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ORIGINAL PAPER

# Identification of genetic loci associated with ear-emergence in bread wheat

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**Abstract** A doubled haploid population constructed from a cross between the South Australian wheat cultivars 'Trident' and 'Molineux' was grown under winter field conditions, under field conditions over summer and under artificial light both with and without vernalisation. The duration from planting to ear-emergence was recorded and QTL associated with heading date were detected using a previously constructed genetic linkage map. Associations were shown with chromosomal regions syntenous to previously identified photoperiod (*Ppd-B1*) and vernalisation (*Vrn-A1*) sensitive loci. Additional QTL associated with time to heading were also identified on chromosomes 1A, 2A, 2B, 6D, 7A and 7B. Comparisons between the genetic associations observed under the different growing conditions allowed the majority of these loci to be classified as having either photoperiod-sensitive, vernalisation-sensitive or earliness per se actions. The identification of a photoperiod-sensitive QTL on chromosome 1A provides evidence for a wheat gene possibly homoeologous to *Ppd-H2* previously identified on chromosome 1H of barley. The occurrence of a putative major gene for photoperiod sensitivity observed on chromosome 7A is presented. The combined additive effects at these loci accounted for more than half the phenotypic variance in the duration from planting to ear-emergence in this population. The possible role of these loci on the adaptation of wheat in Australia is discussed.

**Keywords** Ear-emergence · Earliness per se · Photoperiod · Quantitative trait locus · *Triticum aestivum* · Vernalisation

**Abbreviations**
QTL Quantitative trait locus

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## Introduction

Time to ear-emergence plays a significant role in determining the grain yields achieved by a wheat crop. A flowering time inappropriate for the local environment may subject a crop at critical growth stages to the influences of extreme weather conditions such as frost, drought or heat stress, significantly reducing the crop's grain yield potential. Even in less-stressed environments, the switch from vegetative to reproductive

growth phases will play an important role in driving grain yields through its impact on the development of specific grain yield components.

Although the time to ear-emergence can be altered through cultural practices, significant genetic control is also exerted. Three basic factors control flowering in wheat. In vernalisation-sensitive wheat, a period of cold treatment on a vegetative plant will promote a switch to reproductive growth and therefore reduce the time to flowering (Flood and Halloran 1984b). Photoperiod-sensitive wheat varieties on the other hand will flower more rapidly under long day (more accurately, short night) conditions than during winter months. Finally, wheat cultivars may differ in their inherent rate of development. This last plant development factor is often termed 'earliness per se' and describes the basic development rate of the variety as it relates to growth temperatures (Flood and Halloran 1984a). A summary of previous studies (Snape et al. 2001) reported that genes have been identified on group 5 of wheat controlling vernalisation sensitivity (*Vrn-A1*, *Vrn-B1* and *Vrn-D1*), whilst on group 2, genes exist that control both photoperiod sensitivity (*Ppd-A1*, *Ppd-B1* and *Ppd-D1*) and earliness per se. However, if the genes involved in the control of reproductive development in wheat follow those identified in barley, a number of them are yet to be characterised. Loci on most of the remaining chromosomes have also been postulated to carry genes controlling the duration of the vegetative phase in wheat (Snape et al. 2001) but have not been well characterised.

Recently, a cultivar was produced in Australia that showed very high and stable yields in its target environment (southern Australia). This variety, 'Stylet', arose from a cross between two local cultivars, 'Trident' and 'Molineux'. The work presented here constitutes part of a wider study examining the cause of 'Stylet's' outstanding agronomic performance, in this case the genetic control of flowering time. Toward this end, a genetic linkage map was produced using 182 individuals from a doubled haploid population created from a cross between the two spring cultivars 'Trident' and 'Molineux' (Ranjbar 1997). The maturity of these varieties is typical of varieties grown in southern Australia. In this region, spring habit cultivars are planted in late autumn or early winter and grow through the mild winters and spring and are harvested in early summer. This population showed moderate segregation for time to ear-emergence when grown in the field over winter, but marked variation when grown over summer. Consequently, it was deemed likely that this population would help elucidate a range of genetic factors controlling flowering time in Australian wheat.

## Materials and methods

### Genetic resources

A doubled haploid population (T/M DH) consisting of 182 individuals produced from a cross between 'Trident' (VPM1/5*Cook//4*Spear, released in 1993 by the University of Adelaide) and 'Molineux' (Pitic 62/Festiguay//Warigal, released in 1988 by the University of Adelaide) was used as the basis for this study (Ranjbar 1997). A genetic linkage map was produced using 260 microsatellite and protein markers (Williams et al. 2006).

