	5.5a	−13.4b	1.2a	6.7a
GDDASI	1	144	162	181	0.05	−5.4a	0.4b	1.8b	3.2b
GDDASI	2	28	41	47	0.05	−2.4a	−2.3a	−0.1a	4.8b
GDDASI	2	78	92	99	0.06	2.2a	−5.6b	2.2a	1.3a
GDDASI	4	155	158	165	0.05	0.4ab	3.3a	0.8a	−4.5b
GDDASI	6	106	115	135	0.04	−1.5a	−2.3a	0.3ab	3.5b
GDDASI	8	86	90	99	0.09	−3.4a	7.1b	−0.2a	−3.5a
GDDASI	10	58	60	63	0.18	−4.3a	−3.8a	−1.1a	9.2b
PH	1	224	229	236	0.09	3.7a	−5.2b	−1.4c	2.9a
PH	2	6	53	160	0.04	−2.3a	3.3b	0.2a	−1.3a
PH	3	97	105	114	0.09	−0.8ab	−3.0a	1.3bc	2.5c
PH	5	91	100	105	0.06	1.7a	1.6a	−0.5ab	−2.8b
PH	8	61	66	81	0.10	3.4a	−6.3b	1.7a	1.2a
PH	8	118	123	126	0.06	−2.9a	−1.4ab	3.0c	1.3bc
PH	10	48	53	83	0.05	−0.1ab	−2.0a	−0.8a	3.0b
EH	1	254	276	292	0.06	2.1a	−1.8b	−1.4b	1.1a
EH	2	151	155	164	0.06	0.2a	0.3a	−2.6b	2.1a
EH	3	94	100	120	0.08	0.2a	−2.4b	0.9a	1.3a
EH	4	18	31	80	0.04	1.5a	0.4ab	−1.7b	−0.3ab
EH	7	57	79	91	0.05	−0.9ab	1.6c	0.8ac	−1.6b
EH	8	65	70	73	0.16	0.9a	−5.0b	1.9a	2.2a
EH	8	118	123	126	0.06	−1.3a	−1.3a	3.1b	−0.5a
EH	9	114	118	134	0.05	−2.2a	0.5bc	−0.3ab	1.9c
EH	10	51	78	84	0.07	−0.4a	−1.5a	−0.5a	2.3b
TLN	1	123	144	150	0.08	−0.0ab	−0.2a	0.0b	0.2b
TLN	2	92	103	108	0.12	0.1ab	0.2a	−0.3c	−0.1bc
TLN	3	114	117	122	0.08	−0.0a	−0.2a	0.3b	−0.1a
TLN	5	155	156	171	0.07	−0.1ab	−0.2a	0.2c	0.1bc
TLN	6	0	5	37	0.04	−0.1a	−0.1a	0.2b	0.0a
TLN	7	46	54	63	0.07	0.0ab	0.2a	−0.1b	−0.2b
TLN	8	67	69	70	0.22	−0.1a	−0.4b	0.3c	0.2c
TLN	9	127	128	135	0.09	−0.2a	−0.1ab	0.2c	0.1bc
TLN	10	72	73	82	0.16	−0.3a	−0.2a	0.3b	0.1b
Photoperiodic QTL									
GDDTA	1	119	128	141	0.10	−5.2a	−4.3a	7.0b	2.4b
GDDTA	2	179	182	185	0.07	−4.5a	−2.6a	7.7b	−0.6a
GDDTA	3	109	116	181	0.05	−0.8ab	−5.4a	5.3b	0.9b
GDDTA	4	142	150	153	0.06	−2.2a	−1.8a	8.8b	−4.9a
GDDTA	8	70	73	75	0.12	−4.4ab	−5.8a	9.1c	1.1b
GDDTA	9	114	118	120	0.12	−10.9a	3.5bc	8.5b	−1.1c
GDDTA	10	60	60	62	0.39	−6.0a	−16.2b	13.7c	8.6c
GDDTS	1	119	128	145	0.09	−7.8a	−4.8a	8.6b	4.1b
GDDTS	2	180	183	185	0.09	−7.2a	−3.3a	12.4b	−1.9a
GDDTS	3	77	94	98	0.07	−0.3a	−9.1b	3.8a	5.5a
GDDTS	8	70	73	76	0.07	−6.4a	−4.9a	8.1b	3.3b
GDDTS	9	83	87	90	0.11	−14.3a	3.7bc	10.7b	−0.1c
GDDTS	10	60	60	61	0.40	−10.7a	−20.5b	16.3c	14.9c
GDDASI	3	80	96	127	0.05	1.3a	−4.4b	−0.1ab	3.2a
GDDASI	10	59	60	63	0.16	−3.7a	−4.7a	1.6b	6.8c
PH	2	41	62	100	0.05	−0.6ab	2.1c	0.6ac	−2.0b
PH	3	97	104	134	0.04	−0.9a	−1.3a	0.4ab	1.8b

(*continued*)

TABLE 2

(Continued)

Short-day QTL									
	QTL 2-LOD support interval and peak				Phenotypic	Additive effect			
Trait	Chr	Peak − 2 LOD	LOD Peak	Peak + 2 LOD	*r*2	B73	B97	CML254	Ki14
PH	4	27	72	112	0.04	1.2a	1.3a	−0.9ab	−1.6b
PH	8	66	70	106	0.10	0.2a	−3.4b	1.9a	1.4a
PH	9	57	65	83	0.06	−3.1a	2.6b	1.6b	−1.1a
PH	10	76	78	84	0.10	0.3ab	−3.1c	0.1a	2.7b
EH	8	69	70	78	0.13	−0.1a	−2.6b	1.5a	1.2a
EH	9	87	94	99	0.08	−2.6a	1.1b	0.5b	1.0b
EH	10	77	78	83	0.11	0.4a	−2.3b	0.7a	1.3a
TLN	1	117	144	165	0.04	0.0ab	−0.1a	0.1b	0.0a
TLN	2	95	107	130	0.05	0.0ab	0.1a	0.0ab	−0.1b
TLN	3	49	72	144	0.04	−0.1a	−0.1a	0.1b	0.1ab
TLN	5	90	94	105	0.04	0.1a	0.3a	−0.2b	0.0a
TLN	8	68	70	72	0.17	−0.1a	−0.2b	0.1ac	0.2c
TLN	9	87	89	95	0.16	−0.3a	0.1b	0.1b	0.1b
TLN	10	79	82	85	0.22	−0.1a	−0.3b	0.2c	0.2c

Allelic effects are in GDD for flowering time traits, cm for height traits, and number of leaves for TLN. Allelic effects at a QTL followed by the same letter are not significantly different at $P = 0.05$.

which to search for candidate genes, providing robust tests for candidate genes and simplifying the search for causal genes in forward genetic analyses. Because of the increased precision, power, and parsimony of the connected population analysis, we discuss further only the results of the joint multiple population QTL analyses.

Tests for epistasis: Two forms of epistasis could be directly tested with the joint multiple population analysis. First, the overall significance of interactions between detected QTL and genetic backgrounds (*i.e.*, different mapping families) was tested. This was done by comparing two multiple population analyses: connected (which assumes consistent founder allele effects across backgrounds) and disconnected analysis (which allows founder allele effects to vary across backgrounds). We found that the number, positions, and confidence intervals of the QTL detected by both analyses did not differ significantly. However, the BIC of the combined analysis was superior for the connected analysis for all traits (Table S6). Thus, QTL allele effects were consistent across genetic backgrounds and there was no evidence for epistatic interactions of QTL alleles with genetic backgrounds for any trait.

Second, we tested each QTL for epistatic interactions with all other positions in the genome, including epistasis between QTL pairs as well as between QTL and other genome regions that had no main effect. On the basis of the permutation thresholds computed specifically for this set of tests, we detected no significant epistatic interactions for any trait with the combined connected analysis.

Direct mapping of candidate genes: We mapped 14 candidate gene markers with homology to known circadian rhythm/photoperiod response, floral transition, or floral morphology genes from maize, Arabidopsis, or rice: *CHLOROPHYLL A/B BINDING PROTEIN* (*CAB*), *CIRCADIAN CLOCK ASSOCIATED 1* (*CCA1*), *CONSTANS-LIKE* (*CO-2*), *CRYPTOCHROME 2* (*CRY2*), *HEADING DATE1* (*HD1*), *HEADING DATE 3A/FLOWERING LOCUS T* (*HD3A*), and *LATE ELONGATED HYPOCOTYL* (*LHY* and *LHYC8*; Hayama and Coupland 2004); *INDETERMINATE 1-LIKE* (*ID7*; Colasanti *et al.* 2006); *PHYTOCHROME C1* (*PHYC*; Sheehan *et al.* 2004), *DWARF8* (*D8*; Thornsberry *et al.* 2001), *ZEA MAYS FLORICAULA1* (*LEAFY*) and *ZEA MAYS FLORICAULA2* (*ZFL2*; Bomblies and Doebley 2006); and *FASCIATED EAR2* (*FEA2*; Bommert *et al.* 2005). Each candidate gene mapped to single genome positions distributed across all chromosomes except chromosome 3. Two of these genes control key regulatory steps in the photoperiod response pathways of other species: *CO* of Arabidopsis (closest match mapping to chromosome 2) and its homolog *HD1* of rice (closest match mapping to chromosome 9), and *FT* of Arabidopsis (homologous to *HD3A* of rice, mapping to chromosome 6). *CO*, *CRY2*, *FEA2*, *HD1*, and *LHYC8* homologs mapped within plant height photoperiod QTL intervals, but not within QTL intervals directly affecting flowering time photoperiod response (Table 2; Figure 2; Figure S3). None of the candidate genes that we directly mapped localized within flowering time photoperiod response QTL intervals.

Inferring positions of candidate genes on map: A second approach to testing candidate genes for their effects on photoperiod response was to infer candidate gene positions on the genetic map by referencing the maize physical map and sequence. We identified

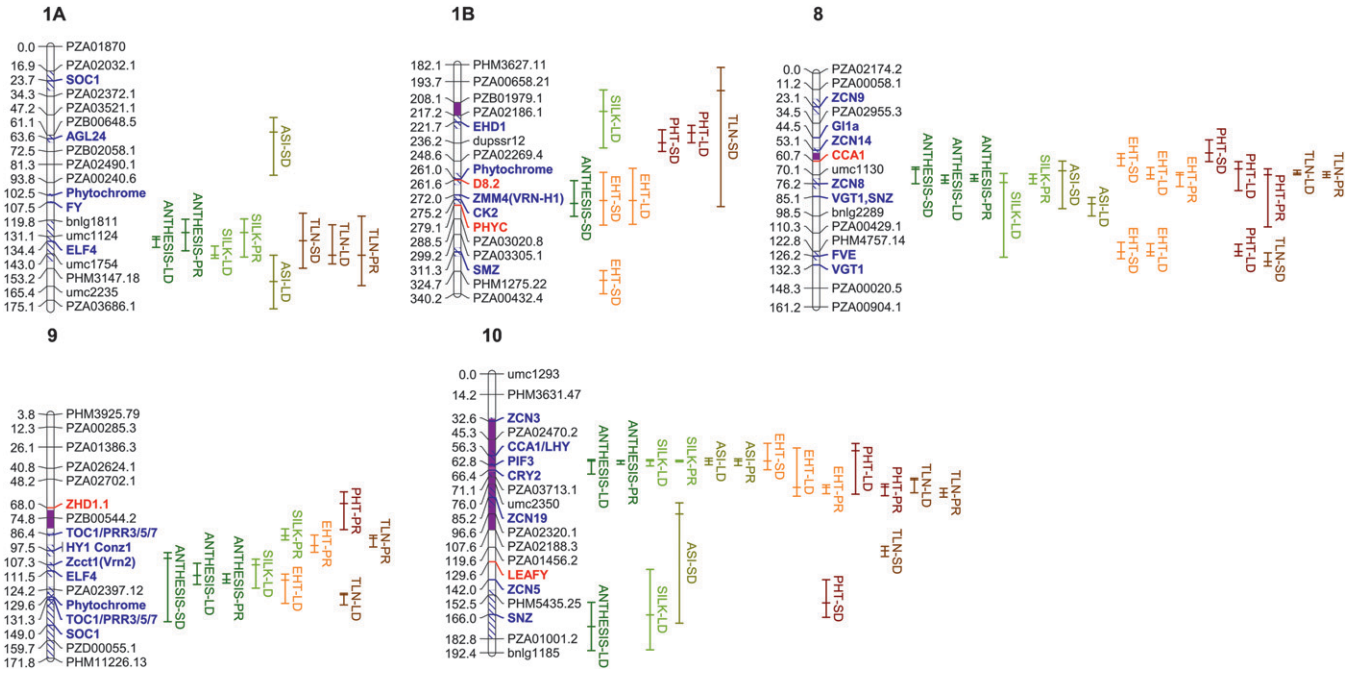

FIGURE 2.—Linkage map of chromosomes 1, 8, 9, and 10 containing the four key photoperiod response QTL regions *ZmPR1–ZmPR4* based on the combined analysis of four RIL mapping populations. For the sake of clarity, chromosome 1 is displayed in two parts and only a subset of marker loci spaced about every 10 cM or more is shown. The complete genetic map with all QTL positions is shown in Figure S3. Candidate genes directly mapped are indicated in red. Map intervals containing candidate genes localized by inference indicated as segments with blue diagonal filling, with the candidate gene name in blue positioned at interval midpoint. Map intervals exhibiting significant segregation distortion in the combined analysis indicated as magenta segments on the linkage group. The map interval on chromosome 10 identified as having undergone a selection sweep by TIAN *et al.* (2009) is indicated by a pink segment on the linkage group. QTL bars represent the 2-LOD support interval of the QTL position; the middle hash mark of a bar represents the maximum likelihood position of the QTL. Trait names for QTL are abbreviated as ANTHESIS for GDDTA, SILK for GDDTS, ASI for GDDASI, EHT for ear height, and PHT for plant height. SD, LD, and PR refer to QTL identified under short-day length or long-day length environments, or for photoperiod response, respectively.

predicted maize genes homologous to candidate genes from Arabidopsis, rice, and barley through the Gramene.org database browser and with direct sequence matching searches through the NCBI and MaizeGDB databases (Table S4). The positions of each gene were inferred on our combined map by reference to mapped SNP markers derived from flanking BACs on ordered BAC physical sequence. In total, we positioned 82 unique candidate gene sequences on the map (Figure S3; Table S4). Three homologs of *TOC1/PRR7*, two homologs each of *CCA1/LHY*, *CRY2*, *ELF4*, and *HY1/SE5*, and single homologs of *CO/HD1*, *CRY1*, *EHD1/2*, *FCA*, *FKF1/ZTL*, *FLD*, *FY*, *LD*, *PIE1*, *PIF3*, *SNZ*, *ZCN1*, *ZCN2*, *ZCN8*, *ZCN10*, *ZCN12*, *ZCN19*, *ZCN21*, and *ZCN25* (together representing 37% of candidate gene positions inferred on the map) mapped with photoperiod response QTL intervals (Figure S3; Table S4), but all other candidate genes tested in this way did not map to genome regions with significant effects for photoperiod response traits.

