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ORIGINAL PAPER

Meta-QTL analysis of the genetic control of ear emergence in elite European winter wheat germplasm

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Abstract Variation in ear emergence time is critical for the adaptation of wheat (*Triticum aestivum* L.) to specific environments. The aim of this study was to identify genes controlling ear emergence time in elite European winter wheat germplasm. Four doubled haploid populations derived from the crosses: Avalon × Cadenza, Savannah × Rialto, Spark × Rialto, and Charger × Badger were selected which represent diversity in European winter wheat breeding programmes. Ear emergence time was recorded as the time from 1st May to heading in replicated field trials in the UK, France and Germany. Genetic maps based on simple sequence repeat (SSR) and Diversity Arrays Technology (DArT) markers were constructed for each population. One hundred and twenty-seven significant QTL were identified in the four populations. These effects were condensed into 19 meta-QTL projected onto a consensus SSR map of wheat. These effects are located on chromosomes 1B (2 meta-QTL), 1D, 2A (2 meta-QTL), 3A, 3B (2 meta-QTL), 4B, 4D, 5A (2 meta-QTL), 5B, 6A, 6B 7A (2 meta-QTL), 7B and 7D. The identification of environmentally robust earliness per se effects will facilitate the fine tuning of ear emergence in predictive wheat breeding programmes.

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Introduction

The timing of the emergence of an ear of wheat from the flag leaf is the summation of several distinct but tightly coupled physiological processes. These include: the developmental shift at the apical meristem from the production of leaves to the production of an inflorescence; the development of spikelets along the length of the immature inflorescence, culminating in the formation of a terminal spikelet; and the elongation of the uppermost stem internodes which will ultimately carry the ear up to mature plant height. The initiation and duration of this process has profound effects on crop performance. Optimum floral initiation and development makes maximum use of resources available throughout the growing season, and exposure of sensitive tissue to biotic and abiotic stress at specific stages of plant development can have a negative impact on grain yield and quality (Worland 1996). The availability of genetic variation controlling ear emergence facilitates its manipulation by plant breeders. Defining this variation will improve the level of control.

In wheat, the genetic mechanisms controlling ear emergence are categorised according to their interactions with the environment. In winter wheat, 4–8 weeks of cold treatment, known as vernalization, is necessary to induce ear emergence in winter wheat varieties. Spring wheat varieties do not require vernalization to induce ear emergence. Genes shown to control the requirement for vernalization include *Vrn-A1*, *Vrn-B1*, *Vrn-D1*, and *Vrn-B3* (Law and Worland 1997; Law et al. 1976). Varieties can also be categorised according to photoperiod requirement. Wheat is

naturally a long-day plant, ear emergence is very late unless long days are experienced. Some genotypes, however, can flower under short days. In bread wheat, this difference is largely controlled by *Ppd-D1* and *Ppd-B1* (Scarth and Law 1984), dominant alleles of which confer early ear emergence through photoperiod insensitivity. These major genes have profound effects on mega-environment adaptation.

However, within mega-environments, the majority of genes shown to regulate ear emergence in the Triticeae have not been shown to be mediators of any specific environmental signal and are loosely categorised as earliness per se (*eps*) effects (Snape et al. 2001). The major vernalization and photoperiod genes confer gross adaptation to an environment, however, it is the *eps* effects which facilitate more subtle manipulation of the life cycle for regional adaptation. Within current UK wheat breeding programmes, progeny tend to segregate within a 5–15-day window for heading time. In most cases this variation is not due to the segregation of the major growth habit or photoperiod response genes as UK wheat varieties are largely photoperiod sensitive, winter, vernalization requiring, types.

In this study four recombinant double haploid populations, developed from crosses between UK adapted parents, were grown in up to ten environments across the UK, Germany, and France. The observed variation in ear emergence and assignment of genes by QTL analysis constitutes the most detailed description to date of the genetic control of ear emergence in elite UK winter wheat, and points towards the deployment of different genes in Western European wheat breeding programmes.

Methods

Plant materials and development of genetic maps

The doubled haploid populations and genetic maps used in this study have been described previously (Snape et al. 2007) and are summarised in Table 1. They are: Charger × Badger (C × B), 93 doubled haploid lines; Spark × Rialto (S × R), 129 double haploids lines; Savannah × Rialto (Sv × R), 126 doubled haploid lines; and Avalon × Cadenza (A × C), 202 doubled haploids. The parents of these populations represent a broad spectrum of the variation present in the UK elite winter germplasm pool, and are generally crosses between varieties developed by different plant breeding companies. All of these varieties carry recessive photoperiod sensitive alleles of *Ppd-D1* and *Ppd-B1*. All are winter types with recessive alleles of *Vrn-A1*, *Vrn-B1*, and *Vrn-D1* except for Cadenza that carries a dominant *Vrn-A1* allele. Allele specific assays (Yan et al. 2004) were used to confirm the presence *Vrn-A1a*.

Framework genetic maps were primarily developed using publicly available single sequence repeat (SSR) markers aiming for a marker density of one every 10–20 cM. Primer sets were used from JIC (*psp*), IPK Gatersleben (*gwm/gdm*), Wheat Microsatellite Consortium (*wmc*), Beltsville Agricultural Research Station (*barc*) and INRA (*cfd/cfa*) collections, see GrainGenes website http://www.wheat.pw.usda.gov/). Targeted markers were selected to provide good genome coverage using published consensus maps (Somers et al. 2004) and for their ease of scoring. DNA fragments were amplified with PCR and run on 5% polyacrylamide gels for separation. The silver staining technique was used to visualize fragments (Bassam et al. 1991). To further improve map density, DNA of S × R, A × C, and Sv × R, populations were subjected to Diversity Arrays Technology (DArT) genome profiling (Wenzl et al. 2004) at Triticarte Pty Ltd, Australia (http://www.triticarte.com.au). Single strand conformation polymorphism (SSCP) analysis was carried out as described by Bertin et al. (2005). The SSCP markers were derived from the following EST accessions: AL503851, BJ544902, and CA008389.

Joinmap v3.0 was used for genetic linkage map construction, set at the default settings with the Kosambi mapping function. Linkage groups were selected at a minimum LOD of three for reliable associations.