### Field-based ear-emergence observations

The T/M DH population was grown in 2001 as single replicate field plots (3.2 m × 1.3 m) at Charlick Research Centre (University of Adelaide, Strathalbyn, South Australia). The Fisher (Puckridge 1983) system was used to assess relative maturity of each DH line (FISH01) when the mean of the population was undergoing anthesis. This scoring system, used by some in Australia, assigns later flowering lines with a low score and early flowering lines with a higher score, one unit representing 2 days, and a score of 31 being ear-emergence. In 2003 (two replicates, randomised complete blocks) and 2004 (three replicates, randomised complete blocks) the population was grown in plots (3.2 m × 1.3 m) at the Roseworthy Agricultural College Campus of the University of Adelaide (Roseworthy, South Australia) and the dates at which 50% of the heads had fully emerged from the flag leaf sheath (heading date) were recorded. The use of heading dates in 2003 and 2004 rather than the Fisher relative score allowed the number of degree days from seeding to heading date (HEAD03 and HEAD04) to be calculated (base temperature of 0°C). Temperature data were retrieved from a nearby (~3 km) weather station operated by the Australian Bureau of Meteorology and used to calculate the average daily temperature. The average daily temperature for the duration of heading in the T/M DH population in 2003 and 2004 was 12.7 and 16.3°C, respectively. During the summer of 2004/2005 the T/M DH population was grown as two replicates (randomised complete blocks) in single observation rows (1 m long, 20 cm apart) and the days from seeding to ear-emergence recorded and degree days to heading calculated (HEAD0405). For the short day, winter experiments, daylight hours averaged 11.4, whilst for the longer day, summer experiment, daylight hours averaged 14.

### Controlled environment ear-emergence observations

A glasshouse-based experiment was undertaken in the autumn of 2005 at Roseworthy, using a subset of the DH population (130 individuals), to help determine the role of each of the QTL associated with heading date. Single plants were grown under long day conditions (artificial incandescent light supplied to extend day-length to 16 h) using a three replicate split plot design with and without vernalisation treatment (UNVERN05 and VERN05). Seeds for the vernalised treatment were germinated on moist filter paper in sealed tubes for 24 h at room temperature and then kept at $5 \pm 3$°C for 6 weeks. For the UNVERN05 treatment, seeds were germinated in the same manner at room temperature but before planting were grown until the coleoptile and root length equalled that of the seeds being vernalised. Two seedlings were planted in a small tube (4 cm diameter, 10 cm deep) and after emergence one was removed to leave a single healthy plant in each tube. The number of days from planting to heading was recorded and converted to degree days.

### Statistical analysis

Best linear unbiased predictors (BLUPs) for each of the heading scores were determined using the REML directive within GENSTAT 6 (Payne et al. 2002). A model incorporating row and column effects from the field was fitted to the data (Gilmour et al. 1997) along with any other significant spatial terms such as seeding direction. The VFUNCTION procedure of GENSTAT was used to calculate broad sense heritabilities (Nyquist 1991). The location of QTL effects for ear-emergence was determined using the interval mapping (Haley and Knott 1992) approach provided by MAP MANAGER QTX (Manly and Olson 1999). A QTL with a LOD between two and three was considered suggestive whilst a QTL with a LOD greater than three was considered significant.

## Results

### Data summary

Relative maturity scores and heading dates for the T/M DH population were most highly correlated between the three winter data sets (Table 1). Due to the alternative scoring system used in 2001, the figures for FISH01 were negatively correlated with all other scores. The heading dates taken from vernalised plants under long day conditions (VERN05) showed the poorest correlation with the three winter field scores, although significant ($P < 0.001$) correlations (0.35–0.4) with the winter data were still observed. Normal distributions for ear-emergence were observed for each of the three winter-derived datasets (Fig. 1). Of the two parents, 'Molineux' took longer to reach 50% ear-emergence ($P < 0.05$) in 2003 although the difference between them was not significant in 2004. In each year they ranked centrally with respect to the DH progeny. In contrast, the variation under longer day conditions showed a less normal distribution. Over summer, this distribution appeared to be bimodal and it was noted that those lines that took longer to reach 50% ear-emergence also showed a winter wheat like growth habit. The other two data sets produced under artificial long day conditions (Fig. 1e, f) showed a more continuous distribution but in the case of the unvernalised plants (Fig. 1e) there was a skew towards an earlier maturing phenotype. Overall, the vernalised plants under artificial long day conditions (VERN05) showed the shortest average period from sowing to heading.

### QTL associated with plant phenology

Chromosomes belonging to groups 1, 2, 5, 6 and 7 showed association with heading date in this population (Table 2). A QTL on chromosome 5A associated with heading date was detected in each of the experiments (Table 2). In addition, this same region was associated (LOD = 26.9) with growth habit (winter vs spring) from the 2004/2005 summer experiment and was the only statistically significant genetic association observed (data not shown). The association between this region on chromosome 5A and ear-emergence was smallest for the VERN05 treatment, accounting for just 11% of the phenotypic variation in time to ear-emergence.

