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J.B. Holland · V.A. Portyanko · D.L. Hoffman
M. Lee

Genomic regions controlling vernalization and photoperiod responses in oat

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Abstract Oat genotypes vary for photoperiod and vernalization responses. Vernalization often promotes earlier flowering in fall-sown but not spring-sown cultivars. Longer photoperiods also promote earlier flowering, and the response to longer photoperiods tends to be greater in cultivars from higher latitudes. To investigate the genetic basis of photoperiod and vernalization responses in oat, we mapped QTLs for flowering time under four combinations of photoperiod and vernalization treatments in the Ogle × TAM O-301 mapping population in growth chambers. We also mapped QTLs for flowering time in early spring and late-spring field plantings to determine the genetic basis of response to early spring planting in oat. Three major flowering-time QTLs (on linkage groups OT8, OT31 and OT32) were detected in most conditions. QTLs with smaller effects on flowering were less-consistently observed among treatments. Both vernalization-sensitive and insensitive QTLs were discovered. Longer photoperiod or vernalization alone tended to decrease the effects of flowering-time QTLs. Applied together, longer photoperiod and vernalization interacted synergistically, often on the same genomic regions. Earlier spring planting conferred an attenuated vernalization treatment on seeds. The major flowering-time QTLs mapped in this study matched those mapped previously in the Kanota × Ogle oat mapping population. Between these two studies, we found a concordance of flowering-time QTLs, segregation distortion, and complex genetic linkages. These effects may all be related to chromosomal rearrangements in hexaploid oat. Comparative mapping between oat and other grasses will facilitate molecular analysis of vernalization response in oat.

Keywords *Avena* · Flowering · Mapping · QTLs

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J.B. Holland (✉)
USDA-ARS Plant Science Research Unit,
Department of Crop Science, Box 7620,
North Carolina State University, Raleigh, NC, USA 27695-7620
e-mail: James_Holland@ncsu.edu
Tel.: +1-919-5134198, Fax: +1-919-5157959

V.A. Portyanko
Department of Agronomy and Plant Genetics,
University of Minnesota,
411 Borlaug Hall, 1991 Buford Cresent, St.Paul, MN 50013, USA

D.L. Hoffman
USDA-ARS, National Small Grains Germplasm Research Facility,
P.O. Box 307, Aberdeen, ID 83210, USA

M. Lee
Department of Agronomy, Iowa State University,
Ames, IA 50010, USA

Introduction

Oat (*Avena sativa* L.) is a long-day plant; longer periods of light alternating with shorter periods of dark each day promote earlier flowering in most genotypes (Sorrells and Simmons 1992). Genotypes vary for responsiveness to photoperiods, however. Oat cultivars from higher latitudes often exhibit greater responses to photoperiod, flowering later under shorter daylengths relative to cultivars from lower latitudes (Sorrells and Simmons 1992). Oat genotypes also vary for response to vernalization, an exposure to cold temperatures during germination. Fall-sown "winter oat" cultivars generally require vernalization to promote flowering, whereas spring-sown oat cultivars respond less, if at all, to vernalization (King and Bacon 1992). Therefore, spring-sown North American oat cultivars tend to be more responsive to photoperiod but less responsive to vernalization compared to fall-sown North American cultivars. The genetic analysis of flowering time in oat is complicated by the frequent interaction of photoperiod and vernalization effects; for example, vernalization can reduce the photoperiod sensitivity of some genotypes (Sorrells and Simmons 1992).

Interactions between responses to photoperiod and vernalization have been dissected with molecular and genetic analysis of flowering-time mutants in *Arabidopsis*. Current models of flowering-time regulation in *Arabidopsis* propose that photoperiod and vernalization affect different signaling genes, but the gene regulation path-

ways initiated by these primary genes partially overlap, causing interactions between photoperiod and vernalization response signals (Koornneef et al. 1998; Levy and Dean 1998; Simpson et al. 1999; Blázquez and Weigel 2000; Samach et al. 2000). Flowering response results from an integration of environmental cues and genetic signals transmitted through both the vernalization and photoperiod response pathways and also distinct environmentally independent pathways (Levy and Dean 1998; Simpson et al. 1999). One approach to understanding the genetics of vernalization and photoperiod responses in oat is to identify oat genes orthologous to cloned *Arabidposis* flowering-time genes. Orthologues of the known *Arabidopsis* flowering-time genes may have similar functions in some grass species (Levy and Dean 1998), but none have yet been identified in oat.

Comparative mapping of flowering-time genes in the grasses represents another approach to understanding the vernalization and photoperiod responses in oat (Laurie 1997). Discrete, major genes affecting photoperiod and vernalization responses have been mapped in barley and wheat (Laurie 1997). The major vernalization response genes *Vrn-A1* and *Vrn-D1* from bread wheat (*Triticum aestivum* L.), *Vrn-H1* from barley (*Hordeum vulgare*), *Vrn-R1* from rye (*Secale cereale* L.) and *Vrn-A^{m}1* from *Triticum monococcum* are orthologous (Dubcovsky et al. 1998). Similarly, the photoperiod response genes *Ppd-H1* from barley and *Ppd* from wheat map to syntenous positions, suggesting that they are orthologous genes (Laurie 1997). Holland et al. (1997) mapped QTLs for vernalization response in the Kanota × Ogle oat mapping population. Dubcovsky et al. (1998) demonstrated that some of the QTLs identified by Holland et al. (1997) map to positions nearly syntenous to the *Vrn* genes of the other cereals, although they were not certain if the oat QTLs represented orthologs of the *Vrn* genes. Burrows (1986) identified a single dominant gene for insensitivity to daylength in oat, *Di1*, and Wight et al. (1994) identified genetic markers linked to *Di1*. Unfortunately, the chromosomal locations of these genetic markers are unknown, preventing comparative mapping of *Di1* relative to the photoperiod response genes of wheat and barley.

QTL mapping of photoperiod and vernalization responses can be used to directly identify genomic regions containing important flowering genes in oat. QTL results can vary across experiments and populations, however, because of genetic heterogeneity, genetic sampling, and genotype by environment interactions (Beavis 1994; Beavis and Keim 1996; Utz et al. 2000). Therefore, we set out to map QTLs for vernalization and photoperiod responses in the Ogle × TAM O-301 oat mapping population developed by Portyanko et al. (2001) in order to test if genomic regions containing flowering-time QTLs identified by Holland et al. (1997) and Siripoonwiwat et al. (1996) in the Kanota × Ogle mapping population would be consistently identified. In addition, the Ogle × TAM O-301 population is more suitable for comparative mapping because it is primarily based on DNA clones previously mapped in other grass species (Portyanko et al. 2001), permitting a better integration of QTL results and candidate gene information from related cereal crop species. The objectives of this study were to: (1) map QTLs for flowering time under field and greenhouse conditions representing different vernalization and photoperiod regimes in the Ogle × TAM O-301 oat mapping population, (2) identify QTLs for photoperiod and vernalization responses, and (3) compare QTLs across oat populations.

Materials and methods

Plant materials

A mapping population of 136 F_6-derived recombinant inbred lines (RILs) was developed by single-seed descent without selection from the cross of oat cultivars 'Ogle' and 'TAM O-301'. Ogle is adapted to spring sowing, whereas TAM O-301 was developed for fall sowing. A linkage map of the population was developed with 441 loci, primarily defined by restriction fragment length polymorphisms (Portyanko et al. 2001). The linkage map consisted of 34 linkage groups, ranging in map length from 4.2 to 174.0 cM.