Field trials

Field trials were conducted at five sites: Norwich, Norfolk, UK; Sandringham, Norfolk, UK; and Balmonth, Fife, UK;

Table 1 Populations used for the detectection of ear emergence QTL and environments tested

Population	Abbreviation	Individuals	Environments
Avalon × Cadenza	A × C	202 DH	CF05, CF06, CF07
Charger × Badger	C × B	93 DH	CF01, CF02, CF03, Ger02, Fr03, San03, Scot03
Spark × Rialto	S × R	129 DH	CF01, CF02, CF03, San01, San03, Fr02, Fr03, Scot03, Ger02, Ger03
Savannah × Rialto	Sv × R	126 DH	CF02, CF03, CF07

Numerical suffixes show the years in which each experiment was carried out

CF Church Farm, Norwich UK. *Ger* Bohnshausen, Langenstein, Germany. *Fr* Froissy, near Amiens, France. *San* Sandringham, Norfolk, UK. *Scot* Balmonth, Fife, UK

Bohnshausen, Langenstein, Germany; and Froissy, near Amiens, France. Experimental details are shown in Table 1. The populations S × R, C × B, and Sv × R were part of parallel experiments grown in the same years, A × C data was collected later but is included here because it is emerging as a UK reference population under the UK Department of Environment, Food and Rural Affairs (DEFRA) Wheat Genetic Improvement Network (WGIN). Each line was grown in three replicate, 5.5 m^2 plots in a randomised design, grown according to standard agronomic practice. Ear emergence time was scored as the day when half of the ears in a plot were more that 50% emerged from the flag leaf, measured from the 1st May in each year/environment. The mean ear emergence times for the varieties used in this study are shown in Table 2.

Statistical analysis

Basic statistical analyses were carried out using Minitab v 15. Analysis of variance was used to demonstrate a genetic contribution to variation in ear emergence for each population and site. Mean values from the three replicates on each site were used to calculate correlations of emergence time between environments and for the detection of QTLs. QTL effects were estimated using single marker analysis and composite interval mapping functions of QTL cartographer version 2.5 (Wang and Zeng 2007) using default settings. QTL with LOD scores greater than two were taken on for inclusion in the meta-analysis. Additive effect and percentage of total variation for each QTL identified was calculated using the multiple interval mapping (MIM) function of QTL cartographer. Epistatic interactions were detected using the 'Refine MIM model' and 'QTL interactions' options in the QTL cartographer MIM module.

Meta-QTL analysis was performed using Biomercator software vs. 2.1 (Arcade et al. 2004). The genetic linkage maps of the four populations were projected onto the published consensus map (Somers et al. 2004) joined with S × R and A × C WheatDArTmapsVersion1.2 (http://www.triticarte.com.au). QTLs and confidence intervals (CI) were projected together with the genetic linkage maps, CI were approximated by the software following Darvasi and Soller (1997). Meta-analysis was carried out separately for all chromosomes with three and more QTLs. The number of meta-QTLs present was determined as the model which minimised the Akaike criterion (AIC).

Results

Extent of variation in time to ear emergence

For each population, the period spanning the emergence of ears from the earliest lines to the emergence of ears from the latest lines, the window of ear emergence, was variable between environments. However, emergence times for each population were well correlated between environments, never falling below an r^2 value of 0.68. All populations exhibited significant genetical variation for the trait within each year/environment combination (ANOVA data not shown). For the A × C population the window of ear emergence ranged from 13 to 17 days with r^2 values between environments ranging from 0.70 to 0.84. For C × B the range varied from 4 to 13 days in, with correlation between environments running from r^2 0.69 to 0.93. For S × R the spread in ear emergence was from 5 to 15 days with a correlation r^2 between 0.68 and 0.90. For Sv × R ear emergence lasted for a minimum of 10 and maximum of 16 days and correlation of heading time between environments was from 0.82 to 0.92.

Identification of QTL controlling ear emergence

A total of 127 QTL were identified. The closest genetic marker, estimated additive effect, and portion of variation accounted for by each QTL are shown in Table S1. Interactions between pairs of QTL were detected in some environments, but never the same interaction in more than one environment. If the assumption is made that QTL identified in the same genetic interval in one population, across multiple environments, are due to the same genes then the numbers of independent QTL can be reduced to 10 in A × C, 16 in S × R, 10 in C × B, and 5 in Sv × R (Fig. 1). Common markers allow the alignment of the genetic maps used in this study and consequently the alignment of QTLs identified in A × C, C × B, S × R, and Sv × R by a meta-analysis. It is possible that allelic variation at the same genes are responsible for the effects detected on: 1B in S × R and C × B; 1D in A × C, S × R and Sv × R, 3A in A × C, Sv × R and S × R; 3B in S × R and C × B, 4D in A × C and S × R; 5A in A × C and S × R; 6A in A × C and S × R; 6B in A × C and C × B; 7A in A × C, S × R and Sv × R; and 7D in S × R and Sv × R. The meta-QTL calculated from this analysis are summarised in Table 3 and a detailed map presented in Fig. S1. These effects are now described in more detail, for each homoeologous chromosome group.

Homoeologous group 1

At least two independent QTL were identified on chromosome 1B. In the CxB and S × R populations an effect in the region of *Xgwm18* was found to be significant in relatively few environments. Early alleles came from Spark and Badger. In the A × C population a separate effect was detected on the distal region of chromosome 1BL with Avalon contributing the early allele, and the QTL being detected in all environments tested.