A second QTL associated with heading date was identified on chromosome 2BS (Fig. 2). This QTL showed a highly significant association with heading date when the population was grown in the field during winter. Based on the average daily temperatures during heading in 2003 and 2004, lines possessing the 'Molineux' 2BS genotype headed 2.8 days earlier than those with the 'Trident' genotype, only a little less than that observed in Europe for the *Ppd-1* series (Worland et al. 1998). A much smaller association with time to heading was also observed on chromosome 2BS for the population when grown under long day conditions (HEAD0405, UNVERN05 and VERN05). A QTL also associated with ear-emergence under short day conditions was located on the long arm of chromosome

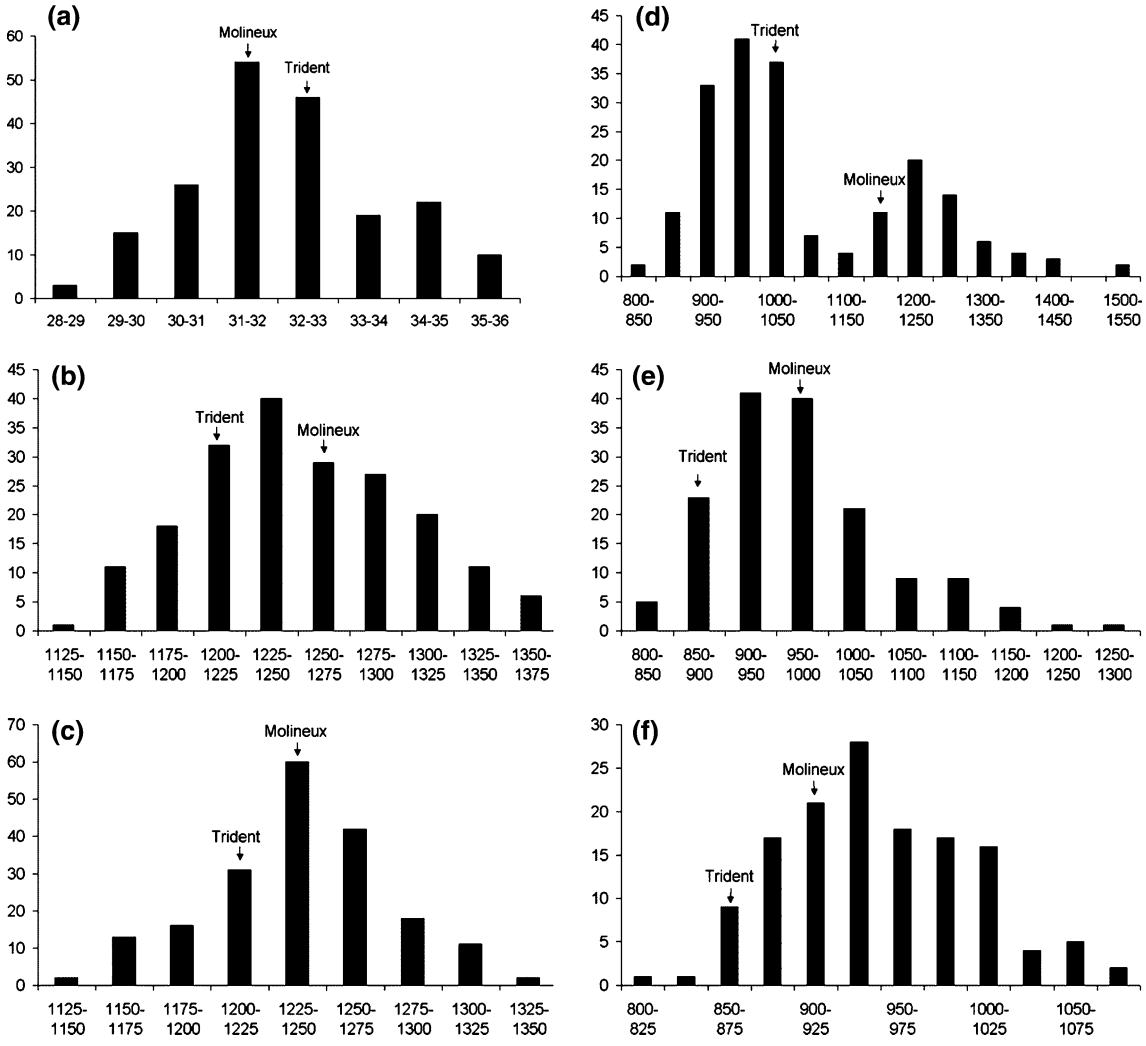


**Fig. 1** Distributions of relative ear-emergence date as measured by **a** Fisher maturity score at Charlick 2001 (FISH01), degree days to heading **b** Roseworthy 2003 (HEAD03), **c** Roseworthy 2004 (HEAD04), **d** Roseworthy summer of 2004/2005 (HEAD0405), **e** under artificial long day conditions without vernalisation (UNVERN05) and **f** vernalised seedlings under artificial long day conditions (VERN05). The *y-axis* indicates the number of DH individuals belonging to each class. The heading date classes for the two parents 'Trident' and 'Molineux' are indicated

