



## Genetic control of pre-heading phases and other traits related to development in a double-haploid barley (*Hordeum vulgare* L.) population

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### ABSTRACT

Extending the phase of stem elongation (SE) has been proposed as a tool to further improve yield potential in small-grain cereals. The genetic control of pre-heading phases may also contribute to a better understanding of phenological traits conferring adaptability. Given that an optimized total time to heading is one of the most important traits in a breeding program, a prerequisite for lengthening SE would be that this and the previous phase (leaf and spikelet initiation, LS) should be under different genetic control. We studied the genetic control of these two pre-heading sub-phases (from sowing to the onset of stem elongation, LS, and from then to heading, SE) in terms of Quantitative Trait Loci (QTL) in a barley double-haploid population derived from the cross Henni × Meltan, both two-rowed spring North European barley cultivars. DH lines (118) and their parents were studied in four field trials in North-Eastern Spain. Genetic control of a number of traits related to leaf appearance and tillering dynamics, which could be important for an early crop canopy structure, were also studied. LS and SE are, at least partially, under a different genetic control in the Henni × Meltan population, mainly due to a QTL on chromosome 2HS. The QTLs responsible for a different control of LS and SE did not seem to correspond with any major gene reported in the literature. Moreover shortening LS, so as to lengthen SE without modifying heading date, would not necessarily imply a negative drawback on traits that could be important for early vigour, such as phyllochron and the onset of tillering.

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### 1. Introduction

Crop phenology, which allows matching crop development with availability of resources (water, radiation, etc.), is the most important single factor influencing yield and crop adaptation to particular environments (Richards, 1991). This is especially relevant in Mediterranean conditions, where water is the main limiting factor and the occurrence of terminal drought and possible late spring frosts defines an optimal window for time to anthesis in order to maximise yield (Richards, 1991; Loss and Siddique, 1994; Cuesta-Marcos et al., 2009). Therefore keeping or achieving an optimised time to flowering is still an important goal in any breeding programme. In some Mediterranean environments, where intensive breeding has been carried out for centuries, either through farmer's selection or breeding programmes, there could be little scope for improving barley adaptability and yield by further adjustments in time to heading (Martiniello et al., 1987; Muñoz et al.,

1998; Slafer et al., 2005). However, knowing the genetic control of different pre-anthesis phases may contribute to a better understanding of phenological traits conferring adaptability (e.g. Limin et al., 2007).

Fine adjustment of phenology could be also important for yield improvement through increasing yield potential. Lengthening duration of the stem elongation phase has been associated to increases in the number of grains/m<sup>2</sup> (Slafer et al., 2001, 2005) which in turn could increase yield potential of small-grain cereals (Fischer, 2007, 2008; Miralles and Slafer, 2007). This should be achieved without modifying total time to anthesis, whose optimisation as shown above, is an important objective providing adaptability in breeding programmes (Slafer, 2003). To attain this goal, a prerequisite would be that the phases before and after the onset of stem elongation should be under different genetic control, as earlier suggested by some authors (Halloran and Pennell, 1982; Slafer and Rawson, 1994; Kernich et al., 1997).

Given the importance of time to anthesis, the genetic control of this trait has been the focus of many studies. Several genes or loci related to the response to photoperiod or vernalisation, or to earliness per se (the three main factors determining head-

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ing time, Slafer and Rawson, 1994) have been found on the seven chromosomes of barley. The most widely known genes related to photoperiod are: *Ppd-H1* on 2HS, expressed under long days (Laurie et al., 1994, 1995) and recently identified as a PRR-like (Pseudo-Response Regulator) gene by positional cloning (Turner et al., 2005); and *Ppd-H2* on 1HL, expressed under short days (Laurie et al., 1995) and for which *HvFT3*, a FT-like (Flowering locus T) gene, could be a candidate gene (Faure et al., 2007). Other reported genes that determine differences in heading time under short photoperiodic conditions are: *Eam7* on 6HS (Stracke and Börner, 1998), *Eam8* on 1HL (Franckowiak, 1997), *Eam9* on 4HL (Franckowiak, 1997; Lundqvist et al., 1997) and *Eam10* on 3HL (Börner et al., 2002). The three most known genes governing the response to vernalization are: *Vrn-H1* (*Sh2*, *HvVRN1* or *HvBM5A*) on 5HL and *Vrn-H2* (*Sh1*, *HvVRN2* or *HvZCCT*) on 4HL (Takahashi and Yasuda, 1971; Laurie et al., 1995) for which gene sequences have been also identified (Trevaskis et al., 2003; Yan et al., 2003, 2004), and *Vrn-H3* (*Sh3* or *HvFT1*) (Takahashi and Yasuda, 1971) which has been recently mapped on 7HS and identified as an orthologue of the *Arabidopsis* FT gene (Yan et al., 2006; Faure et al., 2007). Some loci whose effect could not be related to photoperiod or vernalization response are considered *earliness per se* genes (a group much less studied): *eps2S* on 2HS (or *Eam6*), *eps3L* on 3HL, *eps4L* on 4HL, *eps5L* on 5HL, *eps6L.1* and *eps6L.2*, both on 6HL, *eps7S* on 7HS and *eps7L* on 7HL (Laurie et al., 1995). Other homologues of some of the most important genes controlling flowering time in *Arabidopsis* have been found in barley (*HvCO1* to *HvCO8*, Griffiths et al., 2003; *HvGI*, Dunford et al., 2005; *HvFT1* to *HvFT5*, Faure et al., 2007) although most of them do not correspond to any of the above genes and their effect on heading is unclear. Moreover other QTL for heading date, whose position do not seem to coincide with these genes or loci, have been found in other barley populations and their effect on the response to the three main factors exposed above is unknown (e.g. Hayes et al., 1993; Bezzant et al., 1996; Tinker et al., 1996; Baum et al., 2003; Li et al., 2006). QTL for heading date usually have an effect on other important agronomic characters (yield, height, resistance to diseases, quality traits, etc.) (e.g. Hayes et al., 1993; Bezzant et al., 1996; Tinker et al., 1996; Baum et al., 2003; Li et al., 2006) in accordance with the fact that heading date is a key trait for adaptability.