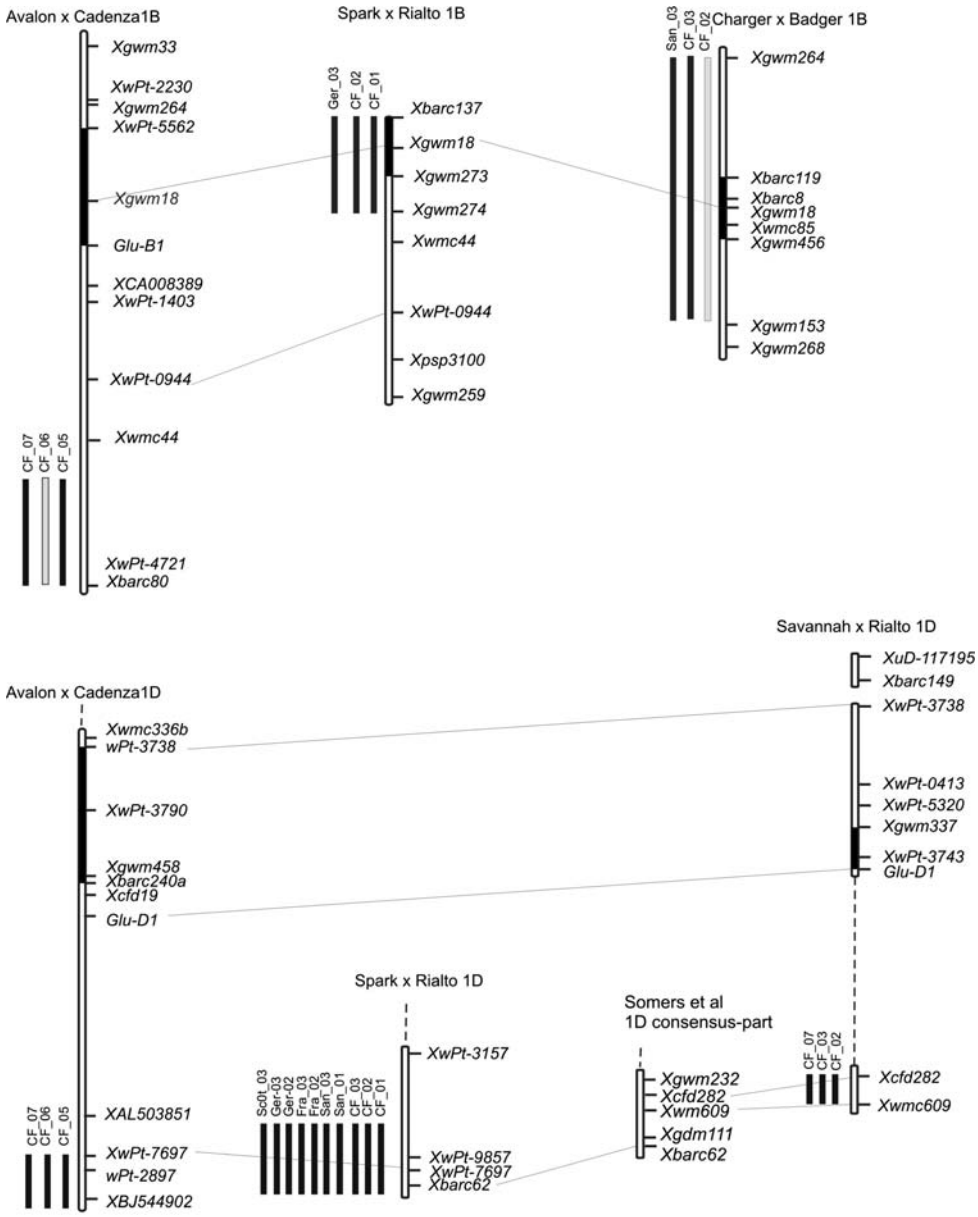


Fig. 1 Chromosomal location of significant heading date QTL identified. Chromosomes are shown as *hollow bars*, centromere containing intervals are *solid bars*. *Bars* corresponding to marker intervals containing QTL are coloured *grey* if LOD is between 2 and 3, and *black* if greater than 3. Common markers between maps are connected. Sections of a wheat consensus map (Somers et al. 2004) are included where it aids map alignment. Linkage groups from the same chromosome are connected by a *dashed line*. Approximate location of QTL identified in other studies that are coincident with those found here are shown as *black bars*, with references

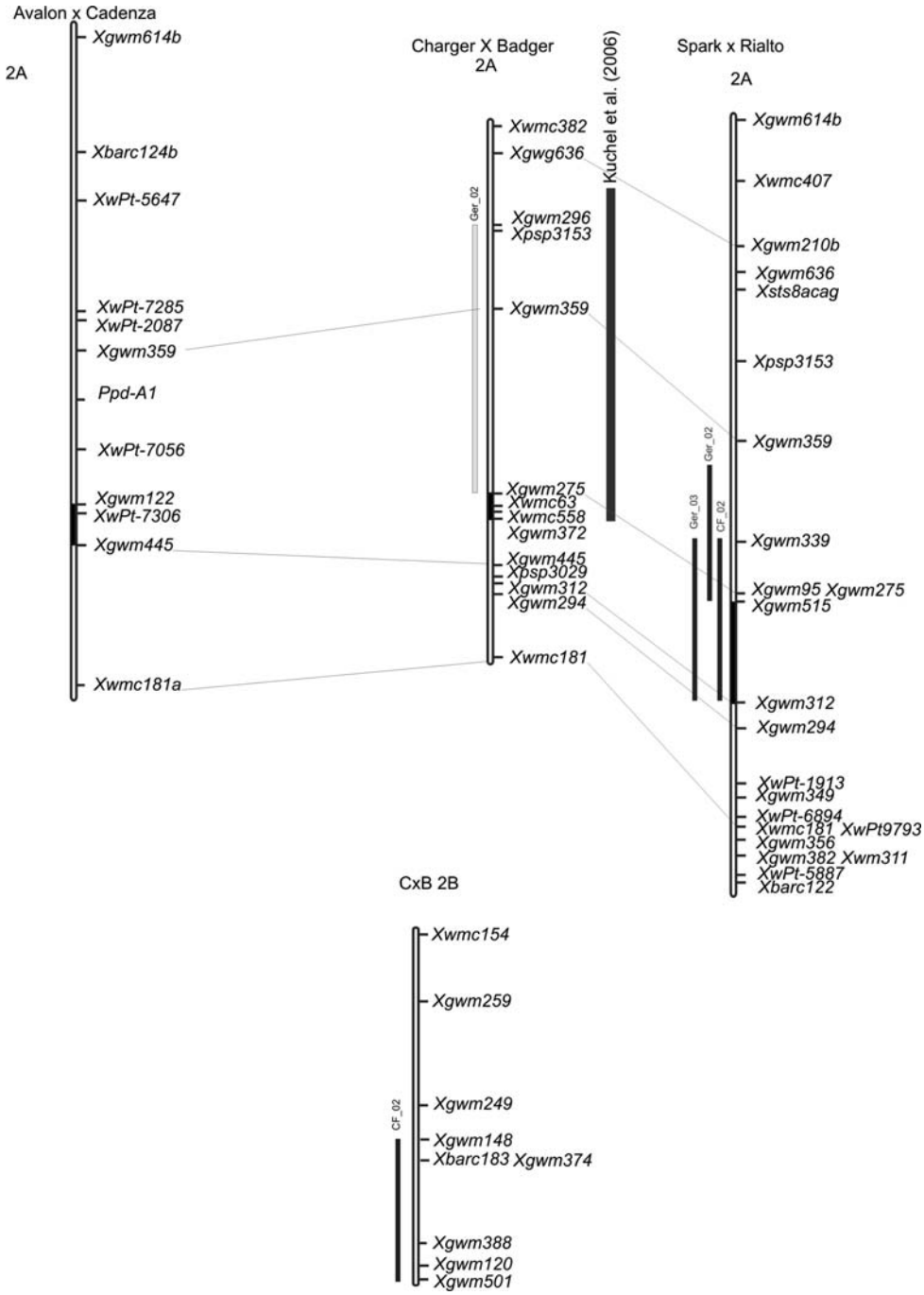
One of the strongest, in terms of additive effect and LOD score, and most environmentally stable effects on time to ear emergence identified in this study was on the distal region of chromosome 1DL. An effect located in this region segregates in A × C, S × R and Sv × R and explains between 10 and 27% of the phenotypic variation in heading data in these populations with a mean LOD score across populations and environments of 12.1. The additive effect ranges from 0.51 to 1.83 days. Earliness was conferred by Cadenza, Savannah, and Spark alleles. The very distal location of the QTL on 1DL and 1BL suggest that these effects could be controlled by homoeoalleles.