**Table 1** Correlations between the heading date measurements are provided below the diagonal. The broad sense heritabilities are listed for each of the replicated experiments in bold along the diagonal

| | FISH01[a] | HEAD03 | HEAD04 | HEAD0405 | VERN05 | UNVERN05 |
|---|---|---|---|---|---|---|
| FISH01 | **N/A** | | | | | |
| HEAD03 | −0.74 | **0.95** | | | | |
| HEAD04 | −0.74 | 0.82 | **0.89** | | | |
| HEAD0405 | −0.43 | 0.58 | 0.59 | **0.96** | | |
| VERN05 | −0.39 | 0.42 | 0.35 | 0.39 | **0.73** | |
| UNVERN05 | −0.50 | 0.49 | 0.43 | 0.53 | 0.68 | **0.83** |

All correlations and heritabilities were highly significant ($P < 0.001$)

[a] The heading score in 2001 was recorded on a single replicate only and consequently a heritability for this figure could not be calculated

1A (*QPpd.agt-1A*). This QTL was observed for each of the three winter experiments (Fig. 3), but was not detected when the population was grown under long day conditions. As with the QTL on 2B, ear-emergence occurred earlier for DH lines with the 'Molineux' *QPpd.agt-1A* genotype when compared to those with the 'Trident' genotype, but this time by an average of 1.8 days across 2003 and 2004.

**Table 2** The significance and extent of association between chromosome regions and time to flowering is indicated by the LOD, percentage variance accounted for (%) and the additive allele effect (Add)

| Trait | Chromosome | Closest marker(s) | LOD | % | Add | Early |
|---|---|---|---|---|---|---|
| FISH01 | 1AL | *Xwmc304-Xgwm497* | 2.6 | 7 | 0.52 | M |
| | 2AL | *Xgwm558-Xwmc198* | 2.4 | 6 | −0.44 | T |
| | 2BS | *Xbarc200-Xgwm148* | 9.5 | 23 | 1 | M |
| | 5AL | *Xgwm271* | 5.6 | 13 | −0.77 | T |
| | 7AS | *Xbarc154-Xbarc108* | 5.8 | 14 | −0.63 | T |
| | 7BS | *Xgwm46-Xgwm333* | 2.2 | 6 | −0.51 | T |
| HEAD03 | 1AL | *Xwmc304-Xgwm497* | 1.8 | 5 | −14.5 | M |
| | 2BS | *Xbarc200-Xgwm148* | 4.1 | 11 | −22.2 | M |
| | 5AL | *Xgwm271* | 9.8 | 15 | 24.1 | T |
| | 7AS | *Xbarc154-Xbarc108* | 7.4 | 18 | 24.8 | T |
| | 7BS | *Xgwm46-Xgwm333* | 3 | 7 | 15.8 | T |
| HEAD04 | 1AL | *Xwmc304-Xgwm497* | 1.7 | 4 | −11.0 | M |
| | 2AL | *Xgwm558-Xwmc198* | 2.7 | 7 | 11.2 | T |
| | 2BS | *Xbarc200-Xgwm148* | 7 | 16 | −17.6 | M |
| | 5AL | *Xgwm271* | 6.9 | 13 | 17.2 | T |
| | 7AS | *Xbarc154-Xbarc108* | 7.8 | 19 | 20.2 | T |
| | 7BS | *Xgwm46-Xgwm333* | 2.3 | 6 | 12.3 | T |
| HEAD0405 | 2BS | *Xgwm614-Xbarc200* | 2.3 | 6 | −47.8 | M |
| | 5AL | *Xgwm271* | 20.8 | 41 | 113 | T |
| | 7AS | *Xbarc154-Xbarc108* | 2.3 | 5 | 36.6 | T |
| UNVERN05 | 2BS | *Xgwm614-Xbarc200* | 3.3 | 11 | −35.3 | M |
| | 5AL | *Xgwm271* | 10.1 | 23 | 51 | T |
| VERN05 | 2AS | *Xbarc220* | 2.2 | 8 | 18.8 | T |
| | 2BS | *Xgwm614-Xbarc200* | 2.3 | 8 | −20 | M |
| | 5AL | *Xgwm271* | 4.4 | 11 | 22 | T |
| | 6DS | *Xgdm141-Xbarc27* | 2.3 | 11 | 19.6 | T |