Growth chamber experiment

An experiment was conducted in growth chambers to investigate the effects of different photoperiod and vernalization treatments on the lines of the mapping population. The parents and 101 randomly chosen RILs were included as entries in the growth chamber experiment. The experiment was a split-split-plot design with three replications. Photoperiod treatments were the whole-plot factor (assigned to different growth chambers), entries were subplot factors, and vernalization treatments were sub-sub-plot factors. Photoperiod treatments were long daylength (16-h photoperiod) and short daylength (11-h photoperiod for the first 60 days, followed by a 13-h photoperiod).

Six seeds of each entry were germinated by first placing them on filter paper soaked with distilled water at 21 °C for 12 h in dark; then transferring them to 6 °C for 21 days in the dark to be vernalized. Six non-vernalized seeds of each entry were germinated at 21 °C for 24 h in the dark. Vernalized and non-vernalized seeds were planted at the same time. Experimental units were 15-cm-diameter pots each containing three vernalized and three non-vernalized seeds of an entry. The potting medium consisted of 200 g kg^{-1} of soil, 400 g kg^{-1} canadian peat moss, and 400 g kg^{-1} of perlite. Pots were randomized within each growth chamber. Growth chambers maintained a constant temperature of 20 °C. Growth chamber lights were a combination of fluorescent and incandescent bulbs producing 960 μmol^{-2} s^{-1} of photon flux density. Pots were thinned to two plants per vernalization treatment approximately 14 days after planting. Days from emergence to flowering (emergence of the first node of the panicle above the flag leaf) were recorded on each plant.

Field experiment

Parent lines, 134 RILs, and eight check cultivars were included as entries in an experiment to measure differences in heading dates among lines in the field. Two RILs were not included in field experiments because of insufficient seed supplies. The experimental design was a split-plot with planting date as the whole-plot factor and entries as the sub-plot factor. Planting-date treatments were an early planting performed as soon as feasible in spring and a late planting 14 days later. Entries within whole-plots were arranged as 12 × 12 lattices. The experiment was replicated twice in 1996 and three times each in 1997 and 1998 at the Agronomy and Agricultural Engineering Research Farm near Ames, Iowa. Planting dates

were April 5 and April 19, 1996; April 3 and April 17, 1997; and April 13 and April 27, 1998. Heading date (date after planting on which the first nodes on half of the plants in the plot had emerged completely above the flag leaf) was measured on each plot.

Data analysis

Days to heading were converted to growing degree days (GDD) to heading using the formula developed by Wiggans (1956, cited in Sorrells and Simmons 1992). Mean daily maximum temperature at the research farm was recorded and heat units for each day were computed as the number of degrees above 4.4 °C. GDD to flowering were computed as the total number of heat units between planting and heading date for a plot. GDD to flowering was perfectly correlated with days to heading in growth chamber experiments because temperatures were constant through every day of the experiment. Therefore GDD for growth chamber experiments were computed by multiplying the number of days from emergence to heading by 15.6 °C, because the temperature was a constant 20.0 °C in the growth chambers. For comparing results of this study to those of Holland et al. (1997), we transformed their QTL-effect estimates from days to heading to growing degree days to heading by multiplying them by 16.6 °C because the maximum temperature was constant in the growth chambers through their experiment and averaged 21.0 °C among replicates.

Vernalization response in the growth chamber study was calculated for each line within each replication and photoperiod treatment as the mean GDD to flowering of non-vernalized plants minus the mean GDD to flowering of vernalized plants. Photoperiod response in the growth chamber study was calculated for each line within each replication and vernalization treatment as the mean GDD to flowering of plants grown in short daylengths minus the mean GDD to flowering of plants grown in long daylengths. Thus, a positive response to vernalization signifies that vernalized plants flowered earlier than non-vernalized plants; a positive response to photoperiod signifies that plants grown under long daylengths flowered earlier than plants grown under short daylengths. Planting-date response in the field study was measured within each replication as the difference in GDD to flowering between early and late-planting treatments. A positive planting-date response indicates that the line required fewer GDD to flower when planted early than when planted late.

For QTL analysis, GDD to flowering under different treatments were considered separate traits. The following traits were mapped: EFLD: GDD to flowering when planted at the early sowing date in the field, LFLD: GDD to flowering when planted at the late sowing date in the field, FLDATE: response to early planting in the field = EFLD – LFLD, NLGC: GDD to flowering in non-vernalized, long-day photoperiod growth-chamber conditions, NSGC: GDD to flowering in non-vernalized, short-day photoperiod growth-chamber conditions, VLGC: GDD to flowering in vernalized, long-day photoperiod growth chamber-conditions, VSGC: GDD to flowering in vernalized, short-day photoperiod growth-chamber conditions, VERN: vernalization response, the mean difference between GDD to flowering under non-vernalized and vernalized conditions in growth-chamber conditions, PHOTO: photoperiod response, the mean difference between GDD to flowering under short-day and long-day photoperiod growth-chamber conditions.

Mixed linear-model analyses were performed for each experiment. Replications (and incomplete blocks and years in the field experiment) were considered random effects. Treatments and entries were considered as fixed effects. Least-square means were estimated for each entry and treatment combination. Heritabilities on a line-mean-basis were estimated by excluding parental and check cultivars and considering RILs to be random effects. Approximate standard errors for heritability estimates were obtained with the delta method (Lynch and Walsh 1998).

QTL analysis was performed using PLABQTL software (Utz and Melchinger 1996). The first steps of the analysis were to perform simple interval analysis and composite interval analysis, with cofactors chosen with stepwise regression (using the default value of F = 3.5 to enter the model). The marker loci nearest to putative QTLs detected by either of these methods were then used as cofactors in a second round of composite interval mapping. If new putative QTL positions were detected, these were then fitted as cofactors in a third round of composite interval mapping. This procedure was iterated until no new putative QTL positions were detected. If different sets of QTLs were discovered with the different methods or in different iterations of composite interval mapping, models with different subsets of putative QTLs were tested. The model with minimum Akaike's information criterion (Lynch and Walsh 1998), and all factors fitting with significant (P = 0.05) effects for a trait, was selected as the best-fitting main-effect QTL model for that trait.

Epistatic interactions between QTLs were detected using the Epistacy routine (Holland 1998) in SAS. Updated SAS code for EPISTACY is available at http://www4.ncsu.edu/~jholland/Epistacy/epistacy.htm. Epistatic interactions were declared significant if they exceeded the threshold of $P < 0.0001$. This threshold was computed as a Bonferroni adjustment of the comparison-wise error rate to account for the 561 pairs of comparisons made between the 34 linkage groups of the genetic map. Epistatic interactions were then mapped more precisely using PLABQTL by searching for the most-significant interaction between positions at 5-cM intervals between the marker loci detected with epistacy and their flanking markers.

Epistatic interactions were added to the best main-effect QTL models already selected by including the pair of QTL positions defining each interaction along with the QTL positions from the best main-effect QTL model in a PLABQTL sequence statement with the additive by additive epistatic interaction model. Backward stepwise regression was used to identify the best model including epistatic interactions for each trait. The model with a minimum Akaike's information criterion and all factors fitting with significant (P = 0.05) effects, except for main effects of significant interactions, was selected as the best-fitting QTL model. Partial r^2 values were calculated for each QTL main effect and interaction in the final model as the ratio of the partial sum of squares for the effect divided by the total sum of squares (Holland et al. 1997). This is not equivalent to the default partial r^2 statistic computed by PLABQTL. We chose to use the statistic as defined by Holland et al. (1997) because the sum of the partial r^2 values computed in this way (in contrast to the PLABQTL method) will not exceed the R^2 for the full model.