DISCUSSION

QTL support intervals for all 18 traits covered 60% of the genetic map (Figure S3). QTL with smaller effects had the largest support intervals and comprised the majority of the map coverage (Table 2). Therefore, we focus discussion on the four most important QTL regions for photoperiod response, which were responsible for the majority of the photoperiodic responses in the six traits (each QTL explaining up to 40% of the phenotypic variation). Support intervals for all photoperiod trait QTL covered a combined 25% of the genetic map, but the four key QTL to be discussed here represent only 2% of the genetic map. These QTL also coincide with the four key flowering time QTL detected under long days on chromosomes 1, 8, 9, and 10 (Table 2; Figure 2) and also with the four most important flowering time QTL detected under long-day conditions in the maize NAM population (BUCKLER *et al.* 2009). To facilitate discussion, we named these four photoperiodic response QTL *ZmPR1–4* (for *Zea mays Photoperiodic Response*). *ZmPR1* is located between markers bnlg1811 and umc1754 on chromosome 1 (Figure S3), associated with ~10% of the photoperiodic flowering time response in these populations. This QTL also had a significant effect on TLN, but was not a major contributor to PH or EH variation. *ZmPR2* is located between the markers umc1130 and PHM3993.28 on chromosome 8 (Figure S3) and contributed 9% of the photoperiodic

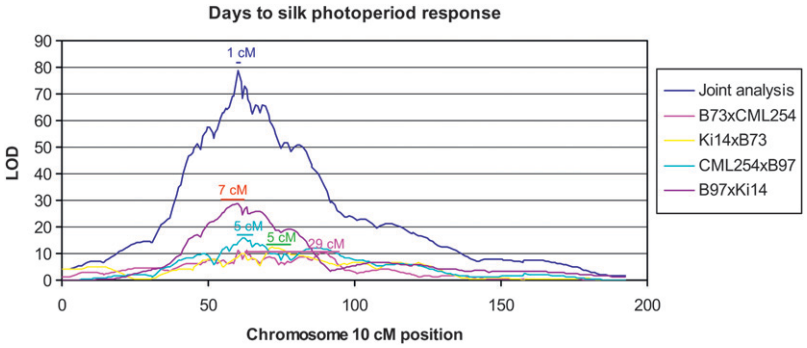

FIGURE 3.—Plots of LOD scores for the presence of a QTL affecting photoperiod response for days to silk along chromosome 10 of maize. Five separate analyses are plotted: the joint analysis (connected model) of four populations simultaneously and four individual population analyses (B73 × CML254, Ki14 × B73, CML254 × B97, and B97 × Ki14). Two-LOD support intervals around the peak QTL position are drawn with horizontal bars, with the length of the support interval presented above the bar.

flowering time response in these populations. The chromosome 9 QTL, *ZmPR3*, is located between markers PZB00547.3 and PZA03057.3 (Figure S3). This locus contributed ~11% of the photoperiodic flowering time variation. *ZmPR4* is located on chromosome 10 between PZA00337.4 and umc1827 (Figure S3), explained 39% of the photoperiodic flowering time response in our study, and also had significant effects on PH, EH, and TLN. Genomic regions with significant segregation distortion across populations coincided with or were linked to all four of these QTL (Figure 2; Table S7), likely due to natural selection against very late flowering during RIL development, further highlighting their importance to adaptation.

Chromosome 1 QTL–*ZmPR1*: An important flowering time QTL in the *ZmPR1* region was previously detected in several populations (Beavis *et al.* 1994; Chardon *et al.* 2004; Blanc *et al.* 2006; Briggs *et al.* 2007; Buckler *et al.* 2009); however, neither of the two previous studies specifically addressing tropical maize photoperiod response detected a significant QTL in this region (Table S8; Moutiq *et al.* 2002; Wang *et al.* 2008), suggesting that *ZmPR1* does not segregate in all temperate × tropical maize populations, as observed by Buckler *et al.* (2009). One flowering time candidate gene mapped to the *ZmPR1* QTL interval: *ELF4*, which is involved in sensing day length and regulation of *CCA1* in Arabidopsis (Doyle *et al* 2002). Buckler *et al.* (2009) also identified a homolog of rice *Ghd7* (Xue *et al.* 2008) in this region.

Chromosome 8 QTL–*ZmPR2*: *ZmPR2* was associated with both the photoperiodic and lateness *per se* flowering time responses. Neither Moutiq *et al.* (2002), Wang *et al.* (2008), nor Briggs *et al.* (2007) detected a flowering time QTL in this region in other populations segregating for photoperiod response (Table S8). This region includes the major flowering time and height QTL *Vgt1*, which was originally identified genetically on the basis of an allelic difference between temperate maize lines (Vlăduţu *et al.* 1999; Salvi *et al.* 2007), although the position of *Vgt1* on our map is uncertain because of disagreements in the maize genome database. The *Vgt1* QTL affects flowering under short-day photoperiods (Salvi *et al.* 2002), similar to the effect that we observed at this QTL region. The noncoding functional polymorphism underlying *Vgt1* regulates the expression of a *Rap2.7*, a maize homolog of an Arabidopsis floral identity gene *APETELA 2* (*AP2*) (Salvi *et al.* 2007).

The known functional variants at *Vgt1* and *Rap2.7* do not segregrate in these populations, however (Buckler *et al.* 2009). Thus, the observed *ZmPR2* QTL effects may be due to *Vgt2*, which is tightly linked to *Vgt1* (Vlăduţu *et al.* 1999; Chardon *et al.* 2005). Danilevskaya *et al.* (2008) proposed that the gene underlying *Vgt2* is *Zea mays CENTRORADIALIS8* (*ZCN8*), which because of its expression patterns and sequence homology, bears the closest resemblance of any gene in the maize genome to the *FT* gene of Arabidopsis. *FT* functions in Arabidopsis as the long-distance floral promoter referred to as florigen (Corbesier *et al.* 2007). *ZCN8* maps to the center of the QTL region.

Chromosome 9 QTL–*ZmPR3*: *ZmPR3* was also observed to affect flowering time and photoperiodic QTL in previous maize studies (Table S8; Moutiq *et al.* 2002; Chardon *et al.* 2004; Briggs *et al.* 2007; but not Wang *et al.* 2008). Several homologs of Arabidopsis and rice flowering time genes are located within the *ZmPR3* interval, including *CONSTANS of Zea mays1* (*CONZ1*), the putative hemeoxygenase *HY1/SE5*, and a homolog of circadian clock-associated genes *TOC1/PRR3/PRR5/PRR7/PRR9* (Chardon *et al.* 2004; Cockram *et al.* 2007; Miller *et al.* 2008).

CONSTANS-like genes have been shown to play important roles in the photoperiodic responses of several plant species, including barley and rice (Griffiths *et al.* 2003), but to date, genetic data indicating that homologs of *CO/HD1* function as activators of the floral transition in maize are lacking (Colasanti and Muszynski 2009). The inferred position of *CONZ1* is inside the 2-LOD support intervals for regions affecting photoperiod response for TLN and EH, but just outside the interval affecting GDDTS photoperiod response. A gene family of *CO/HD1* homologs appears to exist in maize; we also mapped a SNP marker on the basis of an additional *HD1* homolog (ZHD1_1) at least 25 cM distant from *Conz1* on chromosome 9, and a CAPS marker of a *CO* homolog to chromosome 2. ZHD1_1

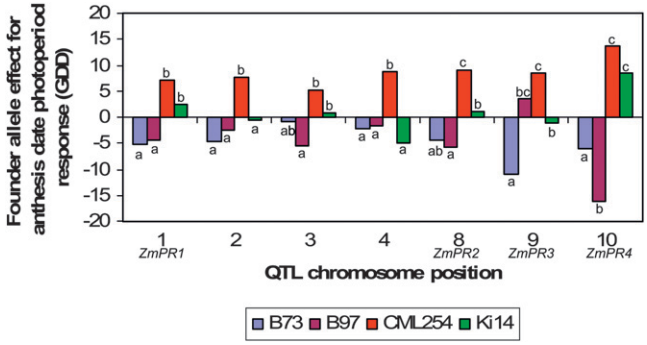

FIGURE 4.—Variation for functional allele effects at seven QTL detected for photoperiod response for anthesis date. At each QTL, four founder allele effects were estimated from the joint population analysis. Allele effects are estimated relative to recombinant inbred line population means: negative effects reduce the photoperiod response and positive effects increase the photoperiod response. Allelic effects within a QTL labeled with the same letter are not significantly different at $P = 0.05$.

mapped outside of the photoperiod response QTL intervals for all traits except plant height and the *CO* CAPS marker also mapped within a broad PH photoperiod response QTL interval on chromosome 2. *CONZ1* is differentially expressed in response to photoperiodic stimuli, and the long-day expression of *CONZ1* in B73 is different from that of photoperiod-sensitive teosinte and CML254 (MILLER *et al.* 2008; T. DLUGI, personal communication). The gene expression results in combination with our genetic data suggest that *CO*-like genes in maize mediate height and leaf number responses to long-day lengths, but do not provide evidence of their effect on flowering time photoperiod responses.

Chromosome 10 QTL–*ZmPR4*: The genome region with largest effect on all photoperiod response traits was *ZmPR4* on chromosome 10, which was associated with up to 40% of the phenotypic variation for photoperiod response. The 2-LOD support intervals of the *ZmPR4* QTL corresponding to GDDTA and GDDTS did not overlap with a tightly linked QTL for PH, EH, and TLN, suggesting that there are at least two distinct genes in the *ZmPR4* region, each with important but unique effects on photoperiod response.

Previous studies have consistently detected major photoperiodic response, flowering time, PH, and TLN QTL in the *ZmPR4* QTL region (ABLER *et al.* 1991; MOUTIQ *et al.* 2002; BLANC *et al.* 2006; BRIGGS *et al.* 2007; LAUTER *et al.* 2008; WANG *et al.* 2008; DUCROCQ *et al.* 2009). *ZmPR4* is syntenic to the major photoperiodic QTL of sorghum (*Ma1*; ULANCH 1999), which has undergone intense directional selection in temperate-adapted sorghum populations (KLEIN *et al.* 2008). Together, these results suggest that the gene or genes promoting photoperiod sensitivity at *ZmPR4* are conserved in tropical maize, teosinte, and sorghum populations. TIAN *et al.* (2009) reported a >1-Mb region that underwent a selection sweep during maize domestication or improvement which maps immediately adjacent to the *ZmPR4* region (Figure 2). The QTL appears to be outside the region of the selection sweep, although map ordering in this region is difficult because it exhibits reduced recombination (DUCROCQ *et al.* 2009; MCMULLEN *et al.* 2009; TIAN *et al.* 2009) and differences in SNP locus orders between the physical BAC sequence and both the NAM genetic map and the combined map from this study. Physical rearrangements of this region among maize lines may be associated with these phenomena.

DUCROCQ *et al.* (2009) recently mapped a photoperiod response QTL to a 170-kb region inside the *ZmPR4* region in a different maize cross. This interval included a noncoding sequence adjacent to a homolog of *Ghd7*, which encodes a CCT protein domain and regulates flowering time in rice (XUE *et al.* 2008). In addition to *Ghd7*, a number of other candidate gene homologs are more loosely associated with *ZmPR4*, including *PHYTOCHROME INTERACTING FACTOR3* (*PIF3*; ODA *et al.* 2004), a cryptochrome gene (*CRY2*), a circadian clock-associated gene (*CCA1/LHY*), and one *FT* homolog, *ZCN19* (CHARDON *et al.* 2004; DANILEVSKAYA *et al.* 2008).

Effects of maize genes defined by major mutations: Aside from *Vgt1*, which has a quantitative effect on flowering time, the other maize flowering time genes cloned to date, *D8*, *ID1*, and *DLF1*, are associated with major effects on flowering time. None of these three latter genes coincided with photoperiod response QTL in this study. Despite previous studies indicating the importance of *D8* to flowering time and latitudinal adaptation in maize (THORNSBERRY *et al.* 2001; CAMUS-KULANDAIVELU *et al.* 2006), *D8* colocalized only with QTL for ear height under long- and short-day lengths (7% of the variation) and TLN in short days (5% of the variation of a QTL with a very large support interval). *D8* encodes a transcriptional regulator of the gibberellin flowering pathway, which controls flowering time independently of photoperiod in Arabidopsis (PENG *et al.* 1999; SIMPSON and DEAN 2002), so it was not expected to have an effect on photoperiod response.

Our experimental approach may fail to identify causal genes as candidates if they are not well annotated in the genome databases, or if QTL interval position estimates are incorrect. Annotation of the maize genome sequence is ongoing, and many gene predictions are preliminary. An additional problem with the maize genome sequence is the possibility that some contigs were not placed correctly on the physical map on the basis of FPC alignments used here; we noted several cases where our SNP markers place a BAC on our genetic map in a different chromosome than they are currently positioned in the maize sequence. In addition, some candidate genes may affect photoperiod response in other crosses but could not be detected in this study because

they were not segregating for functional nucleotide variants. Our approach also has the converse problem of potentially identifying incorrect candidate genes. The QTL intervals often encompass many genes, so any gene within the interval by coincidence may be considered a candidate until the interval can be narrowed by further genetic analysis. Many of the candidate genes we searched for appear to exist as gene families in maize, increasing the chance of a gene homologous to a known flowering regulator from another species residing within a genetic interval. Nevertheless, our results clearly indicate that at least some homologs of important photoperiod regulatory genes are not associated with significant photoperiod responses in these mapping families. There may be related genes that we did not detect in these genome regions or maize may have a unique regulatory pathway for photoperiod response that has not yet been observed in other species.

Genetic architecture of photoperiod sensitivity in maize: We compared the results of this study with those of previous genetic analyses of photoperiod sensitivity in tropical maize (Moutiq *et al.* 2002; Wang *et al.* 2008; Table S8). The main photoperiodic QTL on chromosomes 8, 9, and 10 were observed to affect flowering time across the vastly different environments and with distinct genetic materials represented by these studies. Indeed, some of these photoperiodic alleles may be functionally equivalent to their ancestral teosinte ortholog, on the basis of their importance to photoperiod-dependent flowering time in a maize × teosinte cross (Briggs *et al.* 2007). Across each of these populations, the *ZmPR4* QTL explained >30% of the variation for photoperiodic flowering time response. A study by Blanc *et al.* (2006) of temperate European maize lines also identified a large flowering time allele in the *ZmPR4* region that affected flowering time in long-day environments, which might indicate that photoperiod-sensitive alleles of *ZmPR4* can be found in temperate populations. On the basis of a meta-analysis of 22 maize flowering QTL mapping studies (representing both temperate and tropical germplasm and long- and short-day environments), Chardon *et al.* (2004) suggested that six QTL, including the four ZmPR QTL identified here, affect flowering time across many populations.

Comparisons of QTL across studies are generally confounded by differences in allelic composition, evaluation environments, and methodology. Thus, it can be difficult to determine whether the detection of a QTL in one population but not another is due to true differences in the QTL effects across populations, QTL-by-environment interactions, or statistical issues, such as limited power in small population sizes (Beavis 1998; Melchinger *et al.* 1998). The combined analysis of multiple mapping populations evaluated in common environments permits direct comparison of the effects of specific genome regions across genetic backgrounds. Our results indicate largely consistent QTL regions, but heterogeneity of allelic effects at the *ZmPR* loci within both tropical and temperate inbred line groups (Table 2). For example, CML254 alleles at many of the *ZmPR* loci delay flowering time more than the Ki14 alleles in the long-day environment, particularly at *ZmPR2* and *ZmPR3* (Table 2; Figure 4). Across all QTL detected, the temperate alleles differed significantly from each other at 41% of QTL, the pair of tropical alleles differed significantly at 39% of QTL, and temperate and tropical-derived allele effects differed at an average of 57% of QTL (Table 2). These results suggest the existence of allelic series at the *ZmPR* loci across diverse maize germplasm. Flowering time under long-day conditions in the maize NAM population also is controlled by QTL with allelic series, with significant variation among the allelic effects of tropical founder lines (Buckler *et al.* 2009). Our results suggest substantial standing genetic variation for photoperiod response in tropical maize (perhaps due to adaptation to environments with slight photoperiod differences and precipitation cycles) and multiple potential evolutionary trajectories to reduced photoperiod response. The apparently simpler genetic architecture of flowering time photoperiod response observed here compared to the more numerous genes with smaller effects on flowering time identified in the NAM population (Buckler *et al.* 2009) may be due in part to the smaller number of families derived from parents with very distinct photoperiod responses evaluated in this study.

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Genetic Control of Photoperiod Sensitivity in Maize Revealed by Joint Multiple Population Analysis

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FILE S1

Supporting Methods and Results

METHODS

Characterization of Maize Inbred Line Photoperiodic Responses

Phenotypic characterization of mapping populations required more space than was available in controlled environments, therefore the RILs were evaluated in fields under long day lengths (North Carolina summer) and short day lengths (Homestead, FL winter). To verify that the differential responses in flowering time, height, and leaf number were primarily due to differences in photoperiods between these two field environments, we conducted a photoperiod transfer study to define the magnitude of the long-day photoperiodic responses of eight diverse maize inbred lines under controlled environment conditions (see Supporting Methods and Results for experimental details).