The possibility that some of the group 1 genes are orthologous to heading time effects identified on other Triticeae group 1 chromosomes was investigated using genic markers flanking these effects. These include *Ppd-H2* (Laurie et al. 1995; Faure et al. 2007), *eam8* (Borner et al. 2002) on barley 1HL, and a temperature sensitive *eps* effect identified in *Triticum monococcum* (Valarik et al. 2006). SSCP markers derived from barley ESTs homologous to genes in regions of rice collinear with genes closely linked to *PpdH-2* (*XCA009389*) and *eam 8* (*XAL503851* and *XBJ544902*) were placed on chromosomes 1D and 1B using the Avalon × Cadenza population (Fig. 1).

Homoeologous group 2

Ear emergence QTL in the interval *Xgwm359–Xgwm445* were identified on chromosome 2A in environments CF02, Ger03, and Ger02 in S × R and Ger02 in C × B with

Fig. 1 continued



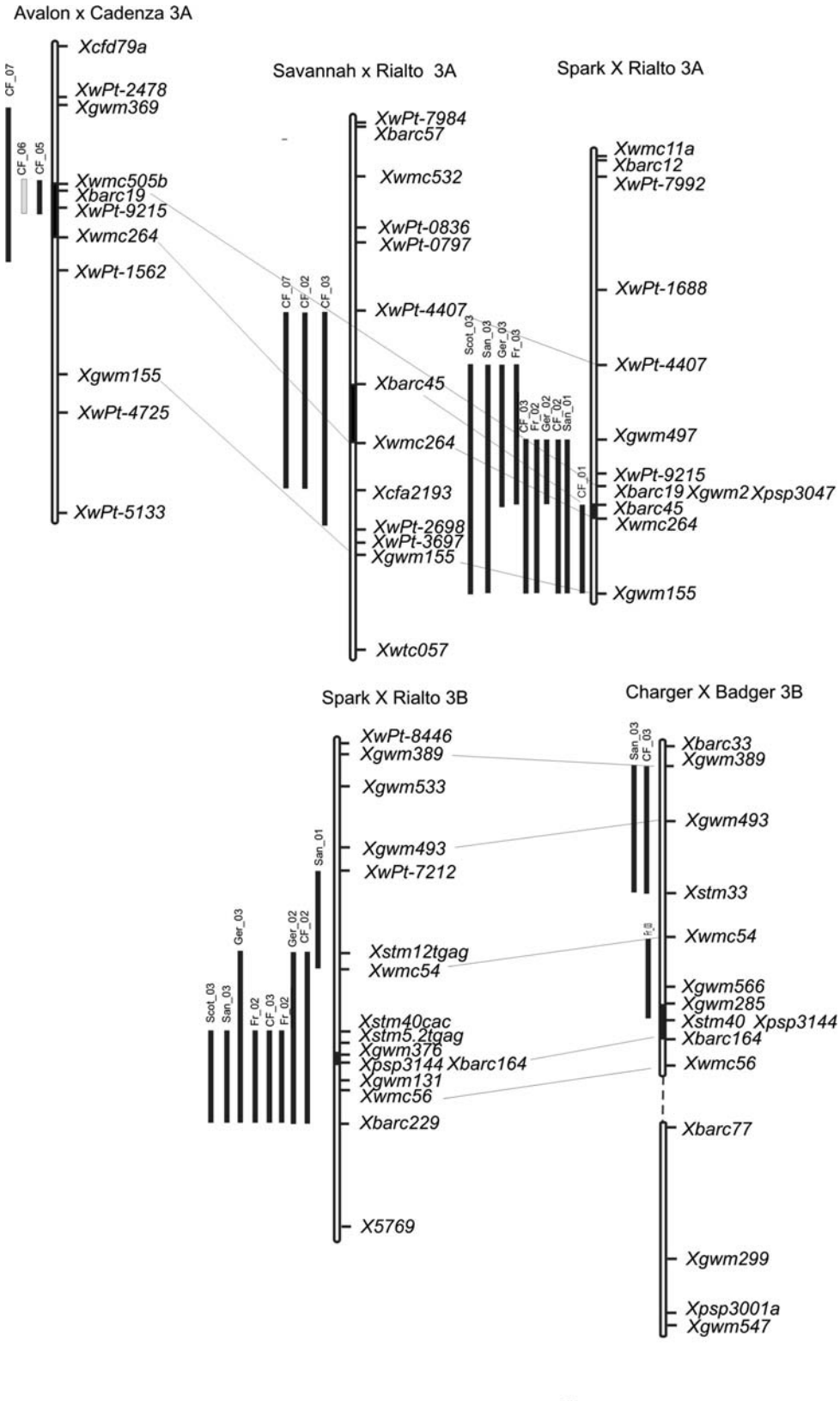
additive effects of 0.3–0.5 days. Earliness was conferred by Rialto and Badger alleles. An ear emergence effect on chromosome 2B was detected around *Xgwm501* in the C × B and A × C populations, in each case the QTL was only significant in one of the environments tested.

Homoeologous group 3

The heading time effects mapped around *Xbarc45* on chromosome 3A have some of the largest additive effects on days to ear emergence identified in this study. As for the strong effects on 1DL, these QTL are identified in S × R, Sv × R and A × C and are detected in the majority of environments sampled. Additive effects range from 0.28 to 1.29 days and explain between up to 25.4% of the phenotypic variation in heading data. In this case alleles conferring earliness were from Avalon in A × C and possibly the same Rialto alleles in both S × R and Sv × R.

On chromosome 3B the *Xwmc54–Xbarc229* interval was associated with a heading time effect in nine out of the ten

Fig. 1 continued



environments tested with the S × R population. The additive effects of the 3B QTL range from 0.34 to 1.82 days and explain between 3.4 and 12.4% of the phenotypic variation in heading time. Earliness is from the Rialto allele. In C × B there appear to be two QTL for days to ear emergence located on chromosome 3B. One is in a similar