The closest marker(s) is provided for positional reference, while the parent providing the earliness allele is also listed (T = 'Trident', M = 'Molineux')

In the winters of 2003 and 2004 a QTL on the short arm of chromosome 7A (*QPpd.agt-7A*) was found to be strongly associated with time to heading, achieving LODs of 7.4 and 7.8, respectively (Fig. 4). A QTL on chromosome 7A was also associated with (LOD 5.8) the relative development score (FISH01) from the winter of 2001. This locus accounted for a greater proportion of the genetic variance for ear-emergence than observed for the QTL on 2B in 2003 and 2004. Progeny from the T/M DH population carrying the 'Trident' genotype at *QPpd.agt-7A* headed on average 3.2 days earlier in 2003 and 2004 than those lines possessing the 'Molineux' genotype at this locus. In comparison, no association between heading date and chromosome 7A markers was observed in the long day glasshouse experiments. However, a minor suggestive association with heading over summer was recorded. A region syntenous to *QPpd.agt-7A* on chromosome 7B (*QPpd.agt-7B*) was also found to be associated with heading date under the winter short day conditions. In 2001 and 2004, the association between *QPpd.agt-7B* and heading was suggestive, but in 2003 the association was significant. Under the natural long day conditions of summer and the artificially long days invoked in the glasshouse experiment, no association between chromosome 7B and heading date was observed.

Two additional suggestive QTL for heading date were detected under the VERN05 treatment where the effects of vernalisation and photoperiod sensitivity were reduced or removed entirely. These were not associated with heading in any of the other experiments. One of these QTL was located on the short arm of chromosome 2A (LOD 2.2) while the other was positioned on the short arm of chromosome 6D (LOD 2.3). A final suggestive genetic association with ear-emergence was identified for the data collected over winter in 2001 (LOD 2.4) and 2004 (LOD 2.7). This QTL on chromosome 2AL was not associated with ear-emergence in the winter of 2003, over summer or in either of the two controlled environment experiments.

## Discussion

The extent of variation observed for the duration to ear-emergence in this population was large, indicating the possible action of several genes resulting in the