Plants of inbred lines B73, B97, Ki3, Ki14, CML247, CML258, CML277, and Tzi8 were grown at the Southeastern Plant Environment Laboratory (the North Carolina State University Phytotron; http//:www.ncsu.edu/phytotron) to evaluate their responses to different photoperiods. We had insufficient CML254 seeds available for this experiment, and in its place we grew a related line, CML258 (Srinivasan, 2001; Liu et al., 2003). Prior to planting, seeds were germinated on moistened paper towels in the dark for one week to promote uniform seedling emergence and were then transplanted to 3.8 L volume soil pots. Experimental units consisted of a single plant per pot. We assigned three replicates of each of the eight genotypes to each of six short day treatments (11 hours light/ 13 hours dark; 30/ 26ºC). These treatments were exposure to zero, five, 10, 15, 20, 25, or 30 days of short-day photoperiod. After the assigned short-day treatment was completed, plants were moved to a long-day photoperiod greenhouse (11 hours light/ 10 hours dark/ three hour night interruption; 30/ 26ºC). A thermostat malfunction during the first 10 days of the experiment produced lower temperatures than those that were assigned in the long-day greenhouse, but these temperatures were not recorded. Pot positions were randomized both in the short-day growth chamber and again in the long-day greenhouse. Measurements of days to tassel emergence (DTE), days to anthesis (DTA), days to silking (DTS), and total leaf number (TLN) were collected for each plant. DTE was defined as the number of days from planting until a tassel was visible from a horizontal observation of the leaf whorl. DTA and DTS were defined in this study as the number of days from planting until approximately 50% of the anthers were shedding pollen or about 50% of the silks were visible on a plant, respectively. SAS

Version 9.1 Proc GLM (SAS Institute, 2002-2004) was used to analyze the effects of genotypes and length of short-day treatment on each phenotype.

Heritability Estimation

Trait heritability on an entry mean basis was estimated for each population separately as $\hat{h} = \frac{\hat{\sigma}_g^2}{\hat{\sigma}_g^2 + \frac{\hat{\sigma}_{ge}^2}{e} + \frac{\hat{\sigma}_\varepsilon^2}{n}}$, where σ^2_g is the genetic variance, σ^2_{ge} is the genetic by environment interaction variance, σ^2_ε is the residual error variance, e is the harmonic mean of the number of environments, and n the harmonic mean of total number of plots, in which each RIL was measured (Holland *et al.*, 2003). Approximate standard errors of heritability estimates were obtained with the delta method (Holland *et al.*, 2003). Heritabilities of photoperiod response traits were estimated by considering each year in which the trait was measured both in short- and long-day length environments to be a replicate. BLUPs for each trait-year combination were computed, and then the photoperiod responses were computed for each year. Heritability of photoperiod response traits were then estimated from an analysis of photoperiod response BLUPs across years as $\hat{h} = \frac{\hat{\sigma}_g^2}{\hat{\sigma}_g^2 + \frac{\hat{\sigma}_e^2}{y}}$, where y is the harmonic mean of the number of years in which photoperiod response was measured on the RILs.

Trait Correlations

SAS Version 9.1 Proc Corr (SAS Institute, 2002-2004) was used to estimate the Pearson correlation between the traits utilizing the combined data of all of the RIL populations. Correlation measurements were made separately for long- and short-day environments, and comparisons were made between the two environments.

Segregation Distortion

Marker genotypes from the combined map and individual maps were used to test segregation distortion of temperate to tropical alleles by using a chi-square test with significance declared when P < 0 .0025 for both individual and combined populations. This threshold was obtained by dividing P = 0.05 by 20, the number of chromosome arms in maize, which is a minimum estimate of the number of independent regions tested.

RESULTS

The timing, duration, and magnitude of photoperiod sensitivity among inbred lines

The parents of our RIL populations (excluding CML254, which was not tested) were found to be photoperiod-sensitive in the controlled environment of the phytotron (Table S2). However, the magnitude of the photoperiodic responses of the tropical lines was much greater than that of the temperate lines (Table S2). The duration of the photoperiod-sensitive phase varied among inbred lines, terminating after plants received between 15 and 30 days of short-day light exposure, congruent with previous findings in maize (Kiniry *et al.*, 1983; Tollenaar and Hunter, 1983). The difference between the photoperiodic responses of temperate and tropical inbreds was similar in both the phytotron experiment and in the field studies (Table 1; Table S2), suggesting that phenotypic differences observed in the field between long- and short-day environments primarily reflect photoperiodic responses. Although other environmental factors such as moisture, temperature, and soil type differed between field locations, the use of GDD largely removed the confounding effects of temperature differences and replication across three years mitigated the effects of other random environmental factors on the observed traits. Many unusual flowering phenotypes were observed in the tropical maize lines in this experiment (Figure S4) when exposed to <25 days of short-day treatment, demonstrating the developmental instability of tropical maize lines under long day lengths.

RIL Field Experiment

We measured six phenotypic traits related to plant development in each RIL populations in both long-day (North Carolina summer) and short-day (Homestead, FL winter) locations: GDDTA, GDDTS, GDDASI, EH, PH, and TLN. All of these traits were highly heritable in long-day environments, with average heritabilities exceeding 80% for all traits (Table S6). The heritabilities of GDDTA, GDDTS, and PH were significantly lower under short day lengths, but the heritabilities

of EH and TLN remained nearly constant in both environments. The heritabilities of photoperiod response traits were lower on average than those of both long- and short-day environments, but were all greater than 49%.

Flowering time traits GDDTA and GDDTS were highly correlated within both long-day (r = 0.96, P < 0.001) and short-day (r = 0.90, P < 0.001) environments, as were the height measurements PH and EH (r = 0.66, P < 0.001 in long-days; r =0.76, P < 0.001 in short-days) (Table S10). Correlations among the other traits measured in long- versus short- day environments were much lower. Unexpectedly, the flowering time traits (GDDTA and GDDTS) were negatively correlated with the height traits (PH and EH), indicating that on average, later flowering lines were shorter than early flowering lines. Flowering time in the short-day environments was not highly related to flowering time in the long-day environments (r=0.05 and 0.22 for GDDTA and GDDTS, respectively). In contrast, GDDASI, PH, EH, and TLN phenotypes were moderately correlated between long- and short-day environments (r = 0.64, 0.65, 0.69, 0.79, respectively).

Of the six traits measured, the temperate parents of our RIL populations had significant photoperiodic responses only for PH, EH, and TLN in the field (P<0.05; Table 1). The tropical parents, on the other hand, displayed significant photoperiodic responses for all six traits (Table 1). Temperate and tropical parents were differentiated more by flowering time than other traits. Among the four parents, the photoperiodic responses measured by the differences in GDDTA, GDDTS, and TLN between long- and short-day environments were greatest in CML254, followed by Ki14, B97, and B73. CML254 silked 433 GDD (almost 25 days) later and had a 31% increase in leaf number under long-day compared to short-day conditions (Table 1). The greatest photoperiodic responses for GDDASI and EH were exhibited by Ki14, followed by CML254, B97, and B73.

Population Distributions

In the short-day environment, the values for the flowering time traits (GDDTA, GDDTS, and GDDASI) were distributed approximately normally around the mean in each of the four populations. In the long-day environments, all populations flowered substantially later and exhibited large increases in GDDASI. On average across the four populations, increases of 101 GDDTA, 130 GDDTS, and 32 GDDASI due to long-day photoperiod were observed. Under long days, GDDTA and GDDTS in the CML254 populations and ASI in the Ki14 populations were strongly skewed toward the temperate parent values.

PH and EH values in the RIL populations were evenly distributed around the mean in both the long- and short-day environments. PH and EH increased on average by 46 cm and 19 cm, respectively, in response to long daylengths. Transgressive segregation was frequent for PH and EH in the long-day environment, but much less common among the other traits.

TLN values in the two Ki14 populations were evenly distributed around the mean in both long- and short-day environments; however, in the long-day environment, the distribution of TLN in the CML254 populations was highly skewed towards the temperate parent values. The average photoperiodic TLN response in the RIL populations was an increase of 3.8 leaves.

Genetic Maps and Segregation Distortion

Genetic maps were produced for each of the RIL populations independently, with total map lengths ranging from 1574 to 1780 cM. A combined map was also produced, measuring 1961 cM with an average distance of 1.5 cM between adjacent markers (Figure 2).

We detected 11 regions of segregation distortion among the four individual populations (Table S8). These regions of segregation distortion were detected in common genomic regions, particularly on chromosomes 4, 8, 9, and 10. At seven of the ten major regions of segregation distortion, temperate alleles were significantly more frequent than tropical alleles. At the distorted region on chromosome 4, the temperate allele was significantly more common in the B73 × CML254 population, but significantly less common in the Ki14 × B73 population. This was the only instance where segregation distortion favored alleles of different origins across populations. Combined across populations, we observed four regions of segregation distortion (Table S8). Temperate alleles were favored in the distorted regions of chromosomes 1, 9, and 10, but recovered less frequently in the distorted region of chromosome 8.

Flowering time QTL

QTL affecting flowering time were detected on every chromosome except chromosome 7 (Table 2; Figure 2). Under short-day conditions, the cumulative effect of the temperate QTL alleles did not significantly differ from the

corresponding cumulative effects of tropical alleles (P = 0.56 for GDDTA, P = 0.20 for GDDTS, and P = 0.11 for GDDASI). In contrast, the cumulative effect of tropical QTL alleles significantly delayed anthesis by 180 GDD and silking by 220 GDD in long-day environments (P <0.0001 for GDDTA, GDDTS).

The positions of several flowering time QTL were consistent in both long- and short-day environments (Table 2; Figure 2; Figure S2). However, the QTL effects were reduced in short-day environments (Table 2): the average proportion of variation explained per QTL in short-days was 6% for GDDTA and 6% for GDDTS, compared to 11% for GDDTA and 10% for GDDTS QTL in long-day environments. In addition, fewer flowering time QTL were detected in short-days than long-days. Four prominent long-day QTL located on chromosomes 1, 8, 9, and 10 consistently were associated with a relatively large proportion of the long-day flowering time variation. At each of these QTL, the tropical alleles were responsible for delaying flowering time in the long-day environment.

Plant Height, Ear Height, and Total Leaf Number QTL

Generally, PH and EH QTL were consistent in position and effect across long- and short-day photoperiods (Table 2; Figure 2; Figure S2). Only one QTL, on chromosome 8, was associated with more than 10% of the ear or plant height variation. The cumulative effects of temperate and tropical alleles on height QTL were not significantly different in either long- or short-day environments.

The cumulative effect of tropical alleles at TLN QTL was to significantly increase TLN, but only in long-day environments (P = 0.0042 in long days; P = 0.10 in short days). The QTL with the largest effects on TLN were detected in the same regions as those for the largest flowering time and height QTL, suggesting that some QTL may act pleiotropically on these traits.

A compressed folder is available at http://www.genetics.org/cgi/content/full/genetics.109.110304/DC1 that includes files for genotype scores and trait BLUPs for RILs used in the experiment, combined linkage map, and data formatted for analysis with MCQTL software.

References to Supporting Methods and Results

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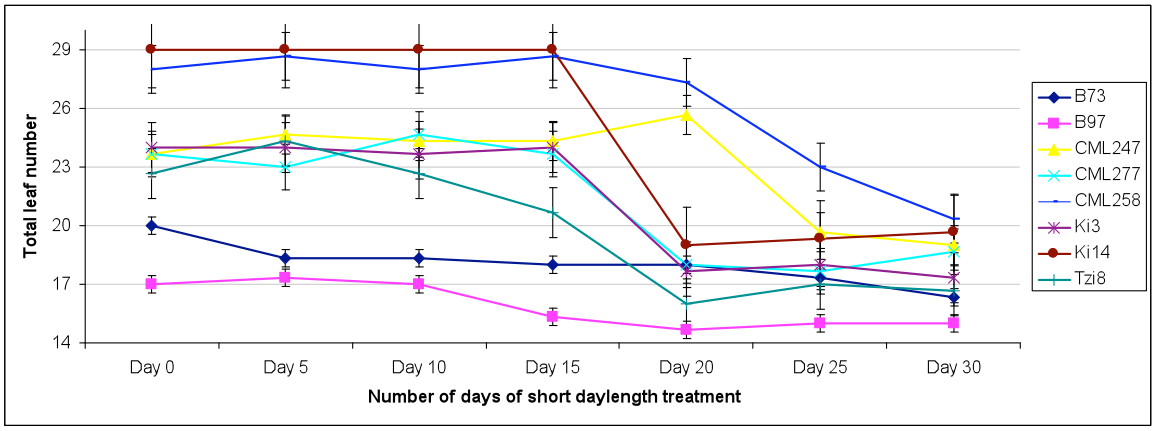
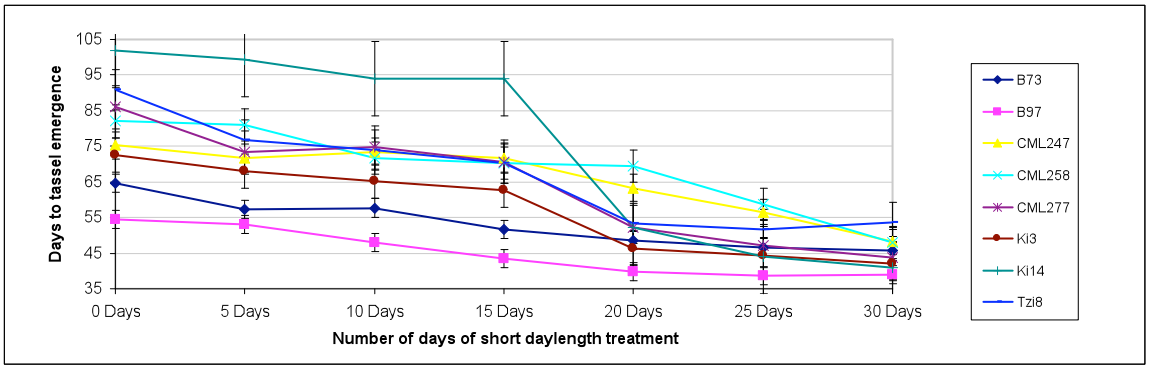
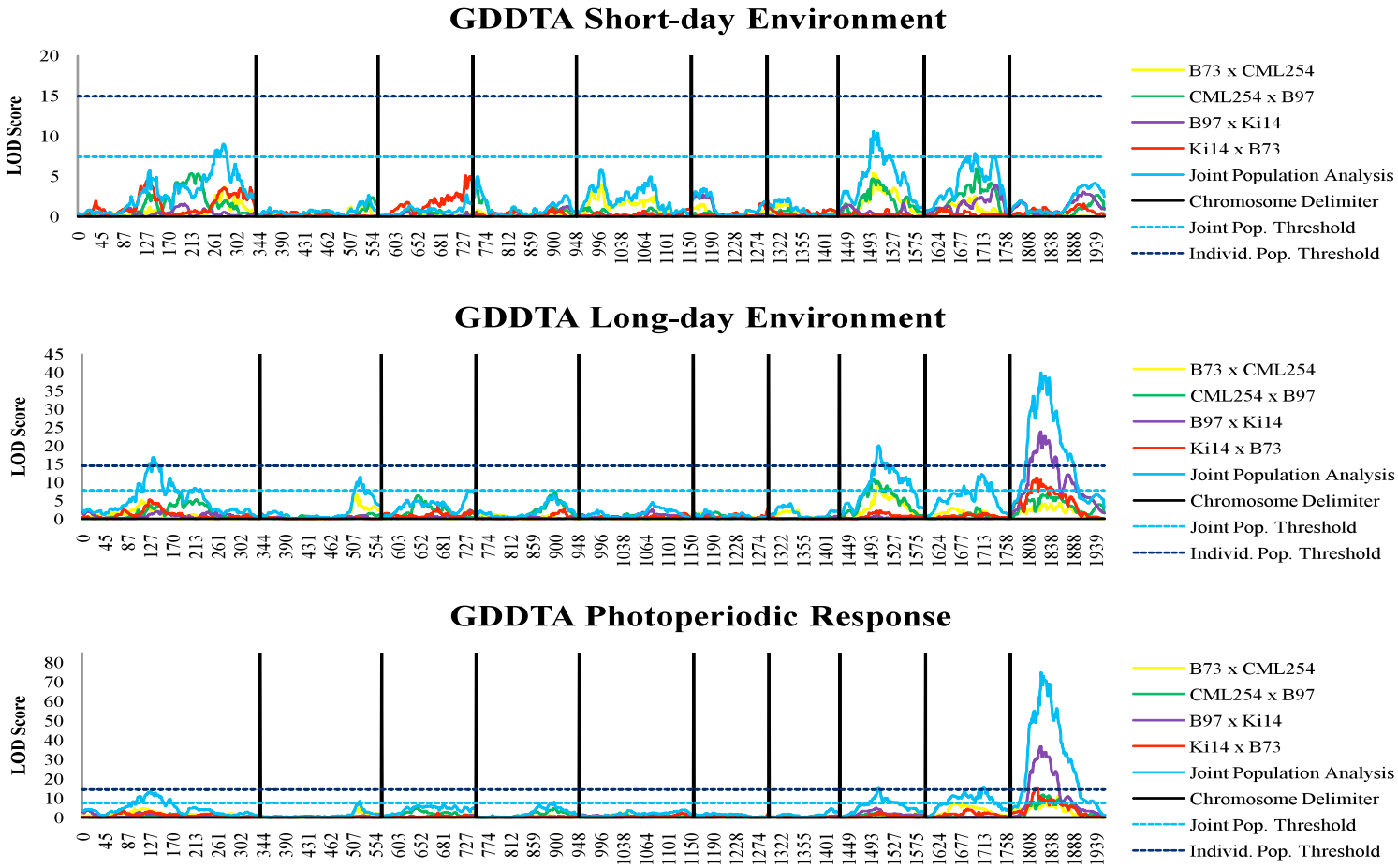