Uncertainty of the map positions of QTLs is illustrated with boxes spanning 20 cM and centered on the maximum-likelihood position of each QTL. In reality, the precision of QTL positions can vary within the same study and confidence intervals are not necessarily symmetrically distributed around the maximum-likelihood position. Unfortunately, however, procedures to estimate confidence intervals for QTLs detected with composite interval mapping are unknown, and LOD-support intervals from interval mapping are downward-biased estimators of confidence intervals (Visscher et al. 1996). Therefore, we followed Cardinal et al. (2001) in using 20-cM approximate confidence intervals to indicate that QTL positions are not known with certainty.

Results

Growth chamber experiment

The main effects of vernalization and photoperiod treatments as well as their interaction were highly significant ($P < 0.01$). The average effect of vernalization was to reduce days to heading from 1,226 GDD (78.6 days) to 1,089 GDD (69.8 days) after emergence. The average effect of long daylength photoperiods was to reduce days to heading from 1,496 GDD (95.9 days) after emergence to 819 GDD (52.5 days) after emergence. The interaction

Table 1 Parental line means, difference of parental line means, recombinant inbred line (RIL) population mean, extremes of the RIL population, least significant difference (LSD) for line mean comparisons, heritability of line means (and their standard errors), and adjusted R^2 values of best multiple QTL models including or excluding epistasis for each of nine flowering-time traits measured on 133 RILs in early and late-field plantings, and on 100 RILs in short-day and long-day photoperiod growth chambers with or without vernalization

Item	Heading date in field experiments			Heading date in growth chamber experiments					
				Non-vernalized treatment		Vernalized treatment		Means across vernalization treatments	
	Early planting (EFLD)	Late planting (LFLD)	Response to early planting (FLDATE)	Long daylength (NLGC)	Short daylength (NSGC)	Long daylength (VLGC)	Short daylength (VSGC)	Vernalization response (VERN)	Photoperiod response (PHOTO)
GDD									
TAM O-301	1,320	1,382	61	1,037	1,710	725	1,268	367	597
Ogle	1,273	1,230	–45	744	1,376	733	1,365	12	633
TAM O-301 - Ogle	47	152*	106*	293*	334*	–8	–97	355*	–36
RIL population mean	1,327	1,371	44	880	1,569	757	1,421	137	683
RIL minimum	1,057*	1,111*	–60	652	1,175*	593	1,175	27	440*
RIL maximum	1,584*	1,670*	142*	1,239*	2,218*	955*	1,713*	515*	1,151*
LSD (0.05)	117	107	79	147	151	145	153	133	170
Heritability of line means	0.92 (0.01)	0.89 (0.02)	0.58 (0.07)	0.84 (0.03)	0.89 (0.02)	0.93 (0.01)	0.85 (0.03)	0.85 (0.02)	0.75 (0.16)
Full-model adjusted R^2 including epistasis	0.61	0.66	0.53	0.73	0.59	NA[a]	0.30	0.68	NA
Full-model adjusted R^2 without epistasis	0.59	0.61	0.45	0.68	0.52	0.62	0.19	0.62	0.18

*Significantly different from both parental means at $P \leq 0.05$
[a] NA, not applicable because the best model did not include epistasis

Table 2 Correlations among growing degree days to flowering measured in growth-chamber and field experiments based on means of 101 to 134 recombinant inbred lines and parents of the Ogle TAM O-301 mapping population

Trait	Heading date in field experiments		Heading date in growth-chamber experiments					
			Non-vernalized treatment		Vernalized treatment		Means across vernalization treatments	
	Late planting (LFLD)	Response to early planting (FLDATE)	Long daylength (NLGC)	Short daylength (NSGC)	Long daylength (VLGC)	Short daylength (VSGC)	Vernalization response (VERN)	Photoperiod response (PHOTO)
EFLD	0.94****	0.28 ***	0.77****	0.72****	0.85****	0.69****	0.45****	0.35***
LFLD		0.58****	0.82****	0.78****	0.75****	0.63****	0.60****	0.36***
FLDATE			0.54****	0.56****	NS[a]	NS	0.69****	0.21*
NLGC				0.80****	0.63****	0.53****	0.81****	0.28**
NSGC					0.49****	0.77****	0.81****	0.67****
VLGC						0.61****	NS	NS
VSGC							0.29**	0.72****
VERN								0.43****

*, **, ***, **** Significant at $P \leq 0.05$, 0.01, 0.001, or 0.0001, respectively
[a] NS, not significant at $P \leq 0.05$

between vernalization and photoperiod treatments was due to a difference in the magnitude of the vernalization effect under the different photoperiod treatments: vernalization reduced heading by 123 GDD (7.9 days) under long daylengths, and by 151 GDD (9.7 days) under short daylengths. The main effect of entry, the interaction of entry and vernalization and the interaction of entry and photoperiod were all significant ($P < 0.0001$) for heading date. The three-way interaction of entry, vernalization, and photoperiod, however, was not significant ($P = 0.97$).

The parental line responses to photoperiod and vernalization generally followed the trend of the overall means. Without vernalization, Ogle flowered 293 (18.8 days) and 334 GDD (21.4 days) earlier than TAM O-301 ($P < 0.05$) under long- and short-day photoperiods, respectively (Table 1). With vernalization, however, there were no significant differences between Ogle and TAM O-301 under either photoperiod (Table 1). Parents did not differ for photoperiod response (Table 1). Transgressive segregation for later flowering was observed

Table 3 Effects on flowering time at photoperiod-sensitive QTL positions estimated by simple interval mapping in the Ogle × TAM O-301 mapping population under different combinations of photoperiod and vernalization treatments in growth chambers

QTL position		Growing degree days to flowering in growth-chamber experiments						
Linkage group	Map position (cM)	Non-vernalized treatment			Vernalized treatment			Mean response to photoperiod (PHOTO)
		Short daylength (NSGC)	Long daylength (NLGC)	NSGC – NLGC	Short daylength (VSGC)	Long daylength (VLGC)	VLGC – VSGC	
OT2	4	62*	21 NS[a]	40	33*	10 NS	23	28*
OT8	110	–50*	–26 NS	–24	–35**	–20*	–15	–29*
OT19	4	14 NS	0 NS	14	6 NS	–10 NS	16	21 NS
OT31	130	145**	87**	58	36**	13 NS	23	37**

*, ** Significant at 0.05 and 0.01 probability levels, respectively
[a] NS, not significant at the 0.05 probability level

under all treatments, whereas transgressive segregation for earlier flowering was observed only under non-vernalized, short daylength conditions (Table 1). Transgressive segregation was also observed for greater vernalization and photoperiod responses. The RIL means were approximately normally distributed, but with a skew toward earlier flowering and a longer tail for late flowering for heading date under all treatments.

Field experiment

The main effect of early planting on the RIL population mean was to decrease GDD to flowering from 1,371 to 1,327 averaged over years, but this was not significant. The effect of planting date was significant ($P < 0.01$) and consistent within 1997 and 1998, however. Both entry and entry by planting date interactions were significant ($P < 0.01$) within each year and in the combined analysis. Averaged over years, Ogle and TAM O-301 did not differ for GDD to heading date when planted early, but Ogle flowered 152 GDD (6.1 days) earlier than TAM O-301 when both were planted late ($P < 0.05$).

Trait correlations

Many positive correlations were observed among the traits measured in the growth chamber and field studies (Table 2). Early planted field flowering (EFLD) was most highly correlated with late-planted field flowering (LFLD) and vernalized long-daylength growth chamber flowering (VLGC, Table 2). LFLD was most highly correlated with EFLD and non-vernalized long-daylength growth chamber flowering (NLGC, Table 2). Response to early planting in the field was most highly correlated with vernalization response (Table 2).