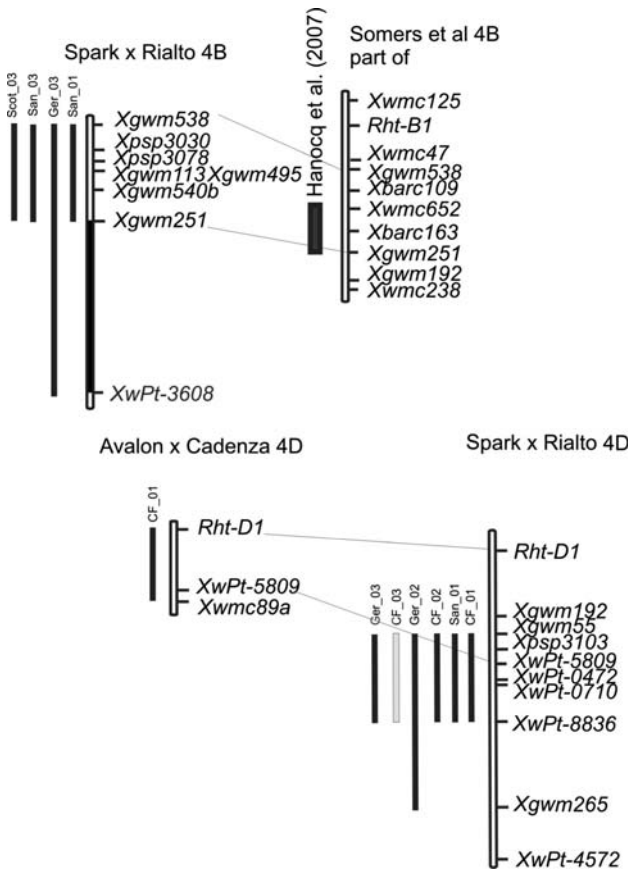


Fig. 1 continued

location to the SxR effect but was detected in only one of the seven environments sampled for this population, Fr_03. The second effect located more distally on chromosome 3BS was detected in two of the seven environments.

Homoeologous group 4

Effects for days to ear emergence were detected on chromosome 4BS in S × R. The QTL in S × R were detected in four of the ten environments sampled, with Rialto possessing the early allele. On chromosome 4D, effects for days to ear emergence were detected in A × C and S × R. For A × C ear emergence was delayed by the Avalon allele in 1 year at CF_01. In S × R the 4D effect was identified in six out of ten environments, the early allele comes from Spark with an additive effect between 0.26 and 1.57 days. The proximity of these QTL to Rht1 homoeoalleles shows that the 4B and 4D effects might be controlled homoeologous genes. The QTL does not appear to be a pleiotropic effect of *Rht-D1*.

Homoeologous group 5

Multiple QTL controlling time to ear emergence were identified on chromosome 5A (Fig. 1). Under the parameters used in this study meta-analysis reduced this number to 2 (Fig. S1). In S × R, the most distal effect on 5AL was detected in the largest number of environments, six out of ten, and on average had the largest additive effect, with the early allele coming from Rialto. For A × C an effect was detected in three of the four environments and mapped to the equivalent region of 5AL. The two other 5A effects identified in S × R were each detected in only two environments. On chromosome 5BL QTL were detected in S × R in environments Fr02 and San_01 and in CxB in just one of the seven environments tested. The segregation of *Vrn-A1* was scored in A × C using allele specific PCR assays (Yan et al. 2004). Due to the paucity of other segregating marker in this region there was insufficient genetic linkage with other 5A markers to map *Vrn-A1*. However, single marker regression analysis showed no association of *Vrn-A1* with a flowering time effect.

Homoeologous group 6

QTL for time to ear emergence were identified in equivalent regions of chromosome 6A in A × C and S × R. QTL in both populations had additive effects of around 0.5 days, with early alleles coming from Avalon and Spark. The S × R effects were detected in six out of ten environments and the A × C effects in three out of four.

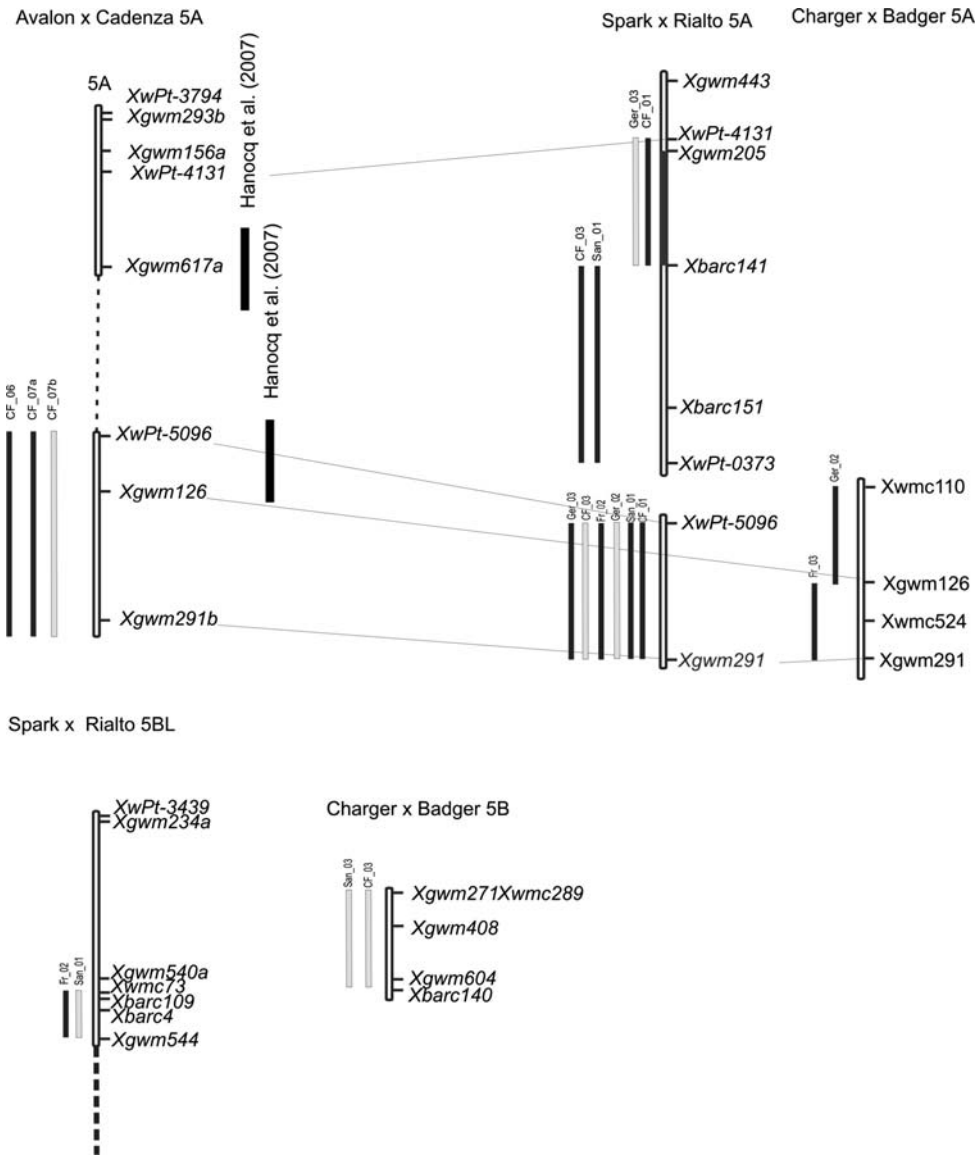
Of the five genomic regions associated with heading time QTL in the CxB population, the 6B QTL were detected in more environments than any other. Ear emergence QTL in this region had additive effects ranging from 0.23 to 0.96 days accounting for 7.2–13.4% of the phenotypic variation. Effects identified on chromosome 6B in A × C could be alleles of the same gene. The early alleles of these effects come from Charger and Avalon.

