

# Molecular and comparative mapping for heading date and plant height in oat

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**Abstract** Selection of oat genotypes combining earliness and short plant height could stimulate oat cultivation worldwide. However, the mechanisms involved with the genetic control of heading date and plant height traits are not fully understood to date. This study aimed to identify genomic regions controlling heading date and plant height in two hulled by naked oat populations and to compare these genomic regions with that of other grass species. Recombinant inbred lines of each population and their parents were genotyped by a 6 K BeadChip Illumina Infinium array and assessed for heading date and plant height in two sowing dates. The quantitative trait loci (QTL) affecting these traits were detected by simple interval mapping. The two oat populations showed different genetic mechanisms controlling heading date. A major QTL was identified in one of the populations, mapped into the ‘Mrg33’ consensus linkage group from the current oat map. Two other QTL were detected into the ‘Mrg02’ and ‘Mrg24’ groups, in the second

population. On the other hand, both populations presented the same genomic region controlling plant height. Six SNP markers, mapping on the same linkage group within each population, were associated with the trait, regardless the sowing date, explaining more than 20% of the phenotypic variation. Five of these six markers were mapped into three different linkage groups on the oat consensus map. Genomic regions associated with heading date and plant height in oat seem to be conserved in *Oryza sativa* L. and *Brachypodium distachyon*. Our results provide valuable information for marker-assisted selection in oats, allowing selection for earliness and plant height on early segregating generations.

**Keywords** *Avena sativa* L. · Heading date · Naked oat · Plant height · Quantitative trait loci · SNP markers

## Introduction

The cultivated oat (*Avena sativa* L.) has attracted attention due to its grain nutraceutical properties, even though its cropped area has been decreasing worldwide (Gorash et al. 2017). In temperate countries oat cultivation competes with soybeans, corn and canola, while in subtropical areas it competes with wheat and barley. Therefore, improvement of agronomic traits and adequacy of flowering are necessary to turn oats more competitive and attractive for farmers. Short

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cycle is especially important under subtropical conditions, where at least two crops are cultivated each year. Short stature may contribute to reduce stem lodging (Berry et al. 2004), a major problem of oats. Oat has been extensively employed in human nutrition due to its high content of beta-glucan, which acts increasing immune function (Davis et al. 2004), reducing cholesterol levels (Karmally et al. 2005), blood pressure (Keenan et al. 2002), and glycemic index (Meyer et al. 2000). Furthermore, oats can be used as animal feed, soil cover and as an alternative crop in rotation systems. Despite the nutritional and agricultural relevance of oats, its breeding efforts have been meager compared to other small grains, such as wheat (*Triticum aestivum* L.) and barley (*Hordeum vulgare* L.). In this sense, oat breeders and researchers are looking into different strategies and tools for developing new cultivars with high agronomic performance.

The selection for earliness and short plant height has been aimed by different oat breeding programs. Heading at the right time, under favorable environmental conditions, is essential for achieving high grain yields, once number of heads per area, and number of florets and grain per head are key yield components. Reduced plant height may help to decrease crop losses due to lodging. However, lodging resistance is more related to stem stiffness, when lodging is related to stem failure (stem lodging). Short stature may even not contribute to lodging resistance when it is related to root lodging (Berry et al. 2004). The use of oat dwarfing genes aiming to improve lodging tolerance has been hampered due to its negative relationship with grain yield and quality in some environments (Milach et al. 2002). In this way, the identification of genomic regions associated with heading date and plant height may represent a decisive step to develop a new oat ideotype.

Linkage mapping on oats has allowed the identification of quantitative trait loci (QTL) affecting traits of major importance, such as heading date (Nava et al. 2012), aluminium tolerance (Schneider et al. 2015), crown rust resistance (Babiker et al. 2015), plant height (De Koeyer et al. 2004; Tanhuanpää et al. 2010), naked grains (Ubert et al. 2017), and grain quality traits (Herrmann et al. 2014). Detection of these QTL may create important tools for oat breeders, allowing marker assisted selection for superior agronomic traits on early segregating generations. A QTL

can be widely applied in plant breeding if detected in different mapping populations. However, its use is often restricted to a specific genetic background. In this context, the proper selection of the parental lines that will compose a mapping population is a decisive step for the detection of useful QTL for plant breeding programs. The development of a mapping population from a cross between hulled by naked parental lines allowed the detection of QTL associated with 16 agronomic, kernel, and chemical composition traits of oat (De Koeyer et al. 2004). Although little effort has been applied to improve naked varieties in comparison to hulled ones, crosses involving hulled by naked genotypes may transfer desirable alleles to the hulled oat germplasm pool (De Koeyer et al. 2004).

An oat consensus linkage map was recently developed using data from a cDNA-derived single-nucleotide polymorphism (SNP) array and genotyping-by-sequencing collected from 12 biparental populations (Chaffin et al. 2016). After evaluating 682 oat lines in different locations and years, Esvelt Klos et al. (2016) identified SNP association with heading date mainly on the consensus linkage groups 'Mrg02', 'Mrg12', 'Mrg13', and 'Mrg24'. However, molecular studies dedicated to identify genomic regions associated with plant height on oats are scarce in the literature. Recently, a genome-wide analysis for plant height in a European oat collection identified genomic regions associated with the trait on consensus linkage groups 'Mrg01', 'Mrg08', 'Mrg09', 'Mrg11', and 'Mrg13' (Tumino et al. 2017). Currently, the selection for plant height on oats is based exclusively on the phenotype. The identification of molecular markers highly associated with this trait could be a decisive step for the genetic progress of the trait on oats. The goals of the present study were to identify molecular makers associated with genomic regions controlling heading date and plant height in two hulled by naked oat populations and to compare these genomic regions with other grass species.