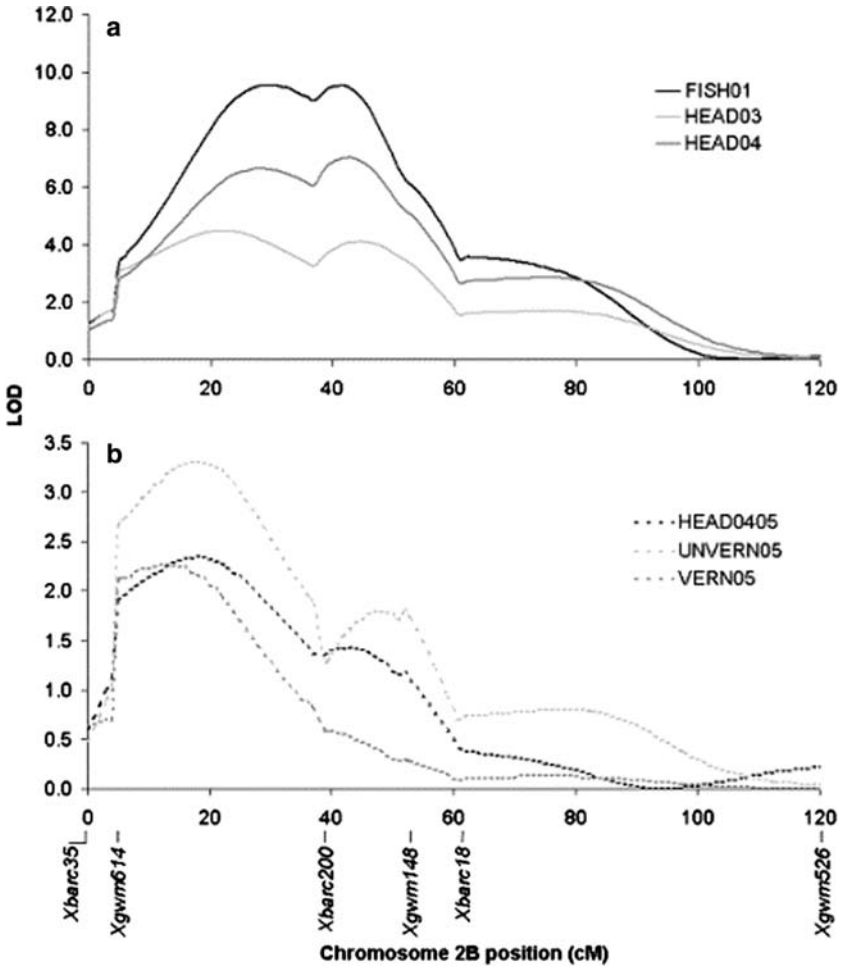


**Fig. 2** Genetic associations between chromosome 2B and ear-emergence under **a** short and **b** long day conditions

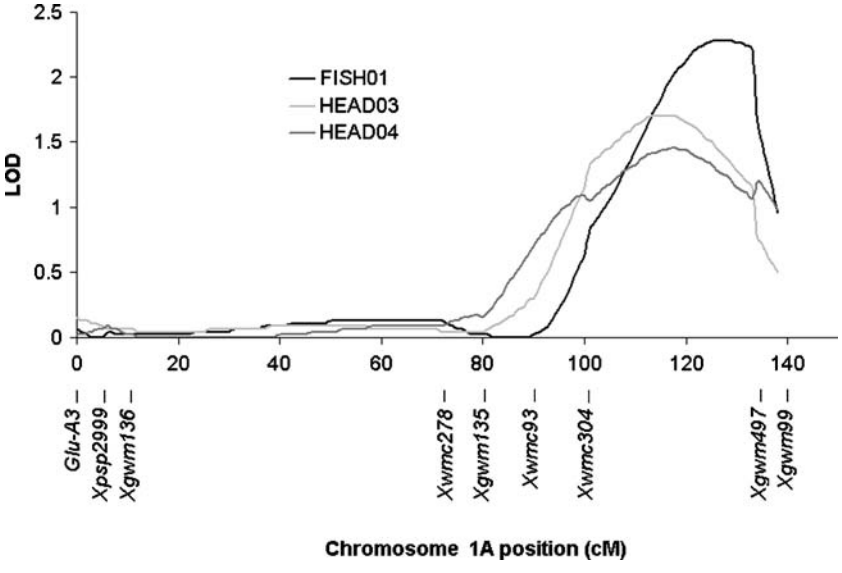


**Fig. 3** A QTL on chromosome 1A associated with heading date in the T/M DH population when grown during winter

observed transgressive segregation. A major locus associated with vernalisation sensitivity, multiple photoperiod sensitivity loci and a number of regions with minor effects independent of these environmental variables seem to control the duration from planting to head emergence in this population.

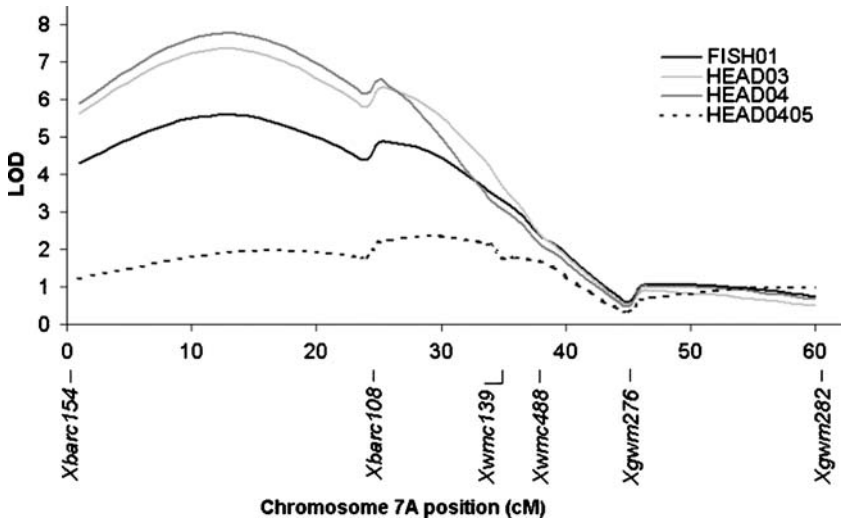


**Fig. 4** Identification of an apparently photoperiod-responsive QTL for heading date on chromosome 7A of wheat

QTL associated with vernalisation sensitivity

Given the apparent interaction of the QTL on chromosome 5AL with cold treatment, its dominance during warm summer conditions, its association with growth habit and its position on chromosome 5AL, it seems likely to be coincidental with the well-characterised vernalisation sensitivity gene *Vrn-A1* (Halloran and Boydell 1967b; Law et al. 1976). Co-segregation with the allele-specific markers (data not shown) developed by Yan et al. (2004) also supports the argument that *Vrn-A1* is the major gene underlying this QTL.