Homoeologous group 7

On chromosome 7A at least two meta-QTL were for days to ear emergence identified. For the QTL in the interval *Xbarc127–Xbarc29* in A × C and S × R early alleles were from Avalon and Rialto. Heading time QTL were also identified on 7AS and 7AL of S × R and 7AL of A × C. QTL were also identified in A × C on chromosome 7BL in the interval *XwPt-1209–XwPt-4814*, with additive effects ranging from 0.39 to 0.41 in CF05, CF06, and CF07.

On chromosome 7D the most significant effects were identified on the long arm in Sv × R and S × R. In the Sv × R population, this QTL was detected in all environments sampled. The additive effect ranged from 0.62 to 1.3 days, explaining between 9.3 and 14.3% of the phenotypic variation. In both cases the Rialto allele conferred later ear emergence. In the S × R population QTL were identified in six of the ten environments sampled in an equivalent location to the Sv × R effects with an additive effect of 0.2–0.5 days.

Fig. 1 continued



Discussion

Comparison with previous studies

In this study, significant QTL effects for heading time were found on chromosomes 1B, 1D, 2A, 3A, 3B, 4B, 4D, 5A, 5B, 6A, 7A, 7B and 7D. It is useful to consider the likely coincidence of the QTL described here with previously described effects.

Homoeologous group 1

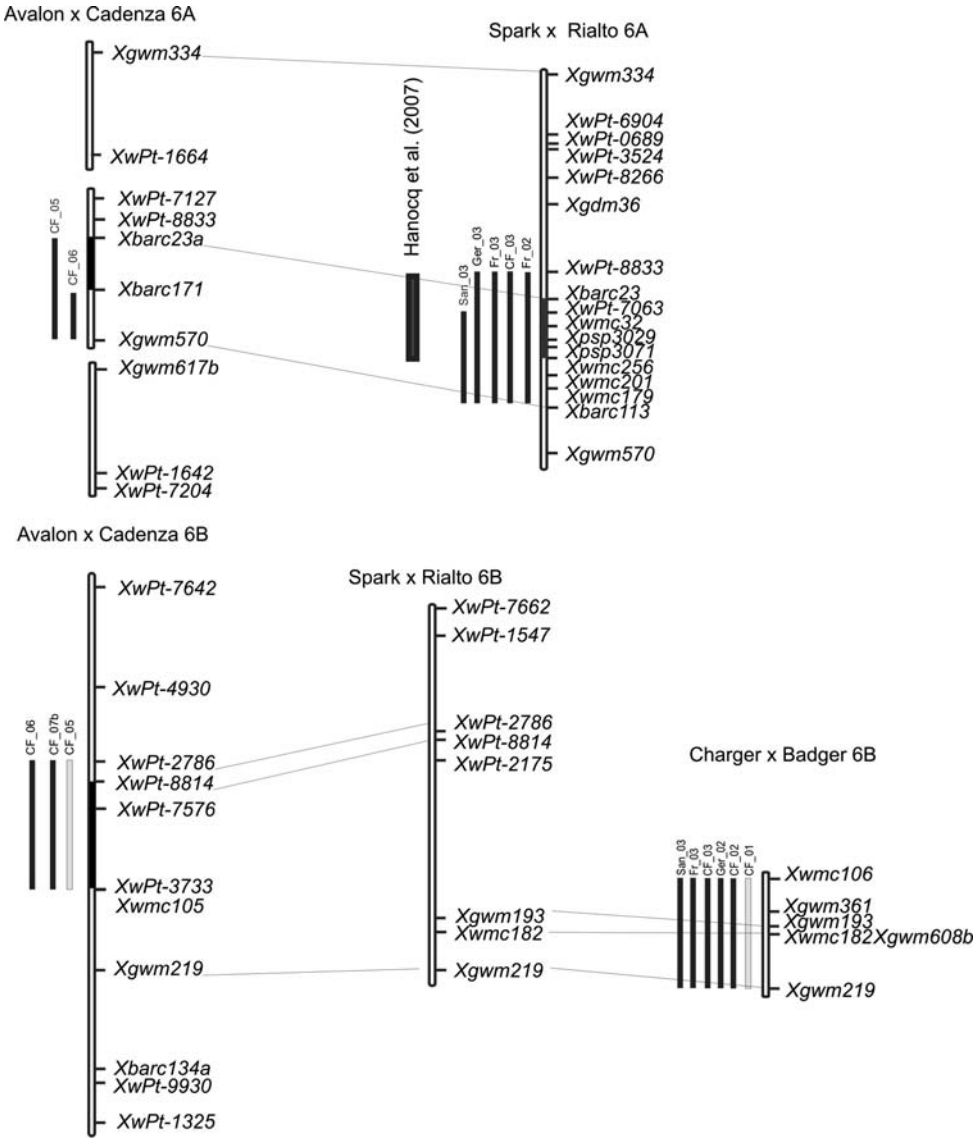
Studies based on aneuploid lines and alien substitution lines (Law et al. 1998) have shown that at least two genes located on all three group one chromosomes influence ear emergence. However, relatively few ear emergence QTL have been identified on the group 1 chromosomes of bread wheat. One exception to this is an effect detected on 1AL in a cross derived from the Australian varieties Trident and Molineux (Kuchel et al. 2006).

The map locations of *XCA009389* showed that the equivalent region to *Ppd-H2* in wheat is likely to be distally linked to the high molecular weight glutenin locus *Glu-D1*, so *Ppd-H2* is a candidate for the S × R and C × B QTL in this region. The distal 1BL and 1DL effects are probably not *Ppd-H2* orthologues but their proximity to *XAL503851* and XBJ544902 shows that they could be orthologous to *eam 8* or the $1A^{M}L$ *eps* effect identified in *T. monococcum* (Valarik et al. 2006).

Homoeologous group 2

Comparison of common SSRs with other studies (Kuchel et al. 2006) shows that the effect located in the interval

Fig. 1 continued



Xgwm359–Xgwm445 on chromosome 2A in S × R and Ger02 in C × B is in a similar location to *Ppd-A1*. The *Ppd-A1* gene sequence was mapped in A × C to an equivalent region to the 2AS QTL identified in this study (Fig. 1). Charger, Badger, Spark, and Rialto are photoperiod sensitive varieties, but it is possible that the relatively weak effects detected in this interval are subtle allelic variants of *Ppd-A1*. Alternatively they are heading time effects linked to *Ppd-A1*.