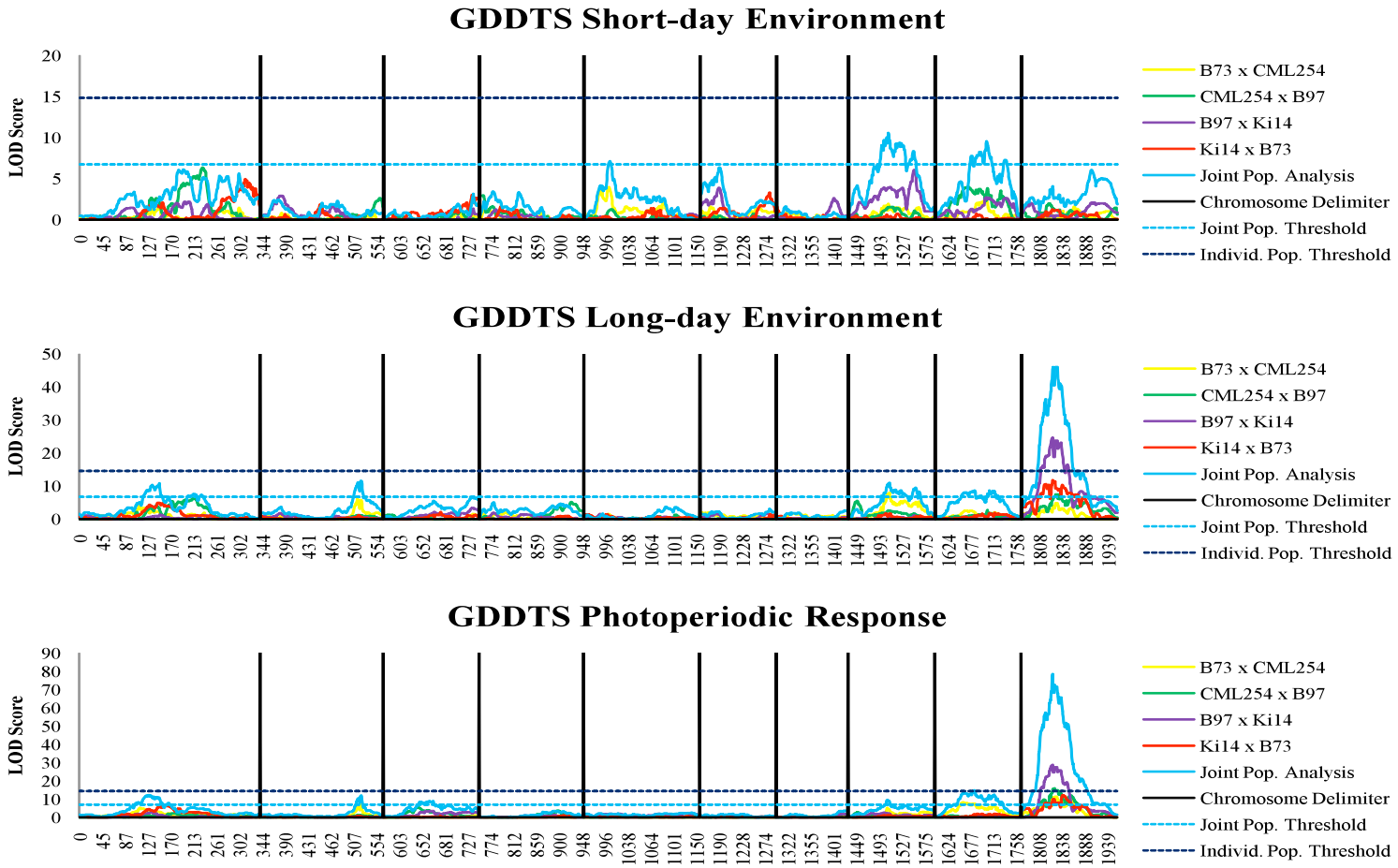
A



B

FIGURE S1.—Effect of short day exposure on total leaf number and days to tassel emergence. Lines given more days of short day treatment flowered faster and produced fewer leaves than those given fewer days of short day treatment. Photoperiod treatment was most effective within the first 25 days after seedling emergence. The tropical lines CML247, CML277, CML258, Ki3, Ki14, and Tzi8 had a greater response to long day photoperiod treatment than did the temperate lines B73 and B97. Graph (A) x-axis is duration of short-day treatment and y-axis is total leaf number. Graph (B) x-axis is duration of short-day treatment and y-axis is the number of days from seedling emergence until tassel emergence.


GDDTA Short-day Environment
LOD Score
0
5
10
15
20
0 45 87 127 170 213 261 302 344 390 431 462 507 554 603 652 681 727 774 812 859 900 948 996 1038 1064 1101 1150 1190 1228 1274 1322 1355 1401 1449 1493 1527 1575 1624 1677 1713 1758 1808 1838 1888 1939
B73 x CML254
CML254 x B97
B97 x Ki14
Ki14 x B73
Joint Population Analysis
Chromosome Delimiter
Joint Pop. Threshold
Individ. Pop. Threshold
GDDTA Long-day Environment
LOD Score
0
5
10
15
20
25
30
35
40
45
0 45 87 127 170 213 261 302 344 390 431 462 507 554 603 652 681 727 774 812 859 900 948 996 1038 1064 1101 1150 1190 1228 1274 1322 1355 1401 1449 1493 1527 1575 1624 1677 1713 1758 1808 1838 1888 1939
B73 x CML254
CML254 x B97
B97 x Ki14
Ki14 x B73
Joint Population Analysis
Chromosome Delimiter
Joint Pop. Threshold
Individ. Pop. Threshold
GDDTA Photoperiodic Response
LOD Score
0
10
20
30
40
50
60
70
80
0 45 87 127 170 213 261 302 344 390 431 462 507 554 603 652 681 727 774 812 859 900 948 996 1038 1064 1101 1150 1190 1228 1274 1322 1355 1401 1449 1493 1527 1575 1624 1677 1713 1758 1808 1838 1888 1939
B73 x CML254
CML254 x B97
B97 x Ki14
Ki14 x B73
Joint Population Analysis
Chromosome Delimiter
Joint Pop. Threshold
Individ. Pop. Threshold


GDDTS Short-day Environment
LOD Score
20
15
10
5
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0 45 87 127 170 213 261 302 344 390 431 462 507 554 603 652 681 727 774 812 859 900 948 996 1038 1064 1101 1150 1190 1228 1274 1322 1355 1401 1449 1493 1527 1575 1624 1677 1713 1758 1808 1838 1888 1939
B73 x CML254
CML254 x B97
B97 x Ki14
Ki14 x B73
Joint Pop. Analysis
Chromosome Delimiter
Joint Pop. Threshold
Individ. Pop. Threshold
GDDTS Long-day Environment
LOD Score
50
40
30
20
10
0
0 45 87 127 170 213 261 302 344 390 431 462 507 554 603 652 681 727 774 812 859 900 948 996 1038 1064 1101 1150 1190 1228 1274 1322 1355 1401 1449 1493 1527 1575 1624 1677 1713 1758 1808 1838 1888 1939
B73 x CML254
CML254 x B97
B97 x Ki14
Ki14 x B73
Joint Pop. Analysis
Chromosome Delimiter
Joint Pop. Threshold
Individ. Pop. Threshold
GDDTS Photoperiodic Response
LOD Score
90
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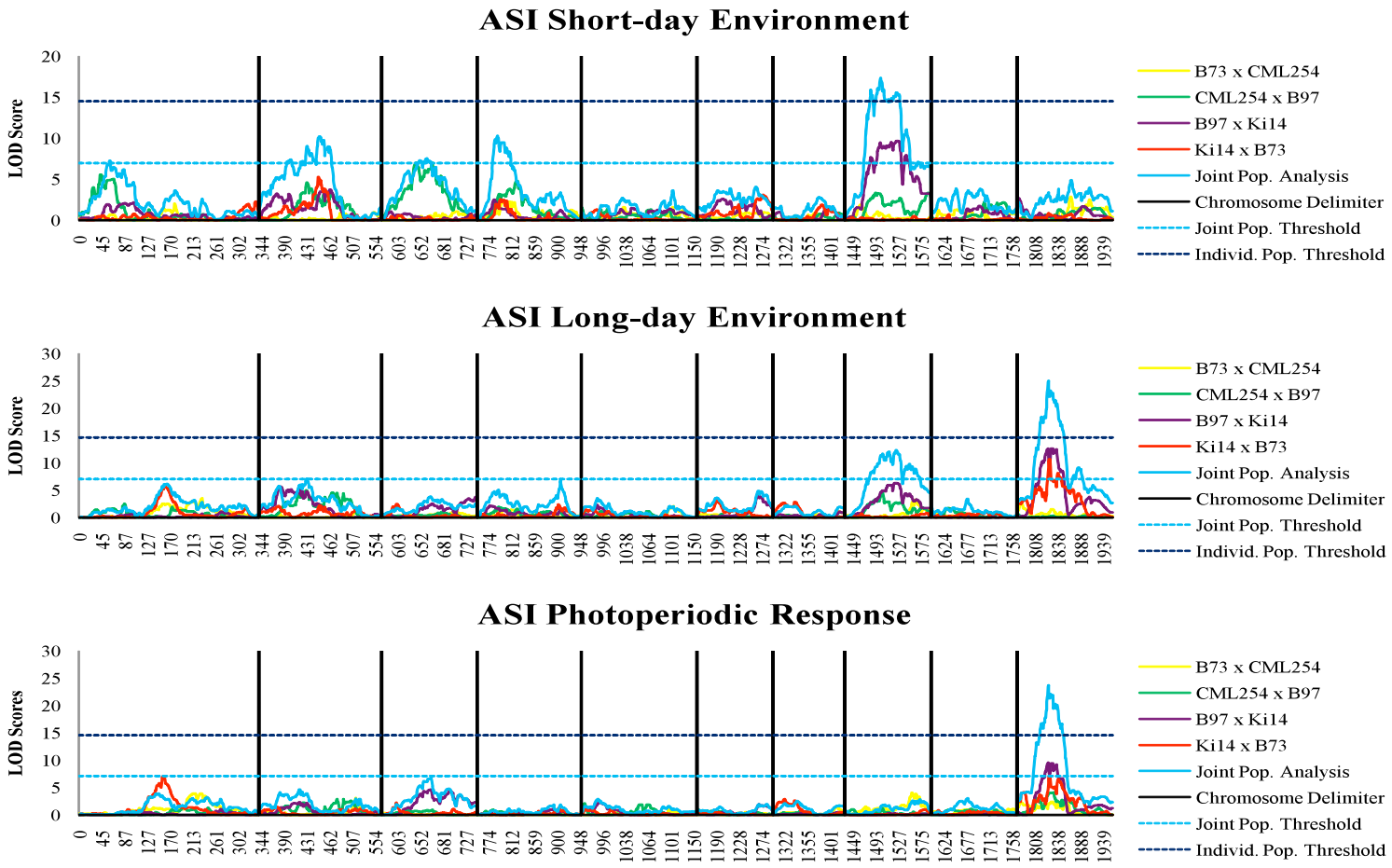
B73 x CML254
CML254 x B97
B97 x Ki14
Ki14 x B73
Joint Pop. Analysis
Chromosome Delimiter
Joint Pop. Threshold
Individ. Pop. Threshold


ASI Short-day Environment
LOD Score
0
5
10
15
20
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B73 x CML254
CML254 x B97
B97 x Ki14
Ki14 x B73
Joint Pop. Analysis
Chromosome Delimiter
Joint Pop. Threshold
Individ. Pop. Threshold
ASI Long-day Environment
LOD Score
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B73 x CML254
CML254 x B97
B97 x Ki14
Ki14 x B73
Joint Pop. Analysis
Chromosome Delimiter
Joint Pop. Threshold
Individ. Pop. Threshold
ASI Photoperiodic Response
LOD Scores
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20
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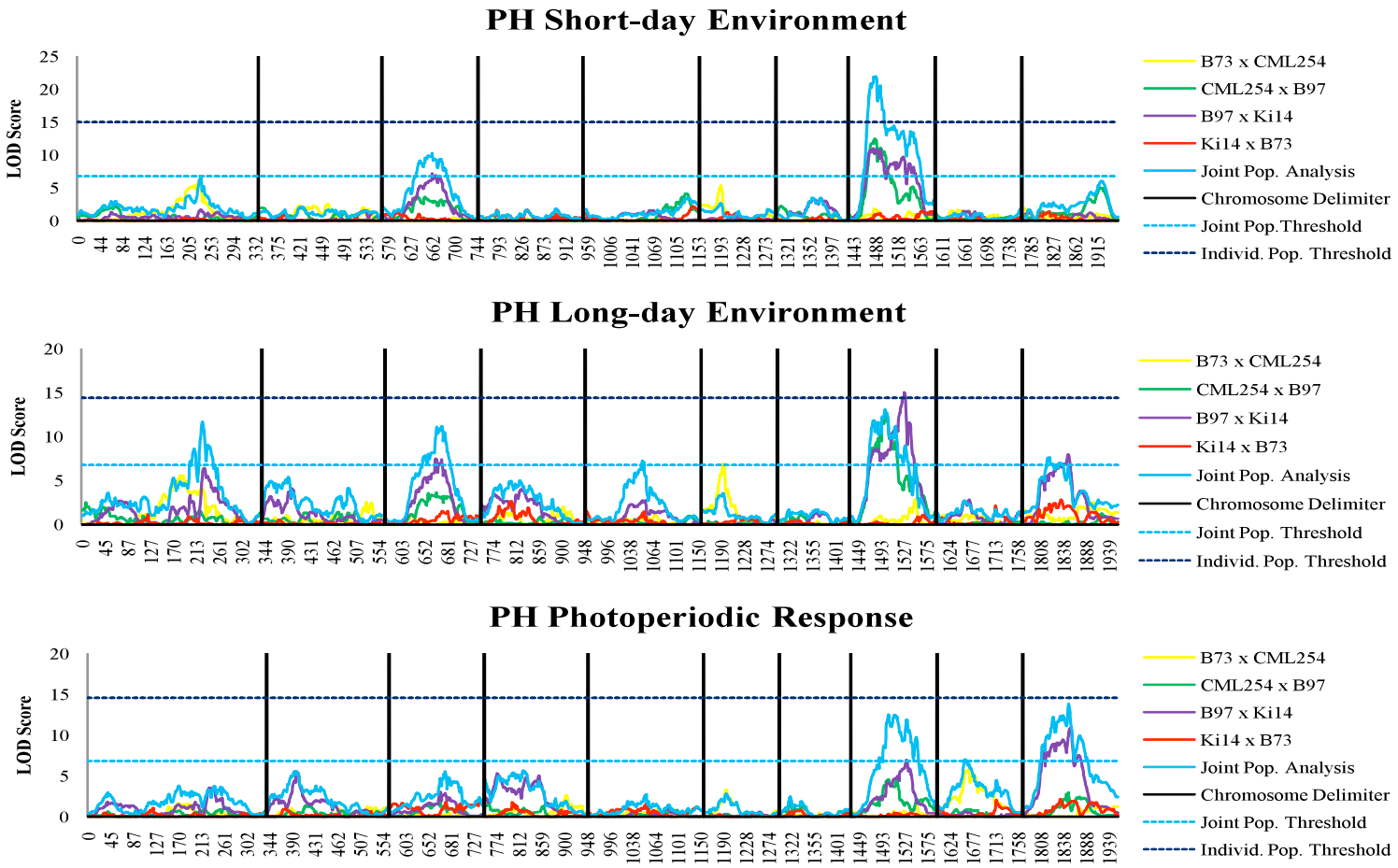
30
0 45 87 127 170 213 261 302 344 390 431 462 507 554 603 652 681 727 774 812 859 900 948 996 1038 1064 1101 1150 1190 1228 1274 1322 1355 1401 1449 1493 1527 1575 1624 1677 1713 1758 1808 1838 1888 1939
B73 x CML254
CML254 x B97
B97 x Ki14
Ki14 x B73
Joint Pop. Analysis
Chromosome Delimiter
Joint Pop. Threshold
Individ. Pop. Threshold