QTL associated with photoperiod response

Four loci were found to be associated with heading date in response to photoperiod in this population. The QTL detected on chromosome 2BS was strongly associated with heading date under the short day winter conditions, but only weakly under long days. This weak association is discussed further in a later section under QTL associated with earliness per se. It seems likely that this QTL is involved with photoperiod response and is coincidental with the gene *Ppd-B1*, previously identified to this chromosome arm (Scarth and Law 1983). Its location distal of *Xgwm148* is the same as that identified by Mohler et al. (2004) and Hanocq et al. (2004) for *Ppd-B1*. Three further genetic associations with heading date appeared to respond to altered day-length. *QPpd.agt-1A* showed differential association with time to ear-emergence under long and short day conditions, so it is likely that this chromosomal region is involved in photoperiod response. Halloran and Boydell (1967a) reported a photoperiod-responsive gene in 1967 on chromosome 1A using substitution lines. More recently, Law et al. (1998) showed that genes for ear-emergence were present on each homoeologous member of the group 1 wheat chromosomes. The action of these genes was not simple; response to both vernalisation and photoperiod was shown in this example. The authors suggested that at least some of the genes were located on the short arms of group 1. This contrasts with the results observed here where a photoperiod-responsive locus has been identified on the long arm of chromosome 1A and did not respond to vernalisation. One cannot rule out the possibility that multiple genes were identified by Law et al. (1998) and that some of these were the same as those identified here and perhaps previously by Halloran and Boydell. (1967a). A study mapping ear-emergence in barley has also located a photoperiod-responsive gene (*Ppd-H2*) on chromosome 1H (Laurie et al. 1995). Given the synteny observed between wheat and barley for the major flowering gene series *Ppd-1* and *Vrn-1*, it has been suggested that a *Ppd-2* series may exist on group 1 of wheat (Laurie 1997; Law and Worland 1997; Snape et al. 2001). Although the statistical significance of the genetic association presented here is weak, its detection across multiple years and its synteny (Fig. 5) with a previously identified gene in barley (*Ppd-H2*) provide added evidence for its association with heading date. To the knowledge of the authors this is the first report of a photoperiod-sensitive gene(s) homoeologous to *Ppd-H2* being mapped by QTL analysis on the long arm of chromosome 1A in wheat. There was no evidence of further QTL associated with time to ear-emergence on chromosomes 1B and 1D in this population.

The association of *QPpd.agt-7A* with heading date was primarily observed under short day conditions indicating some photoperiod response. However, its suggestive association over summer implies that this

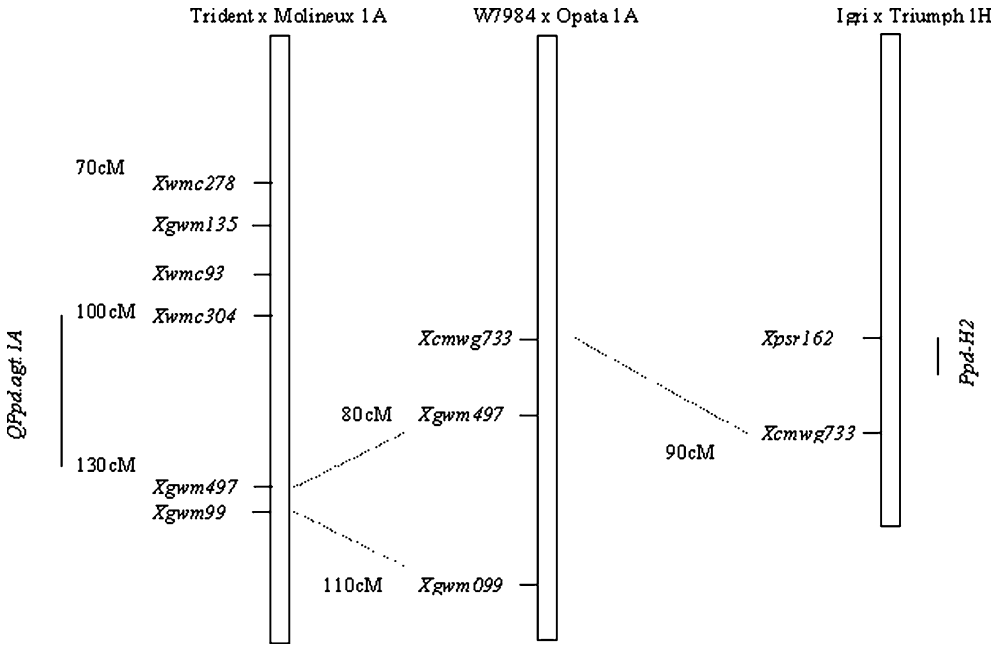


**Fig. 5** Comparative map between *Ppd-H2* in barley and *QPpd.agt.1A* in wheat. The Trident × Molineux chromosome 1A map (Williams et al. 2006) was aligned with the Igri × Triumph chromosome 1A map (Laurie et al. 1995) using the CMap software (http://www.rye.pw.usda.gov/cmap) and the densely covered chromosome 1A map from the ITMI W7984 × Opata population (Song et al. 2005)