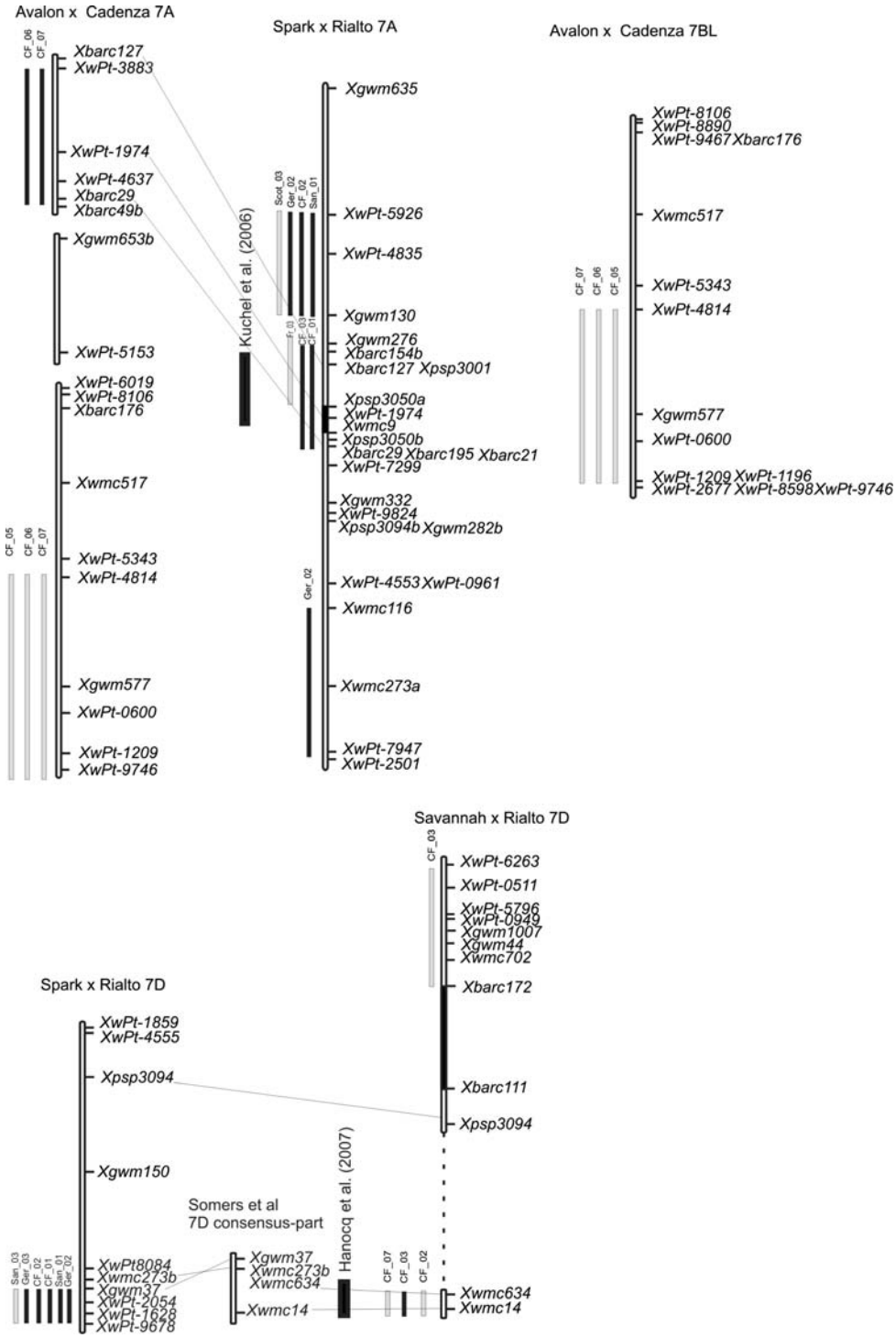
Homoeologous group 3

Studies based on aneuploid lines and alien substitution lines showed that all the homoeologous group 3 chromosomes carry genes controlling ear emergence (Miura et al. 1999; Miura and Worland 1994). Very few QTL based studies have detected group 3 effects in bread wheat. An *eps* effect was detected in a comparison of chromosome 3A from Wichita × Cheyenne (Shah et al. 1999). This effect appears to be located on chromosome 3AL, distal to the QTL described here in the region of *Xbarc45* in SxR, SvxR and AxC. On chromosome 3B Pankova et al. (2008) identified ear emergence effects in a similar location to the S × R and C × B 3B effects described here.

Homoeologous group 4

Analysis of group 4 monosomic chromosomes showed that *eps* genes occur on chromosomes 4A and 4B (Hoogendoorn 1985). A number of QTL studies have also detected effects on 4B. The heading time QTL meta study of Hanocq et al. (2007) collated information from a number of these. Alignment of common markers shows that the 4B meta-QTL is in a similar location to the 4B effect detected in this study in S × R and Sv × R (Fig. 1). The S × R 4D effect does not appear to be coincident with any previously

Fig. 1 continued



described effects. It is possible that the QTL identified on 4B and 4D are homoeologous.

Homoeologous group 5

Many previous studies have detected strong ear emergence effects on the group 5 chromosomes, usually attributable to members of the *Vrn* homoeoallelic series (Law and Worland 1997). The vernalization requirement of the A × C and S × R population was fully met, so none of the effects seen here are likely to reflect segregation for spring habit. The effects located in the interval *XwPt-5096–Xgwm291b* in A × C and S × R are not attributable to *Vrn-A1*. The *XwPt-0373–Xbarc141* and *Xbarc141–XwPt-4131*

Table 2 Heading times (expressed as days after 1st May) of parents of doubled haploid populations used in this study when grown in the environments used here

	Variety						
	Avalon	Cadenza	Spark	Savannah	Rialto	Charger	Badger
Environment							
CF_01	NA	NA	36.50	NA	31.50	30.00	38.00
CF_02	NA	NA	30.00	28.00	26.00	23.30	28.00
CF_03	NA	NA	30.30	27.70	26.00	23.33	29.00
CF_05	32.00	31.70	NA	NA	NA	NA	NA
CF_06	29.00	27.00	NA	NA	NA	NA	NA
CF_07	21.00	19.50	NA	NA	NA	NA	NA
CF_08	32.00	31.50	NA	NA	NA	NA	NA
San_01	NA	NA	48.00	46.00	45.00	42.33	49.00
San_03	NA	NA	34.50	33.00	32.00	31.00	34.00
Fr_02	NA	NA	33.00	32.00	32.00	28.00	33.00
Fr_03	NA	NA	34.00	32.00	31.00	26.00	31.00
Ger_02	NA	NA	38.50	36.00	33.00	31.30	39.00
Ger_03	NA	NA	35.00	35.00	32.00	31.00	35.00
Scot_03	NA	NA	34.00	36.50	37.00	36.00	35.33