PH Short-day Environment
LOD Score
0
5
10
15
20
25
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B73 x CML254
CML254 x B97
B97 x Ki14
Ki14 x B73
Joint Pop. Analysis
Chromosome Delimiter
Joint Pop.Threshold
Individ. Pop. Threshold
PH Long-day Environment
LOD Score
0
5
10
15
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0 45 87 127 170 213 261 302 344 390 431 462 507 554 603 652 681 727 774 812 859 900 948 996 1038 1064 1101 1150 1190 1228 1274 1322 1355 1401 1449 1493 1527 1575 1624 1677 1713 1758 1808 1838 1888 1939
B73 x CML254
CML254 x B97
B97 x Ki14
Ki14 x B73
Joint Pop. Analysis
Chromosome Delimiter
Joint Pop. Threshold
Individ. Pop. Threshold
PH Photoperiodic Response
LOD Score
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0 45 87 127 170 213 261 302 344 390 431 462 507 554 603 652 681 727 774 812 859 900 948 996 1038 1064 1101 1150 1190 1228 1274 1322 1355 1401 1449 1493 1527 1575 1624 1677 1713 1758 1808 1838 1888 1939
B73 x CML254
CML254 x B97
B97 x Ki14
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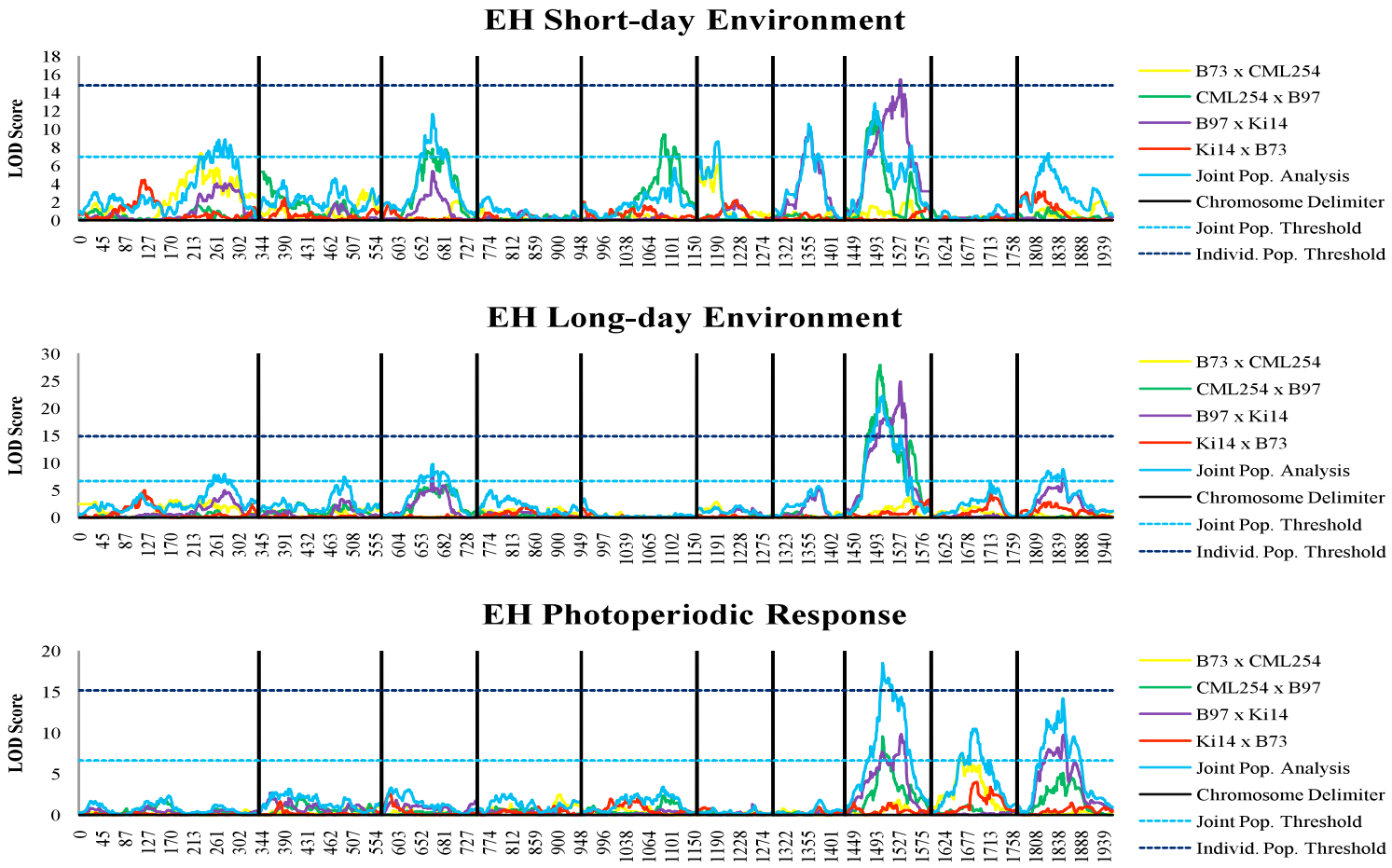
Joint Pop. Analysis
Chromosome Delimiter
Joint Pop. Threshold
Individ. Pop. Threshold


EH Short-day Environment
LOD Score
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B73 x CML254
CML254 x B97
B97 x Ki14
Ki14 x B73
Joint Pop. Analysis
Chromosome Delimiter
Joint Pop. Threshold
Individ. Pop. Threshold
EH Long-day Environment
LOD Score
0 5 10 15 20 25 30
0 45 87 127 170 213 261 302 345 391 432 463 508 555 604 653 682 728 774 813 860 900 949 997 1039 1065 1102 1150 1191 1228 1275 1323 1355 1402 1450 1493 1527 1576 1625 1678 1713 1759 1809 1839 1888 1940
B73 x CML254
CML254 x B97
B97 x Ki14
Ki14 x B73
Joint Pop. Analysis
Chromosome Delimiter
Joint Pop. Threshold
Individ. Pop. Threshold
EH Photoperiodic Response
LOD Score
0 5 10 15 20
0 45 87 127 170 213 261 302 344 390 431 462 507 554 603 652 681 727 774 812 859 900 948 996 1038 1064 1101 1150 1190 1228 1274 1322 1355 1401 1449 1493 1527 1575 1624 1677 1713 1758 1808 1838 1888 1939
B73 x CML254
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Ki14 x B73
Joint Pop. Analysis
Chromosome Delimiter
Joint Pop. Threshold
Individ. Pop. Threshold

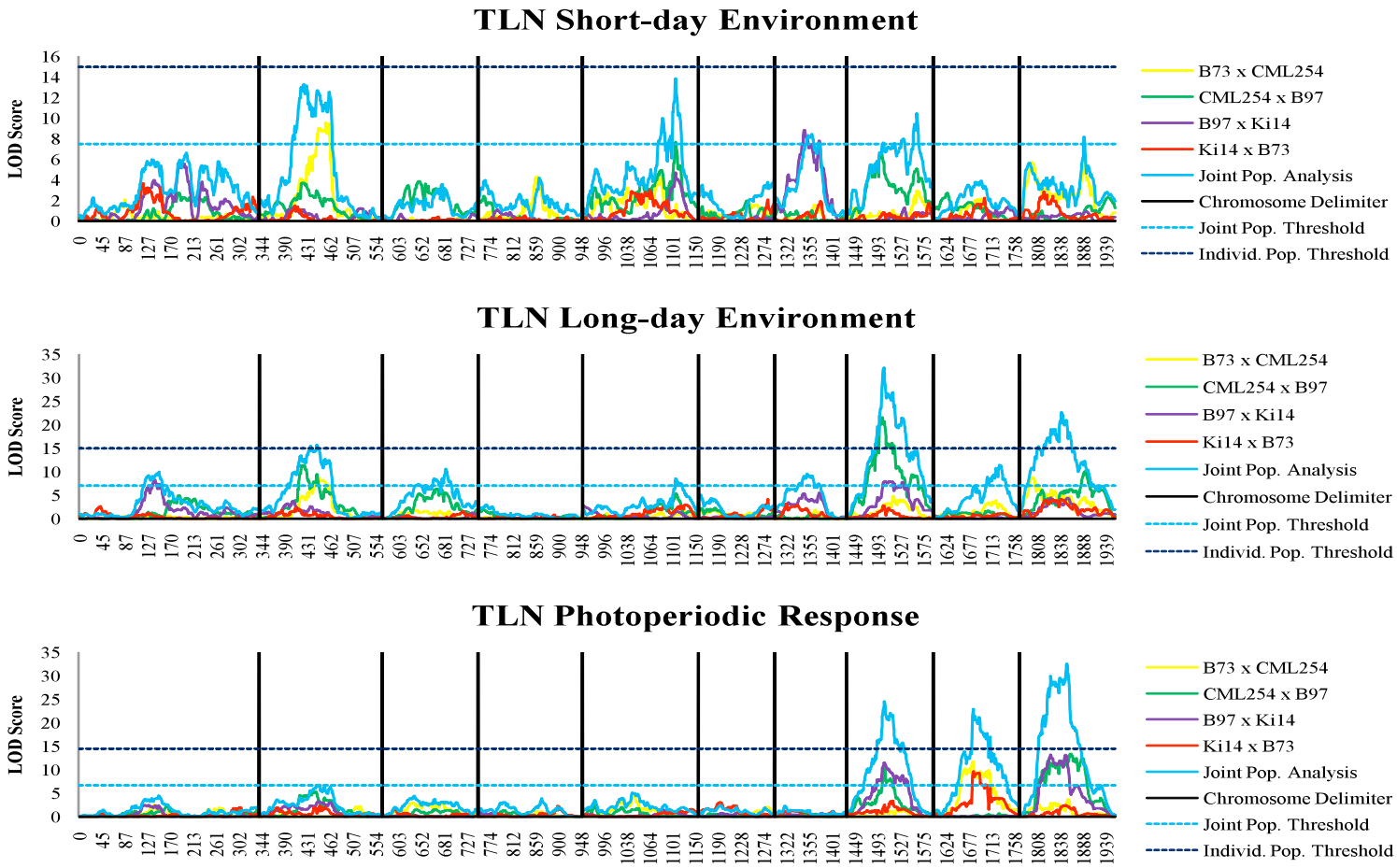
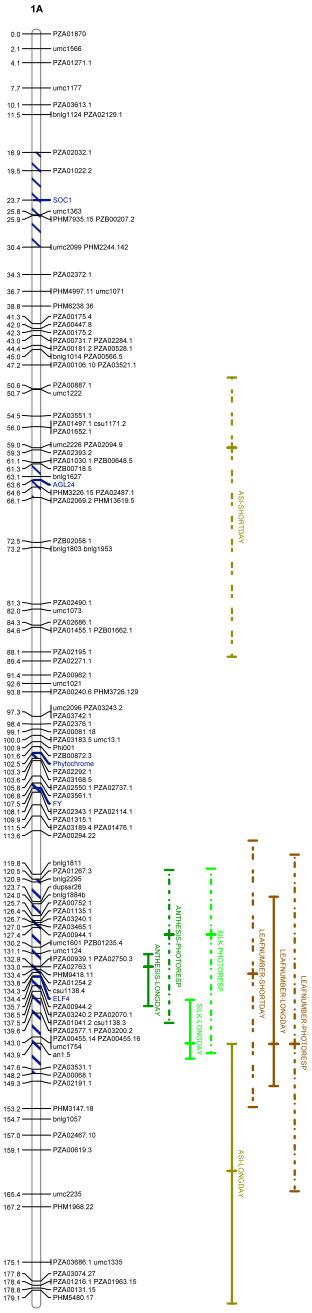


FIGURE S2.—LOD score and significance threshold histograms of each marker-trait association for the three environmental treatments (long-day, short-day, and photoperiodic response). LOD scores are significant where they pass the threshold that

corresponds to the population in question. Y-axes are QTL LOD scores, and X-axes are the map position, measured as the cumulative cM position from the combined population map. Vertical black lines separate different chromosomes.