region may possess some vernalisation requirement that was not met over summer or an earliness per se character as reported previously for this group (Halloran and Boydell 1967a; Sourdille et al. 2000). However, given that no association for this region was observed with heading date for VERN05 and UNVERN05, it is more likely that the average of 14 h daylight (12.5–14.7 h) experienced over summer was not sufficient to overcome all photoperiod sensitivity conferred by this locus. It appears that the greater period of light provided in the glasshouse experiment, however, was enough to render the differences between the alleles insignificant. A final QTL associated with ear-emergence under short days but not under long days was identified on chromosome 7B. Given the apparent response of this QTL to photoperiod and its chromosome location syntenous to *QPpd.agt-7A* (near to the centromere on the short arm of chromosome 7B), it seems plausible that the chromosome 7A and 7B loci presented here are homoeoloci. Further experimentation will be required to confirm these effects in other genetic backgrounds.

The combined effect of chromosome regions carrying vernalisation (5A) sensitive and apparently photoperiod (1A, 2B, 7A and 7B) sensitive QTL explained the majority of the variation in heading date over winter. However, additional QTL for heading date which did not appear to be responsive to day-length or cold treatment were also observed in this study. The QTL on 6D was only detected when plants were subjected to cold treatment prior to planting and were grown under artificial long days suggesting a potential earliness per se action. Islam-Faridi et al. (1996) also identified genes associated with ear-emergence on the group 6 chromosomes of wheat. However, in their study using Chinese Spring ditelosomics, two sets of genes, one sensitive to day-length and the other inhibiting ear-emergence, were located on the long arms of this chromosome group. Also, their study was based on a change in chromosome dosage rather than the identification of allelic variation. Given the relatively low significance of the chromosome 6D QTL observed here, further investigation would be required before confirming its impact on ear-emergence.

As mentioned previously, a minor QTL associated with heading date under long day conditions was detected at or near the *Ppd-B1* locus. *Ppd-B1* may have secondary non-photoperiod-sensitive effects on the timing of flowering, or a second non-photoperiod-sensitive gene may reside nearby. If the later scenario is true, as was suggested by Sourdille et al. (2000) and Shindo et al. (2003), it appears that the QTL in this case may be distal to *Ppd-B1* (Fig. 2b). However, the proximity of this locus to the photoperiod-sensitive QTL makes it difficult to be confident of this result. In support of this hypothesis, a QTL was also identified on the short arm of chromosome 2A for heading date under the VERN05 treatment. Genes for ear-emergence on

the long arms of group 2 chromosomes have been suggested previously by Scarth and Law (1983). However, to the best knowledge of the authors, this is the first time an association independent of vernalisation and photoperiod has been identified on chromosome 2AS. Given their syntenous locality, it is plausible that the QTL for ear-emergence, independent of photoperiod and vernalisation, identified on chromosomes 2AS and 2BS may form a homoeologous gene series for earliness per se.

The mode of action of the QTL associated with heading date in 2001 and 2004 on the long arm of chromosome 2A is more difficult to characterise. No association with this chromosome region was identified under long day conditions, possibly leading to the conclusion that its effect on ear-emergence is subject to photoperiod sensitivity. However, the effect of this QTL was also absent in the winter of 2003. It is possible that this QTL represents the same earliness per se locus identified previously on the long arms of group 2 chromosomes (Law and Worland 1997; Scarth and Law 1983). However, the low significance level for this association makes any conclusions regarding the mode of action of this locus tenuous.

## Conclusion

This study has shown that the genetic control of flowering time in these two southern Australian wheat cultivars is complex. Multiple genes for time to heading, including vernalisation and photoperiod sensitivity as well as earliness per se, have presumably been manipulated either directly or passively by breeders to match the timing of ear-emergence in wheat varieties with their target environment. Interestingly, vernalisation sensitivity has persisted in an elite cultivar in spite of apparent selection for spring habit. This may imply that some adaptive function is conferred by this form of flowering control in southern Australia. The identification of four independent loci for photoperiod insensitivity in this cross suggests that this trait has been particularly important in genetically fine tuning the phenology of wheat for the Mediterranean climate of southern Australia. Locating and characterising the effects of the putative photoperiod-sensitive QTL *QPpd.agt-1A*, *QPpd.agt-7A* and *QPpd.agt-7B* should provide wheat breeders with an improved understanding of the genetic environment in which they work. Further research is required to gain a complete understanding of the impact that these loci exert on grain yield and genotype by environment interaction for grain yield.

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