QTLs for flowering time in the Ogle × TAM O-301 population

The number of QTLs with significant main effects detected ranged from four (for PHOTO) to ten (for EFLD). Multiple QTL models explained from 18% (for PHOTO) to 73% (for NLGC) of the variation in heading-date traits (Table 1). The difference between heritability on a line-mean basis and the multiple QTL model-adjusted R^2 values ranged from to 5 (for FLDATE) to 57 (for PHOTO) percentage points (Table 1). This suggests that some QTLs remained undetected, and that we did not overfit the multiple QTL models.

Several genomic regions exhibited consistently strong effects on multiple traits. The most-important QTL region was on linkage group OT31 (Fig. 1). QTLs for seven of the nine traits were detected in this region. The partial r^2 for this QTL ranged from 7% (for EFLD) to 28% (for FLDATE and NSGC). The TAM O-301 allele at this QTL increased GDD to flowering, particularly when plants were not vernalized. When plants were vernalized in the growth chamber study, the effect of this QTL was reduced or not detected (Tables 3 and 4), suggesting that the effect of vernalization on this QTL was to eliminate the late-flowering effect of the TAM O-301 allele.

Another major QTL was detected on OT32. The TAM O-301 allele at this QTL delayed heading at both planting dates in the field and also in the long-day photoperiod growth chambers (Fig. 1). Vernalization did not alter the effect of this QTL; therefore it represents a flowering-time QTL that acts independently of vernalization. Although this QTL was detected only in the field and in the long-day photoperiod growth-chamber treatments, we found no evidence that it was a photoperiod-responsive QTL. Marker loci in the region of this QTL had significant or nearly significant ($P < 0.06$) effects on heading time in short-day photoperiods, but the effects were not large enough to be included in the final models for these traits. Similarly, the effect of the major QTL on OT34 was consistent across photoperiod and vernalization treatments, although below the threshold of statistical significance in all but vernalized, long-day photoperiod treatments.

A QTL on OT8 was detected for GDD to flowering under all treatments except for vernalized short-day growth chamber conditions (Fig. 1). In fact, however, the QTL effect increased under short-day photoperiod conditions (Table 3), although it was not included in the best

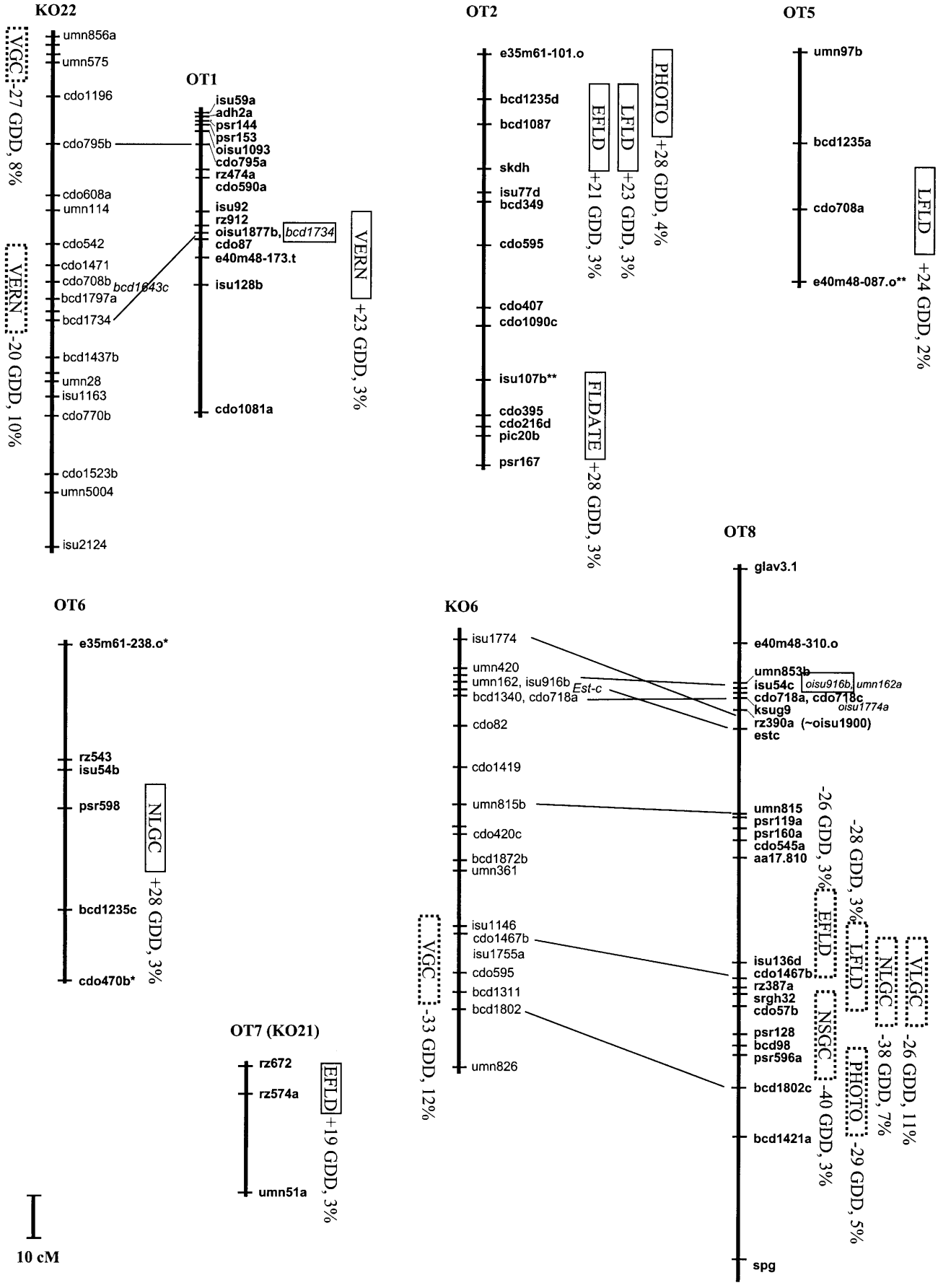
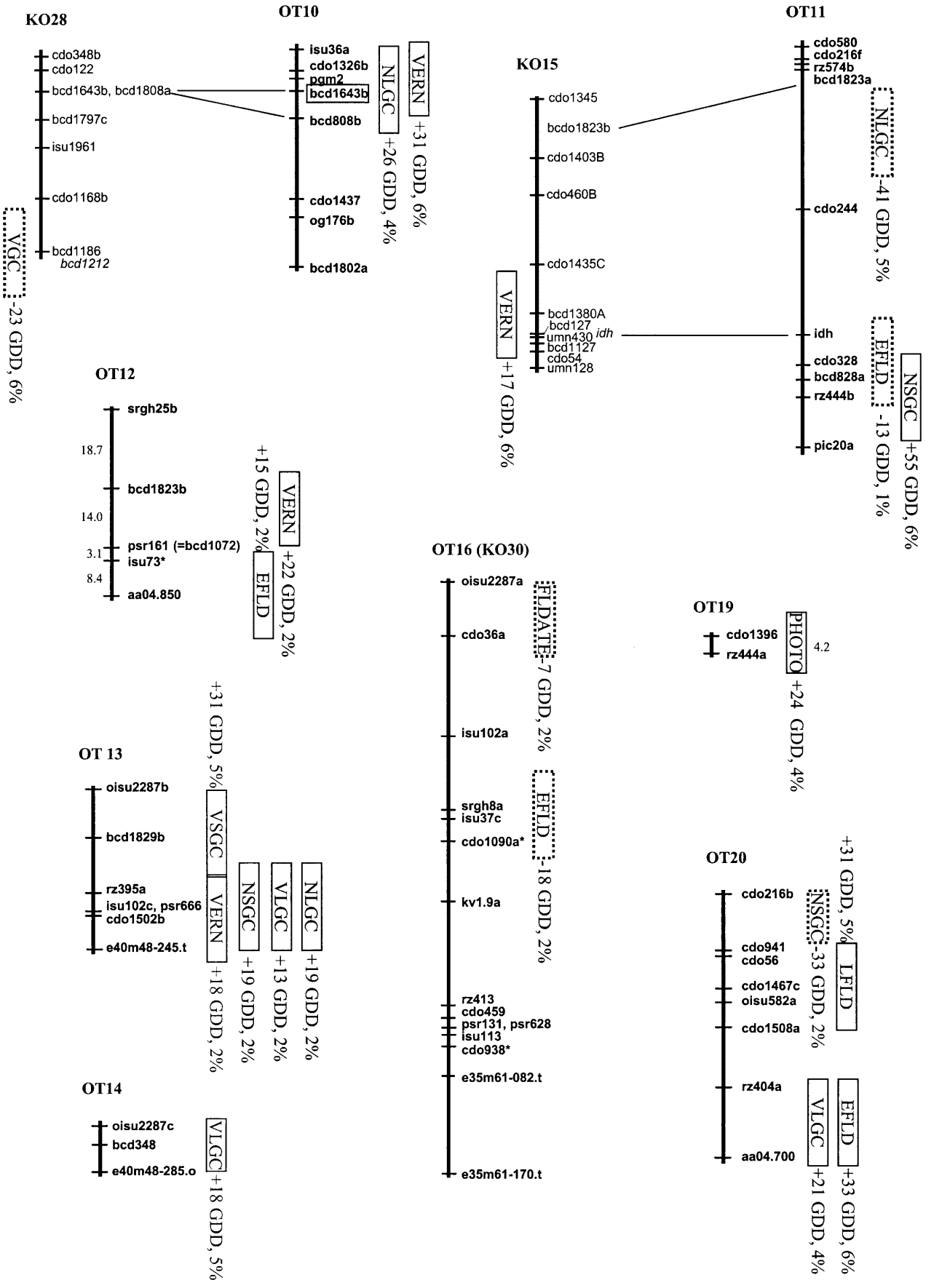