1A
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2.1 umc1566
4.1 PZA01271.1
7.7 umc1177
10.1 PZA03613.1
11.5 bnlg1124 PZA02129.1
16.9 PZA02032.1
19.5 PZA01022.2
23.7 SOC1
25.8 umc1363
25.9 PHM7935.15 PZB00207.2
30.4 umc2099 PHM2244.142
34.3 PZA02372.1
36.7 PHM4997.11 umc1071
38.8 PHM6238.36
41.3 PZA01175.4
42.0 PZA00447.8
42.3 PZA01175.2
43.0 PZA00731.7 PZA02284.1
44.4 PZA00181.2 PZA00528.1
45.0 bnlg1014 PZA00566.6
47.2 PZA00106.10 PZA03521.1
50.6 PZA00887.1
50.7 umc1222
54.5 PZA03551.1
56.0 PZA01497.1 csu1171.2
PZA01652.1
59.0 umc2225 PZA02094.9
59.3 PZA02393.2
61.1 PZA01030.1 PZB00648.5
61.3 PZB00718.5
63.1 bnlg1627
63.6 AGL24
64.6 PHM3226.15 PZA02487.1
66.1 PZA02099.2 PHM13619.5
72.5 PZB02058.1
73.2 bnlg1803 bnlg1953
81.3 PZA02490.1
82.0 umc1073
84.3 PZA02686.1
84.6 PZA01455.1 PZB01662.1
88.1 PZA02195.1
89.4 PZA02271.1
91.4 PZA00962.1
92.6 umc1021
93.8 PZA00240.6 PHM3726.129
97.3 umc2096 PZA03243.2
98.4 PZA03742.1
99.1 PZA02376.1
100.0 PZA00081.18
100.9 PZA03183.5 umc13.1
101.6 Phi001
102.5 PZB00872.3
103.3 Phytochrome
103.6 PZA02292.1
105.8 PZA03168.5
106.8 PZA02550.1 PZA02737.1
107.5 PZA03561.1
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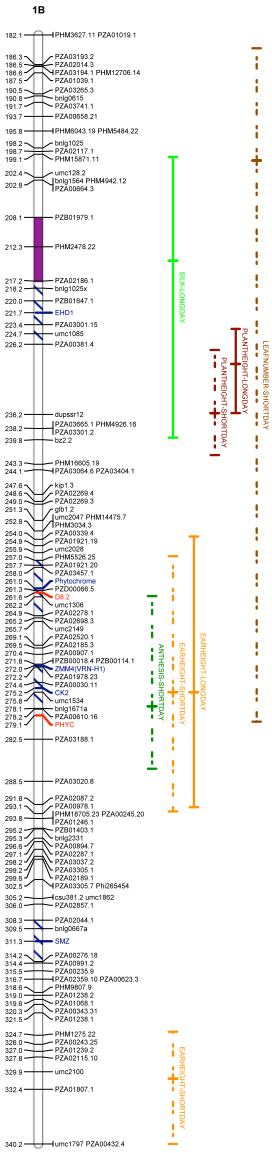
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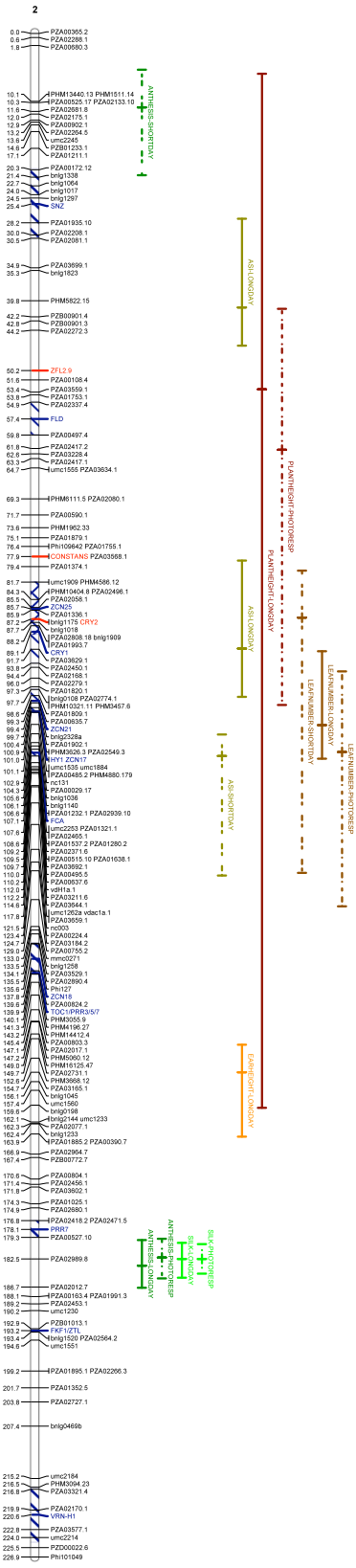
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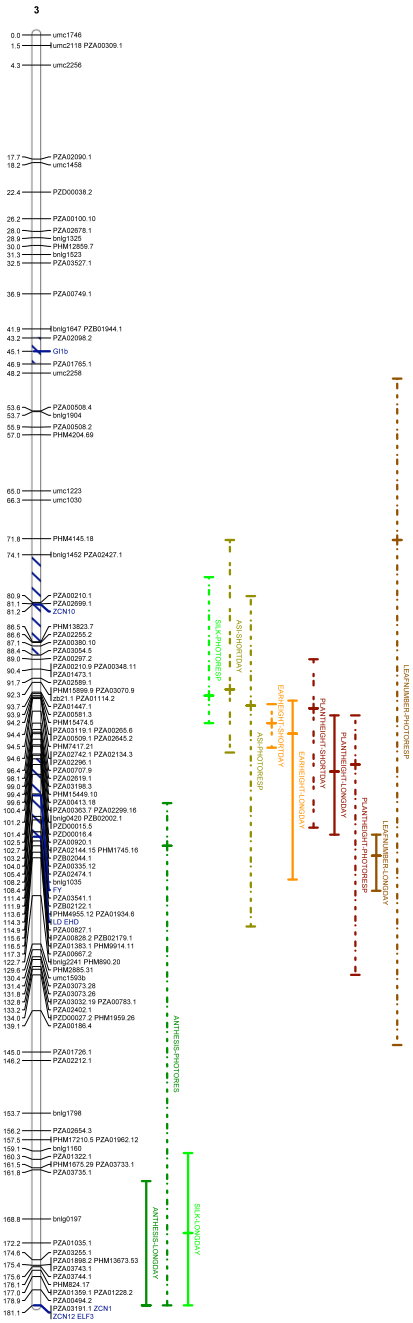
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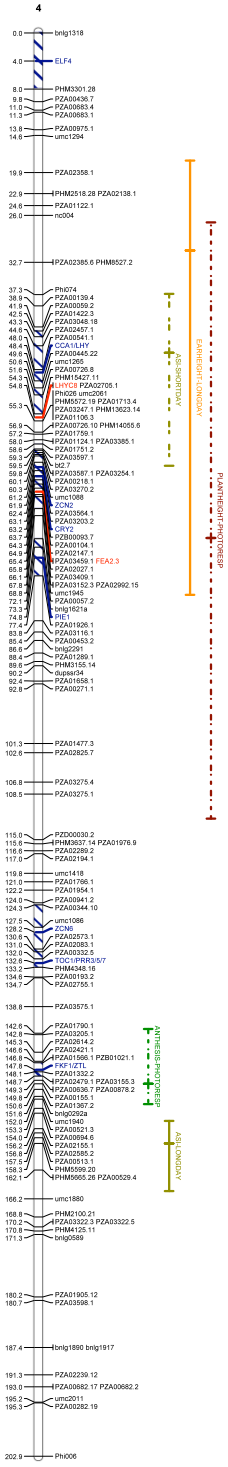
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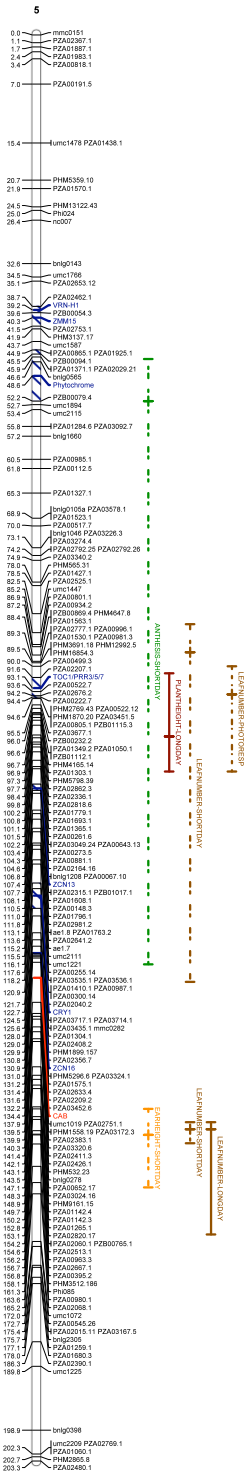
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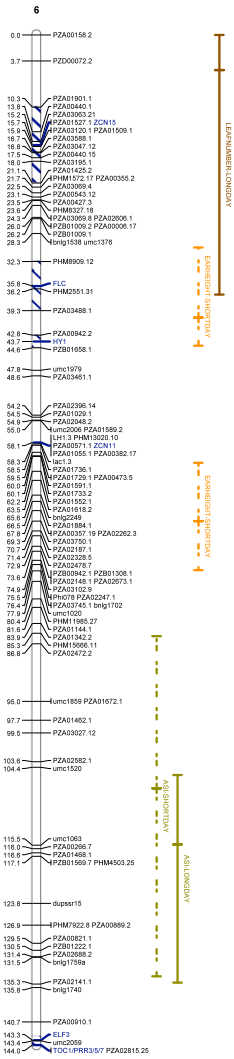
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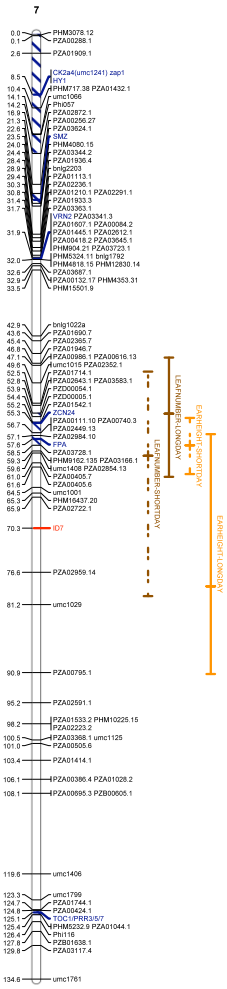
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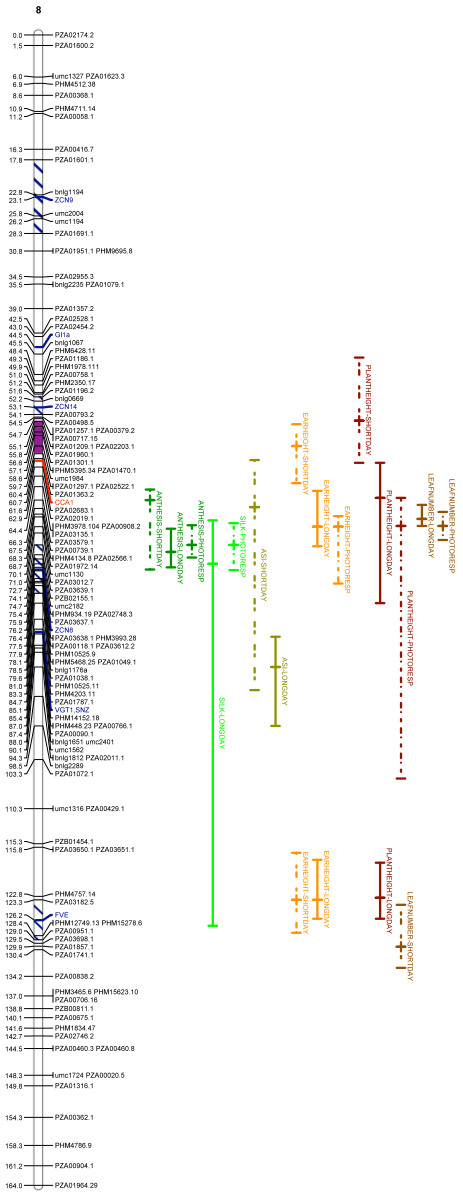
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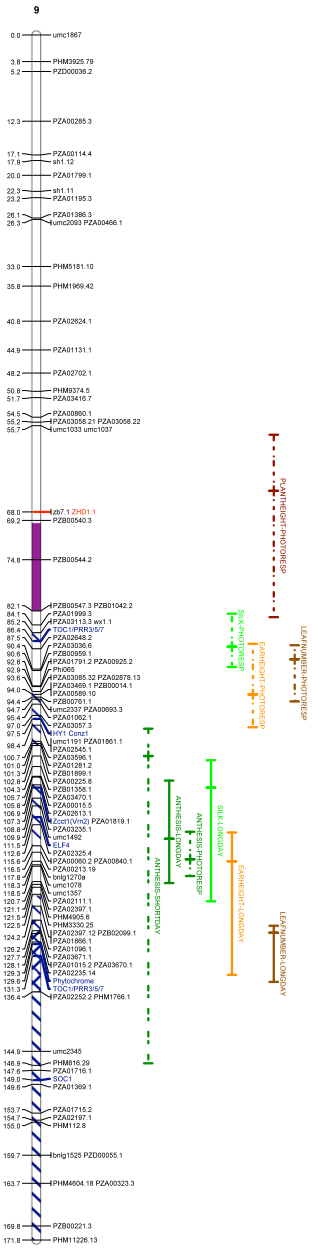
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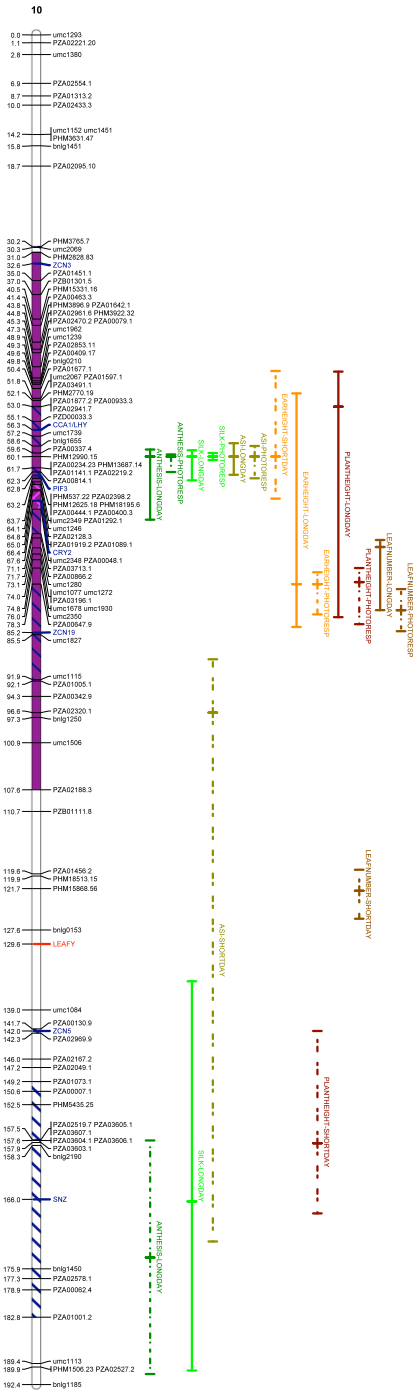
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FIGURE S3.—Linkage map of the combined data from the four RIL mapping populations. This map consists of 241 SSR, 1088 SNP, and 10 candidate gene markers. Total map distance is 1961.2 cM. Candidate genes directly mapped are indicated in red. Map intervals containing candidate genes localized by inference indicated as segments with blue diagonal filling, with the candidate gene name in blue positioned at interval midpoint. Map intervals exhibiting significant segregation distortion in the combined analysis indicated as magenta segments on the linkage group. The map interval on chromosome 10 identified as having undergone a selection sweep by Tian *et al.* (2009) is indicated by a pink segment on the linkage group. QTL bars represent the 2-LOD support interval of the QTL position; the middle hash mark of a bar represents the maximum likelihood position of the QTL.

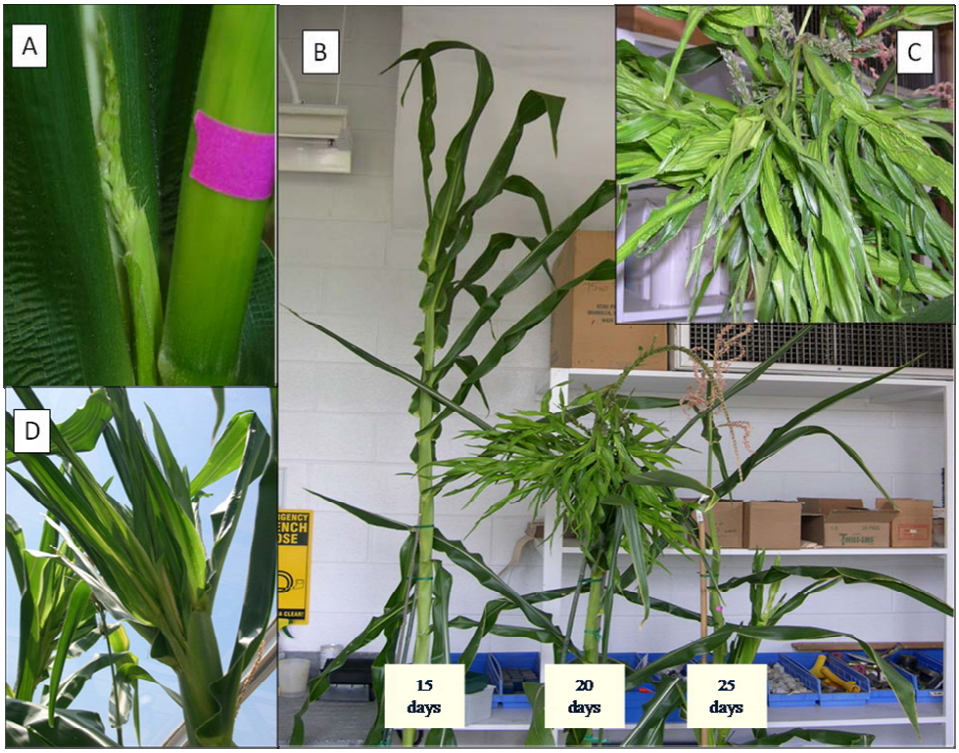

FIGURE S4.—Unusual floral phenotypes from the phytotron. Phenotypes were consistent for the particular treatments shown. A) The tasseled-ear phenotype shown on a Tzi8 plant which received 10 days of short-day treatment before being transferred to a long-day environment. B) Ki14 plants given different amounts of short-day treatment before being transferred to a long-day greenhouse. Plants give greater than 25 days of short-day treatment produced normal-looking tassels which shed pollen and normal-looking ears which produced silks. Plants given 20 days of short-day treatment grew to normal height, but produced giant tassels (measuring up to a meter in length) that were covered in plantlets with roots and shoots. Plants given 15 days or less of short-day treatment grew extremely tall and flowered extremely late. C) Close-up view of plantlets growing on tassels of a Ki14 plant given 20 days of short-day treatment. D) A massive group of leaves surrounding the sterile tassel that emerged from Ki14 plants which received 15 days or less of short-day treatment.

TABLE S1

Number of replications per environment for each of the RIL populations

	Environment						
Population	Summer 2004	Summer 2005	Winter 2005	Summer 2006	Winter 2006	Summer 2007	Winter 2007
B73 × CML254	0	1	2[a]	3	2	3	2
CML254 × B97	0	1	2[a]	3	2	3	2
B97 × Ki14	0	1	2[a]	5	2	4	2
Ki14 × B73	2	0	0	4[b]	2	2	2

[a] The 40 earliest and 40 latest flowering lines in each population in Summer 2005 were planted in the Winter 2005 experiments.