CF Church Farm, Norwich UK. *Ger* Bohnshausen, Langenstein, Germany. *Fr* Froissy, near Amiens, France. *San* Sandringham, Norfolk, UK. *Scot* Balmonth, Fife, UK

Table 3 Heading time Meta-QTL identified in this study

Chromosome	Consensus map interval
1B	*wPt4129–gwm140*
1B	*cfd48–wmc611*
1D	*wmc405–barc62*
2A	*gwm636–wmc474*
2A	*wmc827–cfd168*
3A	*wmc505–wmc527*
3B	*wPt7225–wmc500*
3B	*wmc540–wmc787*
4B	*wPt3608–cfd39*
4D	*wPt8836–gwm165*
5A	*wmc489–cfa2155*
5A	*wmc110–gwm595*
5B	*wmc745–cfa21215B.2*
6A	*Sbarc23–Sbarc113*
6B	*wPt3309–wmc152*
7A	*wmc646–gwm60*
7A	*wmc83–wPt7299*
7B	*gwm344–wPt9746*
7D	*wPt2054–cfd175*

QTL identified in S × R are possibly coincident with two 5A meta-QTL identified previously Hanocq et al. (2007), the alignment of these QTL is shown in Fig. 1.

Homoeologous group 6

Aneuploid studies showed that some of the strongest ear emergence effects were located on the group 6 chromosomes (IslamFaridi et al. 1996; Worland 1996). Allelic variation for ear emergence QTL has been identified in a number of studies. The meta location of Hanocq et al. (2007) aligns with the 6A effect identified in A × C and S × R in the present study. No other heading time QTL seem to have been identified in the same region as the C × B 6B effect. It is possible that this QTL is homoeologous to the 6A QTL.

Homoeologous group 7

The 7A heading time QTL identified in the interval *Xbarc127–Xbarc29* in A × C and S × R occur in a similar location identified by Kuchel et al. (2006). The 7DL effect detected in Sv × R and S × R occurs in a similar location to the meta-QTL described by Hanocq et al. (2007). The major effect identified on the group 7 chromosomes in aneuploid studies was a vernalisation gene, *Vrn-B3* located on chromosome 7BS (Law 1966). No ear emergence time effects were detected on 7BS in the present study. However, *Vrn-B3* has now been cloned (Yan et al. 2006), and shown to be homologous to the *Arabidopsis thaliana* flowering time gene *Flowering Locus T* (*FT*), putative homoeologues of which have been are coincident ear emergence QTL on chromosome 7A and 7D (Bonnin et al. 2008). The 7A copy of *FT* is closely linked to *Xbarc154* showing that the QTL identified on 7AS in S × R and A × C could be homoeologous with *Vrn-B3*.

Implications for the genetic manipulation of ear emergence in wheat

The effects which were notable, in that they were detected in most of the environments tested, occurred on 1BL, 1DL, 3A, 3B, 6B, and 7D. These effects also had the highest additive values. The mean additive values across populations and environments for each effect are: 1D 0.95 days, 3A 0.77 days, 1B 0.65 days, 6B 0.65 days, 3B 0.55 days, and 7D 0.51 days. Summing up the mean additive values for each population for these major QTL provides an estimate of the extent to which they could be deployed to manipulate heading time. In A × C substitution of all late alleles for early alleles would produce a 5.7-day difference in heading date and these QTL explain 45% of phenotypic variation in heading time. For the other populations the equivalent figures are: for Sv × R 5.8 days and 45% S × R 6.5 days and 39%; for C × B 3.7 days and 20%. This allelic

variation is maintained in the UK elite germplasm pool and, bearing in mind the wide representation of Western European winter wheat germplasm represented in this study, these genes are likely to be major determinants of existing varietal differences in ear emergence and maturity date for many UK winter wheat varieties.

By tracking these alleles in segregating populations it will be possible to manipulate ear emergence in wheat breeding programmes, not only to produce varieties with specific ear emergence and maturity qualities, but also to achieve similar ear emergence dates by different genetic routes. There is evidence from this study to suggest that certain allelic combinations of heading time genes are preferable to others. In each case where the major QTL on chromosome 1DL was segregating the effect on 3A was also segregating. This reflects the fact that if a variety carried the late allele for one of these effects it carried the early allele for the other. No epistatic interaction was detected between these loci. These could be maintained by disruptive selection, or it is possible that specific allelic combinations such as this confer advantages in crop performance.

Comparison of the QTL described here with those identified in other studies showed that allelic variation for some, for example effects on 4B, 6A, 7D, appear to occur frequently in diverse germplasm. Others appear unique to this survey, most notably effects on 1DL, 3A, 3B and 6B. Here we found that expression of these QTL is detected across environments, including two sites in continental Europe, but effects in equivalent locations do not appear to have been detected in previous studies. There are two reasons why allelic variation could be maintained at these loci between the winter wheat varieties used in this study but appear infrequently elsewhere. First, it could be a purely historical phenomenon, as appears to be the case for the UK bias towards *Rht-D1b* over *Rht-B1b* alleles of the gibberellic acid insensitive dwarfing genes (Flintham et al. 1997). Alternatively, alleles of these genes might confer advantages in the UK which are not seen in other environments, this could be a direct consequence of the fact that the varieties used here were photoperiod sensitive and that earliness alleles at the 1D, 3A, 3B, and 6B QTL function well in photoperiod sensitive wheat varieties but not in where *Ppd-D1* or *Ppd-B1* confers photoperiod insensitivity.

Some QTL were detected in a limited number of environments. For example, the QTL identified on 2A in S × R was only significant in three of the ten environments tested: Ger_02, Ger_03, and CF_02. In the seven other environments tested, no QTL were detected in this region, even if the LOD detection threshold is reduced to 1. In order to understand the basis of the low heritability of key agronomic traits such as yield and stress tolerance it is important to understand the nature of environmental interactions such as this. However, the lack of some types of data such as detailed weather records for all trial sites means that this analysis is beyond the scope of the present study. In future work it would be useful to identify environmental patterns that coincide with the level of expression of the QTL. It is important to understand the precise mode of action of the genes that have been identified. Ear emergence time can be altered by changing the timing of floral initiation, the developmental rate of the spike, or the rate of stem extension. It is likely that the ability to manipulate these components of ear emergence independently will have effects on other traits such as grain yield (Miralles and Slafer 2007). In rice near isogenic lines (NILs) have provided the platform for revealing the precise function and molecular identity of heading genes (Yano et al. 2001). A similar approach will be pursued with the ear emergence QTL described here.

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