Fig. 1 Legend see page 121



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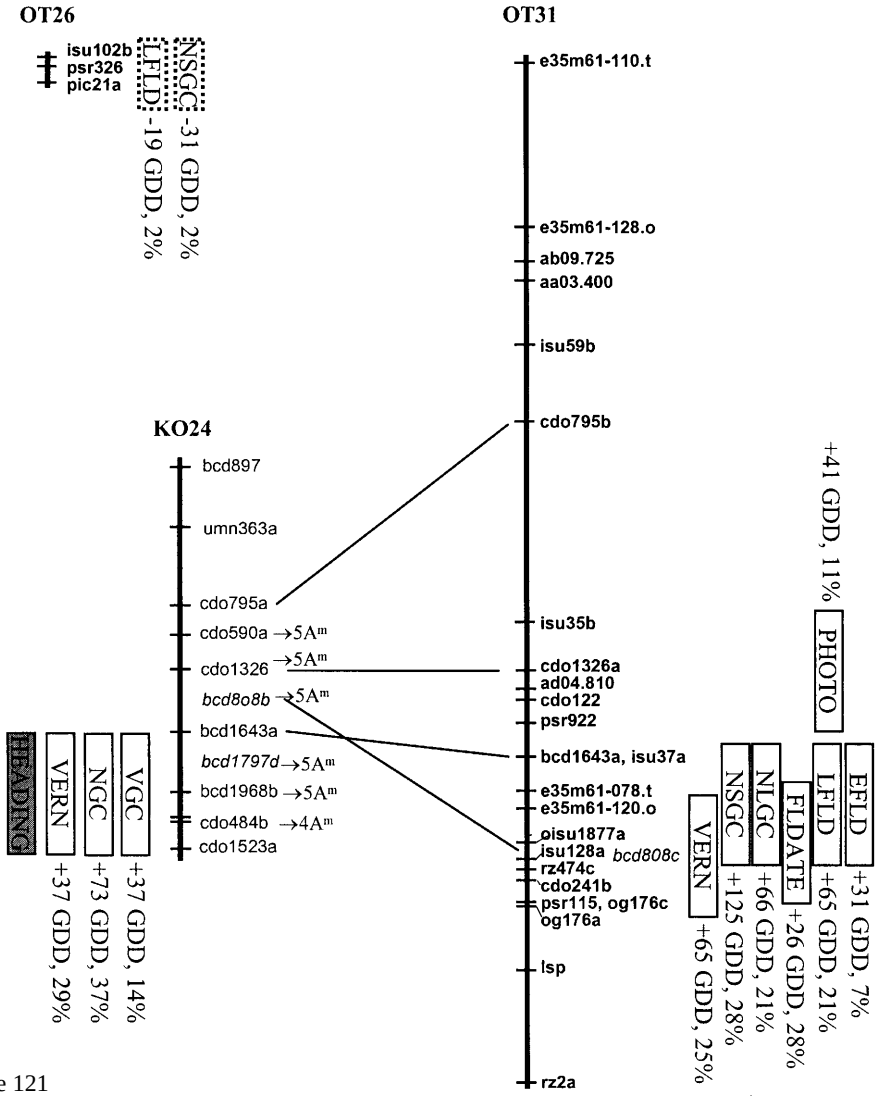

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multiple QTL model for VSGC. This QTL was therefore detected as a photoperiod response QTL (Fig. 1). In contrast to the other major QTLs, the Ogle alleles at this QTL on OT8 and at the QTL on OT34 increased GDD to flowering (Fig. 1).

In general, the major QTLs (on OT8, OT31, OT32 and OT34) were detected across treatments with reasonable consistency, although we found good evidence that the effects of some of these QTLs were altered by environmental conditions. The QTL on OT8 can be described as a photoperiod-sensitive QTL, and the QTL on OT31 is a vernalization-sensistive QTL, whereas the QTLs on OT32 and OT34 represent QTLs for flowering-time *per se* that are relatively unaffected by changes in photoperiod or temperature. In contrast, minor QTLs were detected less consistently across environmental treatments, suggesting that allelic differences between minor QTLs for flowering time are expressed (or exaggerated to the point at which they are detectable) only under specific conditions.

Coincidence of vernalization-responsive and photoperiod-responsive QTLs

To investigate the effects of photoperiod and vernalization treatments on flowering-time QTLs in regions associated with responses to these treatments, simple interval mapping was used to estimate the effects of these regions under each combination of treatments in the growth chamber study (Tables 3 and 4). QTLs for photoperiod response overlapped with other flowering-time QTLs on OT2, OT8 and OT31 (Fig. 1). At each of these regions, the effect of long-day photoperiod was to decrease the QTL effect on flowering time (Table 3). QTLs for vernalization response overlapped with other flowering-time QTLs on OT10, OT13 and OT31 (Fig. 1). In these regions, the effect of vernalization was to decrease the QTL effect on flowering time (Table 4).