[b] Two replications were grown in Clayton, NC and two were grown in Andrews, NC.

TABLE S2

Results of the phytotron study

Parameter	Trait[a]			
	DTA	DTS	DTE	TLN
	days			No. of leaves
Experiment-wide average trait increase per additional day of long-day treatment	1.01	0.78	1.05	0.18
Average increase per additional day of long-day treatment in temperate inbreds	0.56	0.70	0.61	0.10
Average increase per additional day of long-day treatment in tropical inbreds	1.16	1.08	1.12	0.21
Experiment-wide percentage of missing data	12% (male sterile)	30% (female sterile)	4%	1%
Percentage of missing data in temperate inbreds	2% (male sterile)	7% (female sterile)	2%	2%
Percentage of missing data in tropical inbreds	16% (male sterile)	54% (female sterile)	4%	0%

Temperate maize lines (B73 and B97) were compared to tropical maize lines (CML247, CML258, CML277, Ki3, Ki14, and Tzi8) for each of several developmental traits.

[a] DTA: days from coleoptile emergence to anthesis; DTS, days from coleoptile emergence to silk emergence; DTE, days from coleoptiles emergence to tassel emergence; TLN, total leaf number.

TABLE S3

Primer pairs for polymorphic candidate gene markers mapped

Gene	Target Genbank Accession	Forward Primer	Reverse Primer	Marker Type	Enzyme for CAPS/ dCAPS	Comment
CAB	AZM3_105597*	CTTGGCGCAAGTTACTGAAA	ACCAATCCGTTCGCTTCTAA	Indel		
CCA1	CC653945	CGTGAACATGTTTGCTTCTGC	ATCTCCAGCTCCCCCATC	dCAPS	Pst I	
CO	AI622483	GGCAATCAATAAGAGCTTTGC	GGAGGAGCACGAGGAGATGT	dCAPS	Hae III	
CRY1A	AB073546	CACCTTCAACCACCCCTGCAA	ACGTATCCGGTCGTGAACC	dCAPS	Hind III	
CRY2	AF545572	AGCGCCGTTGTTGGTTCTAC	GAACAGCGAGGAGGAGGAC	Indel		
HD3A	BD169090	CGCGTGTATTTCTAGTTCGTAA	ACTTCGCCGAGCTCTACAAC	Indel		
ID7	AY754865	GCAGCAACGTACGATAAGCA	ACGAAATCGTACGGGAAATG	Indel		
LFY	AF378126	ATGTCGAAGCCGTGGCTCG	AAGCCCAAGATGCGGCACTA	dCAPS	Xho I	
LHY	CG833555	TGGAAGGAAGTTTCCGAAGA	GAAATCGCTCATGTTGATGCT	CAPS	BstU I	chr. 10
LHY	N/A**	AGAAAGCCAAACAGGCCATA	TACTTGCCTCGGTCCTCCT	CAPS	Rsa I	chr. 4
PHYC	U56731	CATGCATGTACAACTGAACTG	TGATGGTTAGAATTGCTCAGA	Indel		

* AZM sequence accession code refers to Maize Genomics Consortium Survey Build 3.0

** Partial gene sequence

TABLE S4

Homologs of candidate genes position identified by BLAST-X and BLAST-N searches of maize sequence and positioned on combined genetic map by inference from SNP markers developed from common BAC contigs. Gene list, homologs, and pathway identification adapted from Cockram et al. (2004) and Putterill et al. (2007).

Species	Gene	Homologs	Search method	BAC sequence	Chromo-some	Contig	Predicted gene position on combined map	Within photoperiod QTL support interval?	Comments
Arabidopsis	AGL24		BLAST	AC194144	1	8	61.1 - 66.1		
Arabidopsis	CCA1/ LHY	OsLHY (rice)	BLAST	AC190849	4	164	42.5 - 54.3	PH	
Arabidopsis	CCA1/ LHY	OsLHY (rice)	BLAST	AC213378	10	402	53.0 - 59.6	GDDTS, GDDASI	
Arabidopsis	CK2	Hd6 (rice)	BLAST	AC177884	1	59	272.2 - 278.2		
maize	CK2a4	Hd6 (rice)	MaizeGDB locus search	AC205122	7	293	0 - 16.9		
maize	Conz1	CO (Arabidopsis)	BLAST	AC189064	9	377	93.6 - 101.3	EH, TLN	1
Arabidopsis	CRY1		BLAST	AC190725	2	78	84.3 - 93.8	PH, TLN	
Arabidopsis	CRY1		BLAST	AC210022	5	240	120.9 - 124.5		
Arabidopsis	CRY2		BLAST	AC205484	4	171	58.6 - 67.8	PH	2
Arabidopsis	CRY2		BLAST	AC194432	10	413	61.7 - 71.1	GDDTS, GDDASI	
Arabidopsis	EHD1/ EHD2		BLAST	AC191603	1	47	220.0 - 226.2		3

Arabidopsis	EHD1/ EHD2		BLAST	AC214227	3	129	113.6 - 114.9	GDDTA, GDDASI, PH, TLN	
Arabidopsis	ELF3		BLAST	AC207396	3	149	>181.1	GDDTA	4
Arabidopsis	ELF3		BLAST	AC205040	6	290	142.6 - 144.0		
Arabidopsis	ELF4		BLAST	AC204538	1	17	120.5 - 148.2	GDDTA, GDDTS, TLN	
Arabidopsis	ELF4		BLAST	AC208432	4	156	0 - 8.0		
Arabidopsis	ELF4		BLAST	AC190972	9	384	107.3 - 115.6	GDDTA	
Arabidopsis	FCA		BLAST	AC204717	2	91	106.6 - 107.6	TLN	
Arabidopsis	FKF1/ZTL		BLAST	AC203828	2	108	192.9 - 193.4		
Arabidopsis	FKF1/ZTL		BLAST	AC190896	4	469	146.8 - 148.7	GDDTA	
Arabidopsis	FLC		Gramene gene tree	AC186594	6	272	32.3 - 39.3		
Arabidopsis	FLD		BLAST	AC211468	2	74	54.9 - 59.8	PH	
Arabidopsis	FPA		BLAST	AC198602	7	320	56.7 - 58.5		
Arabidopsis	FVE		BLAST	AC196690	8	359	123.3 - 129.0		
Arabidopsis	FY		BLAST	AC204306	1	14	106.8 - 108.1		
Arabidopsis	FY		BLAST	AC202058	3	128	103.2 - 113.6	GDDTA, GDDASI, PH, TLN	
Arabidopsis	GI (Gigantea1 a)	OsGI (rice)	BLAST	AC193462	8	329	39 - 49.9		
Arabidopsis	GI (Gigantea1	OsGI (rice)	BLAST	AC202834	3	112	43.2 - 46.9		

b)

Arabidopsis	HY1	Se5 (rice)	BLAST	AC197152	2	88	100.9 - 101.1	TLN	
Arabidopsis	HY1	Se5 (rice)	BLAST	AC203340	6	275	42.8 - 44.6		
Arabidopsis	HY1	Se5 (rice)	BLAST	AC217986	7	296	0 - 16.9		
Arabidopsis	HY1	Se5 (rice)	BLAST	AC188985	9	376	93.6 - 101.3	EH, TLN	
Arabidopsis	HY1	Se5 (rice)	BLAST		9	389	126.2 - 171.8		
Arabidopsis	LD		BLAST	AC195792	3	129	113.6 - 114.9	GDDTA, GDDASI, PH, TLN	
Arabidopsis	Phytochrome A/B/C/D/E		BLAST	AC211646	1	12	101.6 - 103.3		
Arabidopsis	Phytochrome A/B/C/D/E		BLAST	AC205798	1	57	257.0 - 264.9		
Arabidopsis	Phytochrome A/B/C/D/E		BLAST	AC216052	5	208	44.9 - 52.2		
Arabidopsis	Phytochrome A/B/C/D/E		BLAST		9	387	122.7 - 136.4		
Arabidopsis	PIE1		BLAST	AC186019	4	181	72.1 - 77.4	PH	
Arabidopsis	PIF3		BLAST	AC191417	10	406	62.3 - 63.2	GDDTS, GDDASI	
Arabidopsis	PRR7		Gramene gene tree	AC198940	2	105	176.8 - 179.3	GDDTAP	5
Arabidopsis	SMZ		BLAST	AC185520	1	64	308.3 - 314.2		
Arabidopsis	SMZ		BLAST	AC188826	7	298	22.6 - 24.4		
Arabidopsis	SNZ		BLAST	AC194075	2	69	20.3 - 30.5		
Arabidopsis	SNZ		BLAST	AC219006	8	354	84.7 - 85.4	PH	
Arabidopsis	SNZ		BLAST	AC204437	10	418	149.2 - 182.8		6
Arabidopsis	SOC1		BLAST	AC194220	1	3	16.9 - 30.4		

Arabidopsis	SOC1		BLAST	AC150630	9	391	126.2 - 171.8		4
Arabidopsis	TOC1/PRR3/5/7/9	Ppd-H1 (barley) Ppd1 (wheat)	BLAST	AC222555	2	101	139.6 - 140.1		
Arabidopsis	TOC1/PRR3/5/7/9	Ppd-H1 (barley) Ppd1 (wheat)	BLAST	AC210735	4	187	132 - 133.2		
Arabidopsis	TOC1/PRR3/5/7/9	Ppd-H1 (barley) Ppd1 (wheat)	BLAST	AC229989	5	219	91.6 - 94.6	TLN	
Arabidopsis	TOC1/PRR3/5/7/9	Ppd-H1 (barley) Ppd1 (wheat)	BLAST	AC206249	6	291	> 144.0		7
Arabidopsis	TOC1/PRR3/5/7/9	Ppd-H1 (barley) Ppd1 (wheat)	BLAST	AC195801	7	325	124.8 - 125.4		
Arabidopsis	TOC1/PRR3/5/7/9	Ppd-H1 (barley) Ppd1 (wheat)	BLAST	AC202398	9	373	85.2 - 87.5	GDDTS, EH, TLN	
Arabidopsis	TOC1/PRR3/5/7/9	Ppd-H1 (barley) Ppd1 (wheat)	BLAST	AC205568	9	387	126.2 - 136.4		
Arabidopsis	VRN2		BLAST	AC212668	7	305	31.9		8
barley	VRN-H1	Vrn1 (wheat)	BLAST	AC211016	2	110	216.5 - 224.6		
barley	VRN-H1	Vrn1 (wheat)	BLAST	AC197034	5	206	38.7 - 39.6		
maize	zap1		BLAST	AC213798/AC205122	7	293	0 - 16.9		4
rice	Zcct1 (Vrn2)		Gramene gene tree	AC204922	9	383	105.7 - 108.8		9
maize	zcn1		BLAST	AC183913	3	152	>181.1	GDDTA	4
maize	zcn2		BLAST	AC208981	4	171-172	60.1 - 63.7	PH	
maize	zcn3		BLAST	AC194104	10	393	30.2 - 35.0		

maize	zcn5		BLAST	AC217051	10	417	141.7 - 142.3		
maize	zcn6		BLAST	AC183820	4	187	124.3 - 132.0		
maize	zcn8		BLAST	AC194866	8	353	72.7 - 79.6	GDDTA, GDDTS, EH, PH	
maize	zcn9		BLAST	AC187287	8	326	17.8 - 28.3		
maize	zcn10		BLAST	AC183315	3	117	74.1 - 88.4	GDDTS, GDDASI, PH, TLN	
maize	zcn11		BLAST	AC200139	6	281	58.1		8
maize	zcn12		BLAST	AC199374	3	141	>181.1	GDDTA	4
maize	zcn13		BLAST	AC207738	5	235	106.8 - 107.7		
maize	zcn14		BLAST	AC192353	8	329	51.6 - 54.5		
maize	zcn15	FT, Hd3a, Vrn-H3	BLAST	AC193989	6	273	10.3 - 21.1		
maize	zcn16		BLAST	AC202071	5	242	130.8 - 131		
maize	zcn17		BLAST	AC206963	2	89	100.9 - 101.1	TLN	
maize	zcn18		BLAST	AC202395	2	100	135.5 - 140.1		
maize	zcn19		BLAST	AC211363	10	413	78.3 - 92.1	EH, PH, TLN	
maize	zcn21		BLAST	AC189755	2	82	97.7 - 101.1	TLN	
maize	zcn24		BLAST	AC199404	7	320	53.9 - 56.7		
maize	zcn25		BLAST	AC190509	2	77	81.7 - 89.6	PH	
maize	Zmm4		BLAST	AC186341	1	57	271.8 - 272.2		10
maize	Zmm15		BLAST	AC231388	5	206	38.7 - 41.9		11

Arabidopsis	LFY (Zfl2)	RFL (rice)	BLAST	AC194054	2		50.2	PH	12
Arabidopsis	Phytochrome A/B/C/D/E		BLAST		1		279.1		12
barley	VRN-H1	Vrn1 (wheat)	BLAST	AC213798	7	293	0 - 16.9		12, 13
Arabidopsis	FT	Hd3a (rice), VRN-H3 (barley), VRN-B3 (wheat)	BLAST	AC193989	6	269	10.3 - 21.1		12, 14
rice	Hd3a	FT (Arabidopsis)	Gramene gene tree	AC193989	6	269	10.3 - 21.1		12, 14
rice	RFT1		BLAST	AC193989	6	269	10.3 - 21.1		12, 14
maize	zcn20		BLAST	AC191066	2	84	100.9 - 101.1		15, 16
Arabidopsis	LFY (Zfl1)	RFL (rice)	BLAST	AC203811	10	416	119.6 - 157.9		12, 17
Arabidopsis	PRR7		Gramene gene tree	AC205568	9	387	126.2 - 136.4	GDDTAP	12, 18
maize	zcn26		BLAST	AC212092	4	197	150.6 - 153.3		15, 19
rice	EHD1		Gramene gene tree	AC191603	1	47	220.0 - 226.2		12, 20
maize	zcn4		BLAST	AC191050	1	53	243.3 - 251.3		15, 21
barley	VRN-H1	Vrn1 (wheat)	BLAST	AC186341	1	57	271.8 - 272.2		12, 22
rice	OsGI		Gramene gene tree	AC193462	8	329	39.0 - 49.9		12, 23
rice	OsGI		Gramene gene tree	AC202834	3	112	43.2 - 46.9		12, 23
Arabidopsis	FT	Hd3a (rice), VRN-H3 (barley), VRN-B3 (wheat)	BLAST	AC192353	8	329	51.6 - 54.5		12, 24
Arabidopsis	CO	Hd1 (rice)	BLAST	AC189064	9	377	93.6 - 101.3	EH, TLN	12, 25
rice	Hd1		Gramene gene tree	AC189064	9	377	93.6 - 101.3	EHP, TLNP	12, 26

Arabidopsis	Phytochrome A/B/C/D/E		BLAST		5		15
maize	dlf1		BLAST		7L		15, 27
Barley	FLC		BLAST	none	none	none	
Arabidopsis	FRI		Gramene gene tree	none	none	none	
Barley	FRI		BLAST	none	none	none	
Barley	FRL1		BLAST	none	none	none	
rice	Ghd7		Gramene gene tree	none	none	none	
Barley	TFL2		BLAST	none	none	none	
Barley	VIN3		BLAST	none	none	none	
Rice	VRN1		BLAST	none	none	none	
Rice	VRN-H2	ZCCT (wheat)	BLAST	none	none	none	
maize	zcn7		BLAST	?			12, 28

Comments:

1	BAC position given by Miller et al., 2008. Note that PZA markers are in flanking contigs 376 and 378. contig 377 not yet directly mapped
2	Both NAM and combined maps differ from physical order in this region, so max uncertainty chosen on position
3	Contig47 position is uncertain. This is current location.
4	This contig maps distal to end of inkage group
5	Homolog of Ppd-H1
6	Contigs 417 - 419 appear inverted in order on combined map vs NAM map
7	Contig291 is most distal contig on chrom 6

8	SNP markers flanking BAC map to same position
9	Rice protein is predicted only, closest match = Q8LGV7
10	Map position given by Danilevskaya et al. (2008) Plant Physiol. 147:2054-2069. BLAST seach of sequence against Maizesequence.org identifies BAC AC186341, which is localized to chrom 1 271.8 - 272.2 on combined map
11	Map position given by Danilevskaya et al. (2008) Plant Physiol. 147:2054-2069. Exact physical position identified by BLAST against Maizesequence.org, identified BAC AC231388, which is flanked by AC21572 (carries PZA02462.1) and AC1914234 (PZB00054.3), so it is localized to 38.7 - 41.5 on combined map
12	Duplicate of sequence already positioned
13	Identifies same sequence as maize zap1
14	Identifies same sequence as zcn15
15	Consider position unknown.
16	Danilevskaya indicated position on chromosome 10. Consider position unknown.
17	LEAFY homolog directly mapped with CAPS marker to position 129.6, consistent with this. So CAPS marker precise position displayed on map
18	Identifies same sequence as TOC1/PRR3/5/7/9
19	Danilevskaya indicated position on chromosome 9.
20	Identifies same sequence as Arabidopsis EHD1
21	BAC is not placed on physical map, appears to be distal to end of chrom 1. Danilevskaya give a position on 2.04. Consider this position unknown
22	duplicate of Zmm4 sequence below
23	Identifies same sequence as GI1a
23	Identifies same sequence as GI1b

24	Identifies same sequence as zcn14
25	identifies same sequence as Conz1, below
26	We identified this as a predicted gene in Gramene. It matches Conz1 already identified.
27	Map position unknown, but it is on 7L. Physical position of sequence matches are beyond end of 7L. Do not map because of uncertainty
28	BLAST locates matches on several unordered BACs plus chr 4 and 8, but not 6 as indicated by Danilevskaya et al. 2008.