Several authors have shown variability in the duration of pre-anthesis phases, comparing different sets of cultivars, and even variability in the late reproductive phase (SE) in varieties with similar time to anthesis, both in wheat (Halloran and Pennell, 1982; Whitechurch et al., 2007) and barley (Appleyard et al., 1982; Kitchen and Rasmusson, 1983; Kernich et al., 1995, 1997; Borràs et al., 2009). However we are not aware of any study in barley nor in wheat providing evidences of the genetic control of different pre-anthesis (sub) phases. The few studies comparing wheat substitution lines, single chromosome recombinant lines or near isogenic lines (differing in *Ppd* alleles) are inconclusive as differences in pre-anthesis phases lengths or in responses to photoperiod in each (sub) phase could not be attributed to particular major *Ppd* genes (see results and comparative review by González et al., 2005). Zhou et al. (2001), using a QTL approach to identify genetic controls of particular phenophases in rice, found some independent QTL for the duration of the vegetative and reproductive phases, either by different magnitude of QTL effects or by opposite allele effects on both phases. Whitechurch et al. (2007) identified variability in the stem elongation phase (SE) independent from the variability in the previous phases of leaf and spikelet initiation (LS) in a rather large set of cultivars, while Borràs et al. (2009) did not find major genetic correlations between both phases (with large genotypic effects and heritabilities for both traits) in the Henni × Meltan barley DH-population. Both results would lead to the suggestion that LS and SE could

be under different genetic control also in wheat and barley. However it would be necessary to identify the particular genetic factors responsible for the genetic variability and for this lack of correlation, so as to explore avenues for manipulating LS and SE without modifying total time to heading. Thus, and following the work by Borràs et al. (2009), the first objective of the present study was identifying main QTL for the LS and SE phases in the Henni × Meltan population and comparing them with other genes or loci for developmental time (heading time) reported in the literature.

In addition, leaf appearance and tillering are important processes that determine the crop canopy structure mainly during phases before the onset of stem elongation. Although possible drawbacks on the crop canopy formation when shortening LS (so as to lengthen SE without modifying total time to heading) could be agronomically solved through, for example, increased sowing (plant) density, traits related to early vigour could also compensate genetically for shorter LS. Moreover early vigour has been shown as a beneficial trait in temperate cereals breeding under some Mediterranean conditions (Richards et al., 2002). Borràs et al. (2009) showed, through genetic correlations, that shortening LS would not bring negative implications in traits that could be important for early vigour (i.e. phyllochron and the onset of tillering, or early vigour itself) in the Henni × Meltan population. Given also that little is known on the genetic control of leaf appearance and tillering parameters, key traits on growth and development, the second objective of this study was identifying the genetic control of traits related to these processes and compare them with the genetic control for pre-heading phases.

## 2. Materials and methods

### 2.1. Population and trials

A population of 118 doubled haploid (DH) lines from the cross Henni × Meltan and both parents were studied in four field trials, two locations by two growing seasons. Henni and Meltan are two-rowed spring barley cultivars from Northern Europe, released in 1995 and 1991 respectively and mainly used for feed. Details on the development of the DH-lines are given in Kraakman (2005). Although there could be a narrow genetic base in terms of phenology, the main advantage of this population is that it represents an actual breeding program, as both parents are modern cultivars within the elite European germplasm, in contrast to other studies that use populations derived from parents with phenology patterns extremely different but without a likely application in a realistic breeding program.

The two locations were Gimennells (41°37'N, 0°22'E, 248 m) and Foradada (41°51'N, 1°0'E, 407 m), both in the province of Lleida (Catalonia, North-Eastern Spain). Gimennells is situated in the middle of an irrigated basin, while Foradada is rainfed. The two growing seasons were 2003/04 and 2005/06. Sowing dates were on 18 December in Gimennells and on 29 December in Foradada in 2003. In 2005 sowing dates were on 19 November and 21 November in Gimennells and Foradada, respectively. The experimental design for the four trials consisted of a latinized row and column design with two complete replicates per DH line and the two parents augmented with four commercial cultivars used as checks (a total of 300 plots per trial arranged in 15 rows and 20 columns). Each plot consisted of 8 rows 0.15 m apart and 4 m long. A sowing rate of 350 seeds m<sup>-2</sup> was used in all cases. Further details on the trials are given in Borràs et al. (2009).

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