QTLs for vernalization response overlapped with QTLs for photoperiod response only at OT31 (Fig. 1). The effect of vernalization was to decrease the QTL's

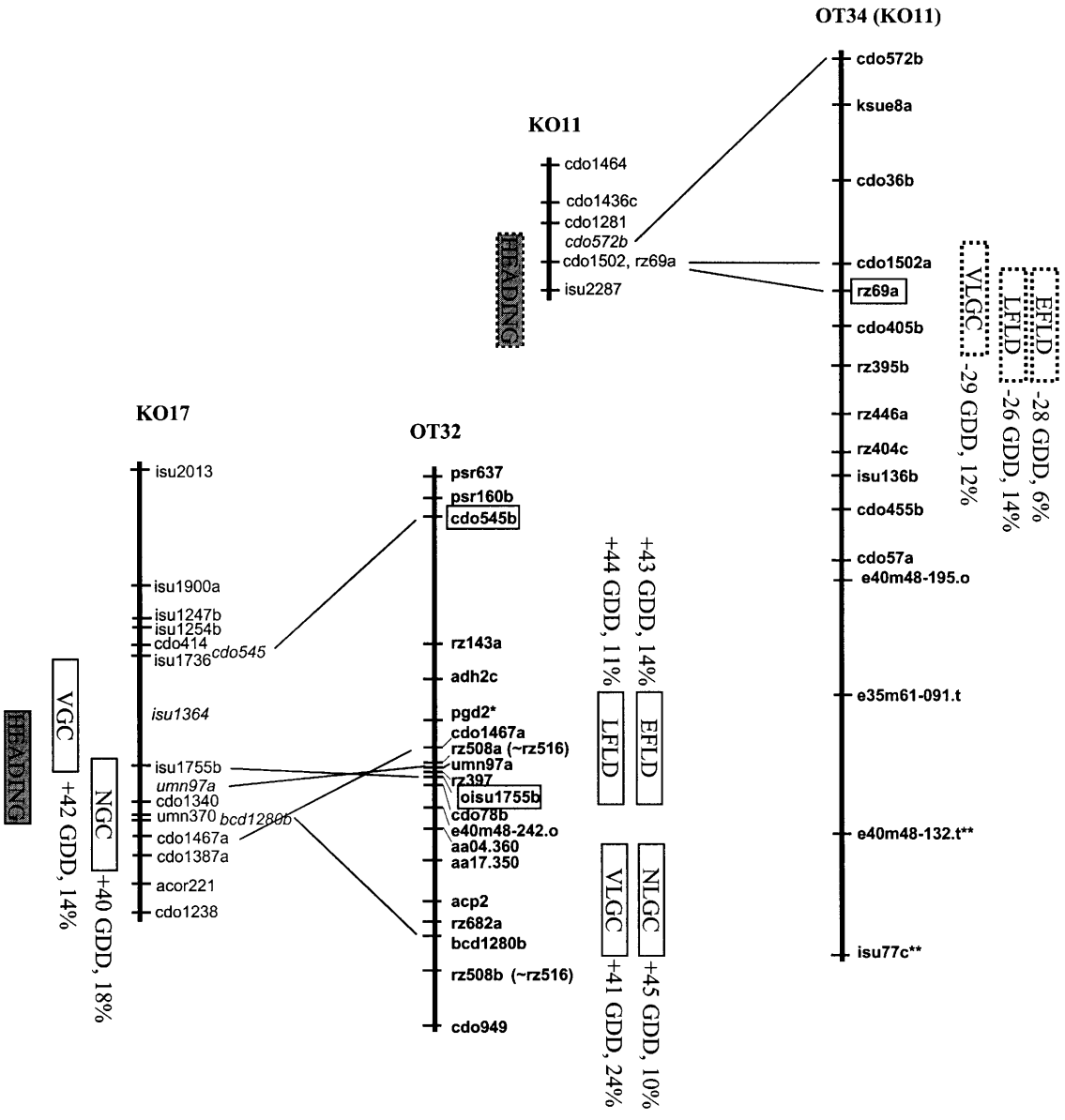

Fig. 1 Flowering-time QTL positions superimposed on the linkage map of hexaploid oat constructed using 136 $F_{6:7}$ recombinant inbred lines from the cross Ogle × TAM O-301 and alignment of homologous or homoeologous linkage groups from the Ogle × TAM O-301 and Kanota × Ogle oat maps containing flowering-time QTLs. Maps are drawn to scale. Only loci assigned to unique positions at LOD > 2.0, demonstrating synteny, or nearest to the most-likely QTL positions, are shown on Kanota × Ogle linkage groups. Probes that produced banding patterns identical to clones included in the framework map are shown in parentheses with the "=" sign. Probes sharing all except one DNA fragment with framework markers are shown in parentheses with the "~" sign. Loci demonstrating segregation distortion at $P = 0.05$ or $P = 0.01$, are marked with * and **, respectively. Marker loci *inside boxes* represent homologues of loci mapped in the Kanota × Ogle oat population. *Arrows* on KO linkage group 24 indicate loci that map to *T. monococcum* chromosomes $5A^m$ or $4A^m$, in the region of a translocation breakpoint and a major vernalization gene (Dubcovsky et al. 1998). *Boxes to the left* of KO linkage groups and *to the right* of OT linkage groups represent the QTL for the flowering-time trait indicated in the box. VGC and NGC represent QTLs for flowering time under vernalized and non-vernalized growth chamber conditions, respectively, in the Kanota × Ogle population. *Shaded boxes* labeled HEADING represent QTLs for flowering time measured in the field by Siripoonwiwat et al. (1995). QTL boxes are centered on the most-likely QTL positions and extend 10 cM to either side of the most-likely position, representing typical QTL confidence intervals. *Boxes composed of solid lines* represent QTLs at which the Ogle allele promoted shorter time to flowering or lower vernalization or photoperiod response. *Boxes composed of dashed lines* represent QTLs at which the Ogle allele promoted longer time to flowering or greater vernalization or photoperiod response

Table 4 Effects on flowering time at vernalization-sensitive QTL positions estimated by simple interval mapping in the Ogle × TAM O-301 mapping population under different combinations of photoperiod and vernalization treatments in growth chambers

QTL position		Growing degree days to flowering in growth-chamber experiments						
Linkage group	Map position (cM)	Short daylength treatment			Long daylength treatment			Mean response to vernalization (VERN)
		Non-vernalized (NSGC)	Vernalized (VSGC)	NSGC – VSGC	Non-vernalized (NLGC)	Vernalized (VLGC)	NLGC – VLGC	
OT1	34	56*	15 NS[a]	41	40**	14 NS	26	34**
OT10	6	62*	14 NS	48	33*	0 NS	33	41**
OT12	24	47 NS	14 NS	33	19 NS	–11 NS	30	33*
OT13	30	49*	24 NS	25	28*	14 NS	14	21 NS
OT31	136	126**	26*	100	75**	7 NS	68	85**

*, ** Significant at 0.05 and 0.01 probability levels, respectively
[a] NS, not significant at the 0.05 probability level

photoperiod response, and the effect of long daylengths was to decrease the QTL's vernalization response (Table 4). Thus, at this QTL region, the effects of photoperiod and vernalization treatments were mutually reinforcing. Since the other photoperiod and vernalization QTLs did not overlap, it is tempting to speculate that they represent regions controlling independent responses to different environmental cues. This may be an artifact of the statistical inability to detect numerous QTLs with small effects in the limited population size used, however. Vernalization consistently decreased the effect of photoperiod response QTLs (Table 3) and long daylengths decreased the effect of vernalization response QTLs (Table 4). This result suggests that long daylengths and vernalization are required together to fully minimize the effects of most genes that confer late flowering in response to these environmental cues. In contrast, the effects of short days and lack of vernalization were to maximize the phenotypic effects of photoperiod and vernalization responsive QTLs. This resulted in the significant interaction between photoperiod and vernalization treatment main effects.