TABLE S5

Heritability (H) estimates on a family mean-basis and their standard errors (SE). Estimates are for each population of traits measured in long- and short-day environments and of photoperiod responses (long-day minus short-day measurements).

B73 × CML254			CML254 × B97			B97 × Ki14			Ki14 × B73		
Trait	H	SE[a]	Trait	H	SE	Trait	H	SE	Trait	H	SE
Short-day environments											
GDDTA	0.86	0.02	GDDTA	0.83	0.03	GDDTA	0.82	0.02	GDDTA	0.65	0.07
GDDTS	0.86	0.02	GDDTS	0.76	0.04	GDDTS	0.86	0.02	GDDTS	0.66	0.07
GDDASI	0.74	0.04	GDDASI	0.72	0.05	GDDASI	0.76	0.03	GDDASI	0.63	0.07
PH	0.60	0.07	PH	0.68	0.06	PH	0.78	0.03	PH	0.66	0.07
EH	0.84	0.03	EH	0.86	0.02	EH	0.85	0.02	EH	0.86	0.03
TLN	0.91	0.01	TLN	0.91	0.02	TLN	0.85	0.02	TLN	0.88	0.02
Long-day environments											
GDDTA	0.96	0.01	GDDTA	0.96	0.01	GDDTA	0.92	0.01	GDDTA	0.92	0.01
GDDTS	0.96	0.01	GDDTS	0.93	0.01	GDDTS	0.91	0.01	GDDTS	0.90	0.02
GDDASI	0.83	0.03	GDDASI	0.80	0.03	GDDASI	0.80	0.03	GDDASI	0.76	0.04
PH	0.91	0.02	PH	0.92	0.01	PH	0.90	0.01	PH	0.79	0.03
EH	0.91	0.02	EH	0.92	0.02	EH	0.87	0.02	EH	0.84	0.03
TLN	0.91	0.02	TLN	0.93	0.01	TLN	0.89	0.02	TLN	0.88	0.02
Photoperiod response (long day - short day measurements)											
GDDTA	0.80	0.03	GDDTA	0.83	0.03	GDDTA	0.58	0.05	GDDTA	0.71	0.05
GDDTS	0.83	0.03	GDDTS	0.85	0.02	GDDTS	0.67	0.04	GDDTS	0.70	0.06
GDDASI	0.48	0.07	GDDASI	0.58	0.07	GDDASI	0.52	0.06	GDDASI	0.63	0.07
PH	0.58	0.07	PH	0.50	0.09	PH	0.75	0.03	PH	0.50	0.09
EH	0.63	0.06	EH	0.55	0.08	EH	0.63	0.05	EH	0.53	0.09
TLN	0.61	0.07	TLN	0.42	0.10	TLN	0.51	0.07	TLN	0.42	0.08

TABLE S6

Comparison of BIC values of connected and disconnected combined population analyses

			LOD Thresholds		Cofactor Thresholds (.9 *						
Trait	Env	Model	5%	1%	5% LOD)	Residual Variance	Total R^2	# QTL detected	Model Parameters	Residual SS	BIC
GDDTA	Short-day	Connected	7.42	8.99	6.68	484.68	0.25	5	19	264636	3600
GDDTA	Short-day	Disconnected	6.35	7.63	5.72	490.14	0.24	4	32	261247	3675
GDDTA	Long-day	Connected	7.72	9.26	6.95	1225.06	0.49	7	25	661532	4157
GDDTA	Long-day	Disconnected	6.45	7.60	5.80	1168.86	0.52	8	60	590274	4314
GDDTA	Photoperiodic	Connected	7.42	9.26	6.67	738.63	0.53	7	25	398858	3870
GDDTA	Photoperiodic	Disconnected	6.40	7.40	5.76	732.47	0.55	8	60	369897	4049
GDDTS	Short-day	Connected	6.73	8.09	6.05	714.87	0.31	7	25	386031	3852
GDDTS	Short-day	Disconnected	5.87	6.90	5.28	734.07	0.29	6	46	380982	3977
GDDTS	Long-day	Connected	6.79	7.65	6.11	1918.06	0.50	8	28	1029998	4426
GDDTS	Long-day	Disconnected	5.57	6.50	5.02	[a]	[a]	5	39	[a]	[a]
GDDTS	Photoperiodic	Connected	7.10	8.15	6.39	1347.05	0.52	6	22	731448	4194
GDDTS	Photoperiodic	Disconnected	5.97	6.77	5.37	1360.27	0.52	6	46	705980	4326
ASI	Short-day	Connected	7.00	8.09	6.30	159.93	0.33	7	25	86364	3004
ASI	Short-day	Disconnected	5.84	5.84	5.26	145.45	0.41	9	67	72436	3171
ASI	Long-day	Connected	7.06	8.62	6.36	428.23	0.38	7	25	231244	3562
ASI	Long-day	Disconnected	6.01	7.09	5.41	428.22	0.39	7	53	219248	3709
ASI	Photoperiodic	Connected	7.11	8.71	6.40	374.44	0.21	2	10	207815	3406
ASI	Photoperiodic	Disconnected	5.82	7.10	5.24	374.83	0.21	2	18	205033	3449
EH	Short-day	Connected	6.98	8.21	6.28	38.54	0.49	10	34	20463	2246
EH	Short-day	Disconnected	6.08	7.15	5.48	35.68	0.54	11	81	17268	2448
EH	Long-day	Connected	6.67	8.01	6.01	81.06	0.49	9	31	43284	2651
EH	Long-day	Disconnected	5.75	6.74	5.17	77.76	0.52	10	74	38181	2853
EH	Photoperiodic	Connected	6.67	7.41	6.00	51.93	0.25	3	13	28663	2304
EH	Photoperiodic	Disconnected	5.62	6.66	5.06	50.27	0.29	4	32	26792	2386

PH	Short-day	Connected	6.76	7.95	6.09	60.15	0.28	4	16	33021	2403
PH	Short-day	Disconnected	5.78	6.78	5.20	60.96	0.29	4	32	32490	2495
PH	Long-day	Connected	6.77	8.14	6.09	177.11	0.39	7	25	95640	3062
PH	Long-day	Disconnected	5.89	7.11	5.30	184.29	0.37	6	46	95645	3195
PH	Photoperiodic	Connected	6.82	7.77	6.14	116.19	0.29	6	22	63092	2807
PH	Photoperiodic	Disconnected	5.66	6.80	5.09	119.79	0.27	5	39	63008	2914
TLN	Short-day	Connected	7.51	8.91	6.76	0.62	0.39	8	28	335	-120
TLN	Short-day	Disconnected	6.47	7.75	5.82	*a*	*a*	*a*	4	*a*	*a*
TLN	Long-day	Connected	7.03	8.21	6.33	0.83	0.50	9	31	441	55
TLN	Long-day	Disconnected	6.31	7.32	5.68	0.82	0.51	9	67	410	242
TLN	Photoperiodic	Connected	6.72	8.18	6.05	0.41	0.45	7	25	219	-379
TLN	Photoperiodic	Disconnected	5.72	6.64	5.15	0.43	0.42	6	46	222	-238
Average over traits	All environments	Connected	7.02	8.31	6.31	439.88	0.39	6.61	23.83	237949	2728
Average over traits	All environments	Disconnected	5.98	6.99	5.38	372.77	0.40	6.47	46.78	192445	2935

Permutation analysis was used to estimate the genome-wide 1 and 5% LOD thresholds for each trait under each model. Based on the 5% threshold, the total # of QTL and their global R2 scores were computed. For each trait, the BIC was compared between the connected and disconnected analysis. The connected model produced the superior BIC value in every instance.

a These models would not converge using 5% LOD thresholds

TABLE S7

Chromosomal regions exhibiting segregation distortion within and across four RIL populations

Genome region		Allelic composition	
Bin	Flanking Markers	% Temperate	% Tropical
	B73 × CML254 Population		
4.06 - 4.08	PZA00057 - PZA02289	67	33
8.03	PZA01301 - PZA00908	40	60
9.02	PZA02624 - PZA00860	64	36
10.02	PHM3631 - PZA00463	63	37
10.04	PZA01089 - PZA00342	64	36
	CML254 × B97 Population		
8.03	PZA01301 - PZA02522	34	66
8.05-8.06	umc1316 - PZA03182	32	68
9.03 - 9.06	PZA02648 - PZA02235	60	40
10.02 - 10.05	PHM3765 - umc1506	69	31
	B97 × Ki14 Population		
9.01 - 9.02	PZA00285 - PZA01131	68	32
	Ki14 × B73 Population		
4.08 - 4.09	PZA02083 - PZA00694	33	67
	Combined across populations		
1.07	PZB01979 - PZA02186	63	37
8.03	PZA01209 - PZA01297	40	60
9.03	PZB00540 - PZB00547	59	41
10.03 - 10.04	PHM2828 - PZA02188	62	38

[a] Significant segregation distortion declared where $P<0.0025$ at more than three consecutive markers.

TABLE S8

Comparison of QTL from different photoperiodic, flowering time, and plant height studies

Candidate Genes			*id1*						*ZmLD*					
Bin[a]	**1.01**	**1.06**	**1.08**	**1.1**	**2.02**	**2.04**	**2.05**	**2.07**	**3.05**	**3.08**	**4.01**	**4.05**	**4.08**	**5.01**
Flowering Time						Short-Day QTL								
GDDTA[b]				0.07							0.04			0.05
GDDTS[b]			0.05	0.05										0.06
Wang *et al.* 2008									0.16					
Moutiq *et al.* 2002							0.11		0.11			0.08		
Briggs *et al.* 2007	0.02				0.02				0.06	0.01				
Height Traits														
PH[b]			0.05						0.08					
EH[b]				0.07					0.09					
Wang *et al.* 2008				0.09		0.05			0.29				0.07	
Briggs *et al.* 2007	0.02		0.06			0.02			0.11			0.02		0.06
TLN[b]		0.05	0.05			0.10								
Scale[c]	0-.049	.05-.099	.10-.149	.15-.199	.20-.249	.25-.299	.30-.349	.35-.399	.40-.449					

Candidate Genes			*id1*						*ZmLD*					
Bin[a]	**1.01**	**1.06**	**1.08**	**1.1**	**2.02**	**2.04**	**2.05**	**2.07**	**3.05**	**3.08**	**4.01**	**4.05**	**4.08**	**5.01**
Flowering Time		***ZmPR1***				Long-Day QTL								
GDDTA[c]		0.13[e]						0.09		0.07				
GDDTS[c]		0.08	0.06					0.09		0.05				
Wang *et al.* 2008												0.03	0.07	
Moutiq *et al.* 2002							0.07		0.05					
Briggs *et al.* 2007		0.03		0.03	0.02				0.05				0.02	0.01
Blanc *et al.* 2007	0.08	0.08				0.09			0.11	0.05		0.03		0.03
Chardon *et al.* 2004		x												
Height Traits														
PH[c]			0.09		0.04	0.05			0.09		0.05			
EH[c]				0.06				0.06	0.08		0.04			
Wang *et al.* 2008		0.09		0.07					0.04				0.13	
Briggs *et al.* 2007		0.02	0.05			0.01			0.08			0.03		0.04
TLN[c]		0.08					0.12		0.08					
Yi *et al.* 2006		x	x	x	x	x			x				x	
Flowering Time						Photoperiodic QTL								
GDDTA[d]		0.10						0.07	0.05				0.06	
GDDTS[d]		0.09						0.09	0.07					
Wang *et al.* 2008									0.03				0.06	
Moutiq *et al.* 2002														
Scale[e]	0-.049	.05-.099	.10-.149	.15-.199	.20-.249	.25-.299	.30-.349	.35-.399	.40-.449					

Candidate Genes									*Vgt1/Vgt2*		*Conz1*			*Zfl1*
Bin	**5.03**	**5.06**	**6.01**	**6.04**	**6.06**	**7.01**	**7.03**	**7.04**	**8.04**	**8.06**	**9.03**	**9.05**	**10.04**	**10.06**
Flowering Time	Short-Day QTL													
GDDTA[b]									0.08			0.06		
GDDTS[b]			0.05						0.08		0.08			0.05
Wang *et al.* 2008			0.08				0.08					0.07		
Moutiq *et al.* 2002											0.11			
Briggs *et al.* 2007				0.02		0.03		0.02			0.01			
Height Traits														
PH[b]									0.16					0.05
EH[b]		0.05	0.07	0.05			0.08		0.10	0.07			0.06	
Wang *et al.* 2008								0.04	0.03				0.02	
Briggs *et al.* 2007						0.03						0.02		0.01
TLN[b]	0.05	0.11					0.07			0.08			0.07	0.08
Scale	0-.049	.05-.099	.10-.149	.15-.199	.20-.249	.25-.299	.30-.349	.35-.399	.40-.449					

Candidate Genes									*Vgt1/Vgt2*		*Conz1*			*Zfl1*
Bin	**5.03**	**5.06**	**6.01**	**6.04**	**6.06**	**7.01**	**7.03**	**7.04**	**8.04**	**8.06**	**9.03**	**9.05**	**10.04**	**10.06**
Flowering Time					Long-Day QTL				***ZmPR2***		***ZmPR3***		***ZmPR4***	
GDDTA[c]		0.03							0.15		0.09		0.25	0.05
GDDTS[c]									0.09		0.07		0.28	0.05
Wang *et al.* 2008												0.10	0.37	
Moutiq *et al.* 2002									0.18		0.09		0.35	
Briggs *et al.* 2007					0.02	0.02			0.01		0.09		0.23	
Blanc *et al.* 2007			0.05						0.07				0.24	
Chardon *et al.* 2004									x x[f]		x		x	x
Height Traits														
PH[c]	0.06			0.04					0.10	0.06			0.05	
EH[c]								0.05	0.16	0.06		0.05	0.07	
Wang *et al.* 2008													0.20	
Briggs *et al.* 2007					0.02	0.04		0.03	0.04			0.07	0.03	0.01
TLN[c]		0.07	0.04				0.07		0.22		0.09		0.16	
Yi *et al.* 2006		x			x		x	x	x	x	x		x	
Flowering Time					Photoperiodic QTL									
GDDTA[d]									0.12		0.12		0.39	
GDDTS[d]									0.08		0.11		0.40	
Wang *et al.* 2008								0.02				0.07	0.33	
Moutiq *et al.* 2002									0.10		0.22		0.40	
Scale[e]	0-.049	.05-.099	.10-.149	.15-.199	.20-.249	.25-.299	.30-.349	.35-.399	.40-.449					

a Approximate bin number where QTL were located in each study according to flanking markers

b Traits measured by Coles et al. (2009) in short-day environments

c Traits measured by Coles et al. (2009) in long-day environments

d Traits measured by Coles et al. (2009) as the difference between long- and short-day environments

e R^2 value of each QTL as reported in each study

f Two separate QTL for flowering time were detected by Chardon et al. (2004) in this interval