Epistatic interactions among QTLs

Including epistatic interactions in multiple-QTL models increased their explanatory power for seven of nine traits (Table 1). When epistatic terms were included in the final model, adjusted R^2 values increased from 2 (for EFLD) to 11 (for VSGC) percentage points (Table 1). Most epistatic interactions had relatively small partial r^2 values (7% or less) except for the interaction between QTLs on OT32 and OT34 for VSGC (partial r^2 = 10%, Table 5). Epistatic interactions were not consistent across traits. The only epistatic interactions that were detected for more than one trait were the interactions between QTLs on OT8 and OT11 (for EFLD and NLGC) and on OT10 and OT13 (for NLGC and VERN, Table 5).

Correspondence of QTLs with segregation distortion

Portyanko et al. (2001) observed that several regions of the Ogle × TAM O-301 map exhibited segregation distortion. The most-severely distorted segment is on OT31, in which many loci had an excess of the TAM O-301 genotype. Similarly, parts of OT32 and OT12 had an excess of the TAM O-301 genotype. Major QTLs were detected on both OT31 and OT32 in the distorted regions, and minor QTL effects were observed for EFLD and VERN in the region of segregation distortion on OT12 (Fig. 1). In addition, segregation distortion in which the Ogle allele was in excess was detected on OT8, OT16 and OT34 (Portyanko et al. 2001). QTLs were detected in all of these regions as well (Fig. 1). In each of these cases, the allele in excess, whether from Ogle or TAM O-301, caused later flowering.

We also observed that the major QTLs detected in this study map to those linkage groups that caused difficulties during linkage-map construction (OT8, OT31, OT32 and OT34, Portyanko et al. 2001). OT1 and OT8 originally contained many loci because of putatively spurious linkages. To resolve disagreements in the two-point and three-point orders, these linkage groups were split into smaller groups at a higher linkage stringency. The resulting linkage groups were OT31, OT32, and OT33 from OT 1 and OT34 from OT8. All of these linkage groups except OT33 had QTLs for flowering traits.

Discussion

Comparisons of flowering-time QTLs detected under different conditions

The mean effect of early planting was to reduce the number of growing degree days from planting to flowering because early planted seeds were exposed to sufficiently cold temperatures in their early development that some vernalization could occur. Photoperiod and temperature differences were confounded in the field experiment,

Table 5 Epistatic effects contributing to best multiple QTL models for flowering-time traits measured on 134 recombinant inbred lines of the Ogle × TAM O-301 mapping population grown in the field across 3 years and on 101 random lines grown in growth chambers

QTL peak position		Nearest marker locus	Additive or additive by additive effect	Partial R^2
Linkage group	Position (cM)			
			GDD	
Early field planting (EFLD)				
8	84	ISU136D	–26	0.03
11	77	CDO328	–13	0.01
		QTL8 × QTL11	–20	0.02
Late-field planting (LFLD)				
7	0	RZ672	NS[a]	0.01
13	10	BCD1829B	NS	0.00
		QTL7 × QTL13[b]	–29	0.04
Response to early field planting (FLDATE)				
2	86	CDO395	6	0.01
4	93	CDO20	NS	0.00
		QTL2 × QTL4	–10	0.04
1	2	PSR144	NS	0.00
16	5	OISU2287A	–7	0.02
		QTL1 × QTL16	10	0.04
Nonvernalized, long-day photoperiod growth chamber (NLGC)				
8	94	CDO1467B	–38	0.07
11	77	CDO328	NS	0.01
		QTL8 × QTL11/77	–21	0.02
10	10	BCD1643B	26	0.04
13	28	ISU102C	19	0.02
		QTL10 × QTL13	23	0.03
Nonvernalized, short-daylength photoperiod growth chamber (NSGC)				
20	0	CDO216B	–33	0.02
31	128	E35M61120.O	125	0.28
		QTL20 × QTL31	–62	0.07
Vernalized, long-day photoperiod growth chamber (VLGC)				
No epistatic effects				
Vernalized, short-day photoperiod growth chamber (VSGC)				
4	62	CDO618	NS	0.02
16	70	KV1.9A	NS	0.02
		QTL4 × QTL16	–36	0.05
32	4	PSR160B	NS	0.00
34	140	E40M48132.T	NS	0.01
		QTL32 × QTL34	44	0.10
Vernalization response (VERN)				
10	6	Pgm2	31	0.06
13	30	CDO1502B	18	0.02
		QTL10 × QTL13	27	0.04
2	80	ISU107B	NS	0.00
28	26	RZ538	NS	0.00
		QTL2 × QTL28	–30	0.04
Photoperiod response (PHOTO)				
No epistatic effects		28		0.04

[a] NS, main effect of epistatic QTL not significant at $P \leq 0.05$ in the final model

[b] QTL*i* × QTL*j*, epistatic interaction effect of QTL on OT*i* and QTL on Ot*j* detected for the trait indicated

when comparing early and late-planting treatments. Nevertheless, the higher correlation between FLDATE and VERN (Table 2) suggests that temperature difference was the primary agent causing planting date response. The mean daylengths of the first 14-day period following the early planting date and the first 14-day period following the late planting date differed by only 35–37 min within each year of the experiment. In contrast, across the 3 years of the field experiment, average minimum daily temperatures at a 25-mm depth in the soil were 3.6 °C for the first 2 weeks after early planting and 6.6 °C after late planting.

Mean photoperiods in the field experiment ranged from 12 h 42 min in April to 15 h 12 min in June, when most genotypes flowered. These daylengths explain why the field flowering times were best correlated to long-

daylength growth chamber flowering times (Table 2). Time to flowering under early planting in the field was best correlated with time to flowering following vernalization in the long-daylength growth chamber, and time to heading in the late planting in the field was best correlated with heading in the long-daylength growth chamber in the absence of vernalization. These results further support the suggestion that the genetically controlled planting-date response observed in the field was primarily an attenuated vernalization response, in combination with smaller genetically controlled responses to other, unidentified, environmental effects.

QTL comparisons between Kanota × Ogle and Ogle × TAM O-301 populations

The Ogle × TAM O-301 (OT) and Kanota × Ogle (KO) maps share a common parent; therefore some homologous RFLP loci could be identified between the two maps (Portyanko et al. 2001). Seven flowering-time QTL regions mapped by Holland et al. (1997) and four mapped by Siripoonwiwat et al. (1996) in the Kanota × Ogle population can be unequivocally aligned with the Ogle × TAM O-301 map based on homologous RFLP loci. Four of the seven QTL regions mapped by Holland et al. (1997) in the KO map (on KO6, KO17, KO22 and KO28) are homologous to linkage groups containing flowering time QTLs in the OT population (Fig. 1). Three of the four QTL regions mapped by Siripoonwiwat et al. (1996) (on KO11, KO17 and KO24) also are homologous to QTL regions identified in the OT population (Fig. 1). Not all QTLs mapped on homologous linkage groups in the two populations were found in both populations, however. Holland et al. (1997) mapped QTLs on KO23 (homologous to OT15), and KO33 (homologous to OT30), and both Holland et al. (1997) and Siripoonwiwat et al. reported a flowering-time QTL on KO3 (homologous to OT3) but no corresponding loci were detected in the OT population. Similarly, two QTLs regions on the OT map that are homologous with linkage groups on the KO map (OT7 with KO21 and OT16 with KO30) lacked corresponding QTLs on the KO map.

In general, the most-important QTLs in the two populations mapped to similar genomic positions. For example, the largest effects tended to be on OT31 and OT32, and both of these regions matched the KO heading-date QTL positions detected by Holland et al. (1997) and also by Siripoonwiwat et al. (1996), who mapped QTLs for flowering date in the KO population grown in the field at Aberdeen, Idaho for 4 years and Ithaca, N.Y., for 3 years. QTLs that did not match between the two populations tended to have smaller effects. Likewise, the gene action effects of the major QTLs were similar in the two populations, but the effects of minor QTLs were less consistent. For example, a vernalization response QTL on OT1 mapped to the same region as a vernalization QTL on KO22, but the effects of the Ogle allele relative to the other parental allele at this QTL were opposite in the two populations. In the OT population, the Ogle allele at this QTL region significantly decreased flowering time ($P \leq 0.05$, based on single-factor ANOVA for both long-day and short-day photoperiod treatments) under non-vernalized growth chamber conditions, but had no significant effect under vernalized conditions. Thus, a positive vernalization-response effect was detected at this region in the OT population. In the KO population, however, the effect of the Ogle allele in this region changed from increasing flowering time under non-vernalized conditions to decreasing flowering time under vernalized conditions, resulting in a negative vernalization response (Holland et al. 1997). Considering the vernalization response of an allele as a shift from conferring later flowering without vernalization to promoting earlier flowering following a vernalization treatment, we hypothesize that the Ogle allele in this region has a small vernalization response, the Kanota allele is relatively insensitive to vernalization, and the TAM O-301 has a large vernalization response.

QTLs were detected for VERN and NLGC on OT10, which is homologous to KO28. A QTL for flowering time under vernalized conditions was detected on KO28, but this QTL was identified about 40 cM from the position homologous to the QTL in the OT population (Fig. 1). Furthermore, whereas the Ogle allele at the QTL on KO28 contributed to later flowering and vernalization did not affect the difference between Ogle and Kanota alleles (Holland et al. 1997), the Ogle allele at the QTL on OT10 promoted earlier flowering and vernalization eliminated the difference between Ogle and TAM O-301 alleles. These QTLs most likely represent different genomic regions.

QTLs were detected on both of OT11 and KO15 (Fig. 1). Portyanko et al. (2001) suggested that these two linkage groups were members of a common homoeology set, and they may be homologous, although this cannot be demonstrated conclusively. The Ogle allele at a QTL for EFLD on OT11 contributed to later flowering, similar to the effect of the QTL on KO15 (Holland et al. 1997).

Major QTLs on OT8 match the position and effect of a QTL on KO6, as do the major QTLs on OT32 and KO17 and on OT34 and KO11. OT31 and KO24 are members of a common homoeologous set (Portyanko et al. 2001) and are likely homologous, based on four loci identified by common RFLP markers (Fig. 1). The Ogle allele at QTLs in this region in both populations promotes earlier flowering, with the effect being greater under non-vernalized conditions, resulting in a positive vernalization response.

Genomic regions that exhibit synteny with oat chromosome 17 seem to be important for adaptation consistently across the cereal crops. Dubcovsky et al. (1998) demonstrated that the vernalization QTL on KO24 maps to a position that is syntenous with part of chromosome $5A^m$ of *T. monococcum* containing the major vernalization gene *Vrn-A^{m}1* (Fig. 1). This region, in turn, is synte-

nous with the chromosomal regions containing the orthologous vernalization loci *Vrn-A1* and *Vrn-D1* in bread wheat, *Vrn-H1* in barley, and *Vrn-R1* in rye (Dubcovsky et al. 1998). The orthology of the oat vernalization QTLs on KO24 and OT31 with these other cereal vernalization genes is not certain, because the oat maps of this region cannot be perfectly aligned with the maps of other cereals yet. Nevertheless, the consistent vernalization effect of this region across oat mapping populations and its near synteny with the cereal vernalization regions is suggestive of orthologous relationships between the major vernalization genes of oat, wheat, barley and rye.

QTL, segregation distortion, complex genetic linkages, and chromosomal rearrangements

Four major QTL regions detected in the OT population (OT8, OT31, OT32 and OT34) corresponded to four major QTL regions mapped in the KO population (KO6, KO11, KO17 and KO24). All of these regions were associated with segregation distortion in the OT map, and three of the corresponding KO regions (KO6, KO11 and KO24) also had segregation distortion. Syntenous regions on OT31 and KO24 and on OT34 and KO11 all had a deficiency of the Ogle allele, whereas the Ogle allele was in excess on OT8 but the homologous region on KO6 had a shortage of the Ogle allele.

The consistent association between major QTL positions and segregation-distortion favoring QTLs promoting later flowering in the OT population is not easily explained. It seems unlikely that selection occurred for alleles contributing to later flowering during RIL development, because no lines were lost during the inbreeding process after the F_2 generation (Portyanko et al. 2001). Portyanko et al. (2001) suggested that genes causing gametic or zygotic lethality might have been responsible for segregation distortion, based on the putative synteny between OT31 and regions of the rice and *Triticum tauschii* genomes carrying gametophytic lethality genes. This does not explain why such loci would be consistently associated with flowering-time QTLs in this oat mapping population, however.

Similarly, the association between major flowering-time QTLs and regions of the genome demonstrating inconsistent two- and three-point linkage estimates when initially grouped could have been caused by several effects. For example, either segregation distortion or chromosomal rearrangements in these regions could have caused spurious linkages. A translocation between chromosomes 17 and 7C is strongly correlated with the rachis disarticulation phenotype that defines the *A. sativa* subspecies *sativa* and *byzantina* (Jellen and Beard 2000). The translocation is also loosely associated with the winter vs spring growth habit (primarily a vernalization response) and with the geographic origin in cultivated oat landraces (Zhou et al. 1999; Jellen and Beard 2000). Chromosome 7C contains linkage group KO3 and chromosome 17 contains linkage group KO24 (Zhou et al. 1999), and these correspond to linkage groups OT3 and OT31, respectively (Portyanko et al. 2001). The restriction of recombination near chromosomal interchanges may be adaptive if it prevents the disruption of co-adapted complexes of loci affecting important fitness traits. In this way, selection in divergent ecological conditions may result in associations between chromosomal interchanges, adaptive QTLs, and geography, such as those reported for winter and spring oat by Zhou et al. (1999) and Jellen and Beard (2000). It may not be a coincidence that the major vernalization gene in *Triticum* is located near a translocation breakpoint that differentiates the A genome from the B and D genomes (Dubcovsky et al. 1998).

We have identified major QTLs for vernalization responses on a region of chromosome 17 in two winter by spring oat crosses, confirming the importance of this region to ecological adaptation. Whereas Kanota and Ogle differed for the form of the 7C-17 interchange, however, Ogle and TAM O-301 both have the translocation (E.N. Jellen, personal communication). Thus, spring growth habit is conditioned by genes that are often, but not always, associated with a translocation between chromosomes 7C and 17. The consistent segregation distortion and the difficulty in constructing consistent linkage groups in the region of the translocation, even when the parents did not differ for the translocation, is curious, however. It is possible that TAM O-301 is heterogeneous for the translocation, such that the plant used to form the mapping population and the plant that was karyotyped carried different forms of the translocation. This hypothesis could be tested by karyotyping a sample of TAM O-301 plants. Another possibility is that cryptic chromosomal micro-rearrangements exist in this region between genotypes that have the same karyotype, resulting in skewed segregation ratios and inconsistent two- and three-point linkage estimates. Conversely, segregation distortion could be the result of selection against certain alleles at the QTLs in this region, because of their pleiotropic effects on gamete or sporophytic viability, or because of linkage to such viability genes. If this were true, then segregation distortion (if it occurred on several linkage groups) could cause spurious linkages, complicating genetic mapping in the surrounding region. However, the association between these viability genes and adaptation QTLs and the translocation would not be understood except as a coincidence. The causal relationships among QTLs for vernalization response, chromosomal translocations, geographic distributions, segregation distortion, and linkage-map complexities remain uncertain and pose a challenge for oat geneticists.

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