## Materials and methods

### Plant materials

Two mapping populations of oat recombinant inbred lines (RILs) were developed by single crosses, involving four oat genotypes: 'UFRGS 01B7114-1-

3' by 'UFRGS 006013-1' and 'URS Taura' by 'UFRGS 017004-2'. The names of these populations are abbreviated hereby as 'U01B/U006' and 'UTau/U017', respectively. The oat populations were obtained by modified single seed descent method, where one panicle from each plant was harvested each generation and around 30 seeds were sown to advance the next one, from  $F_2$  to  $F_5$ , and all the seeds from each RIL were bulked on  $F_{5,6}$ . 'UFRGS 01B7114-1-3' and 'URS Taura' are hulled oat genotypes, while 'UFRGS 006013-1' and 'UFRGS 017004-2' are naked oat lines. The naked lines were derived from the same cross, 'Coker 492/Starter-1//UFRGS 8'. The hulled parent 'UFRGS 01B7114-1-3' has the pedigree 'Pc68/5\*Starter ( $F_4$ )//UFRGS 10', while 'URS Taura' is descent from the cross 'UFRGS 970216-2 ( $F_{3,4}$ )//UFRGS 970461 ( $F_{7,8}$ )'. The 'URS Taura' genitor 'UFRGS 970216-2' is derived from 'UFRGS 881971//Pc68/5\*Starter ( $F_4$ )'. 'URS Taura' is a commercial oat variety, highly appreciated by Brazilian farmers due to its agronomic type, which include reduced plant height, short cycle, lodging resistance, and high grain yield. It is also widely adopted by the milling industry in Brazil due to its high milling yield. All parental lines and RIL populations were developed by the Federal University of Rio Grande do Sul (UFRGS) Oat Breeding Program.

### Field experiments

A sample of 93 and 91 RILs at the  $F_{5,7}$  generation, representing the 'U01B/U006' and 'UTau/U017' mapping populations, respectively, and their parental lines were evaluated in a field experiment carried out in 2014, in two sowing dates, at the UFRGS Agronomy Experimental Station, located in Eldorado do Sul city, RS state, Southern Brazil. The first sowing date was June 12th and the second July 4th. The first half of June is the best sowing window for this region, while July sowing dates usually result in shorter plant cycle and plant growth, leading to lower grain yield potential. The experiment was conducted in a randomized complete block design, with two replicates. Each experimental unit was composed by a hill plot of approximately 15 cm long. Each plot was spaced 0.30 m apart within rows, while rows were spaced 0.40 m apart. Sowing was carried out manually at different densities; hulled genotypes were sown at a rate of 15 seeds per hill, while naked ones were sown

at a rate of 20 seeds per hill. Two sowing densities were used due to the lower germination of naked seeds compared to hulled ones. The base fertilization was  $300 \text{ kg ha}^{-1}$  of a 5-30-15 N-P-K formula, and topdressing nitrogen, in the form of dry urea, was applied twice, when plants showed three and six extended leaves, at a rate of  $33 \text{ kg ha}^{-1}$  of N per application. Pests and fungal diseases were chemically controlled as needed and weeds were manually controlled.

### Phenotypic data

Parental lines and RILs were assessed for heading date and plant height. Heading date was recorded as the number of days from plants' emergence to the moment where 50% of the plants showed panicles emerged from the main stem (stage 55 from Zadoks' scale; Zadoks et al. 1974) in each hill. Plant height was measured as the distance, in cm, from soil surface to panicle's tip, and expressed as the average of three plants measured in each hill. Plant height was recorded when plants reached the physiological maturity stage (stage 89 from Zadoks' scale; Zadoks et al. 1974).

### Statistical analyses

Phenotypic data for heading date and plant height were analyzed separately. Frequency distribution analyses were carried out in order to verify the phenotypic variation in each population by sowing date, using the average of the two replicates from each sowing date. The number of phenotypic classes was defined by  $k = \sqrt{n}$ , where  $k$  is the number of phenotypic classes and  $n$  is the number of RILs in each population. Analysis of variance for each trait was also performed in order to: (1) identify significant differences among RILs within each sowing date and population; (2) identify significant differences among RILs between sowing dates, within population; (3) verify if there was genotype by sowing date interaction. All statistical procedures were carried out using the SAS 9.4 software (SAS Institute Inc., Cary, NC, USA).

### Linkage mapping and QTL analyses

RIL populations and their parental lines were assayed with 6000 genome-wide SNP markers, through a 6 K BeadChip Illumina Infinium array as described by

Tinker et al. (2014). The genotypic analysis was performed at the Biosciences Research Laboratory, United States Department of Agriculture (USDA)—Agricultural Research Service, located in Fargo, North Dakota, USA. A genetic linkage map was generated for each population using the JoinMap 4.0 software (Van Ooijen 2006), as described by Ubert et al. (2017). Linkage groups were formed using a logarithm of the odds (LOD) score threshold of seven and a maximum frequency of recombination of 40%. The Haldane mapping function was used to convert recombination frequencies into centimorgans (cM). QTL affecting heading date and plant height traits were detected by simple interval mapping using the Mapping of Quantitative Trait Loci (MQTL) software (Tinker and Mather 1995), taking the average of each sowing date for each trait. The main effect of a QTL was estimated by statistical tests that determine the likelihood ratio, indicating if this QTL is located between linked adjacent markers. A QTL was declared as true when the maximum estimated value for the statistical test was above the established significance level. The experiment-wide false positive rate for QTL main effects was estimated based on 10,000 random permutations. Results of the statistical tests were transformed to LOD scores by multiplying by 0.2171 to facilitate the interpretation of the results, as described by Xu (2013). Manhattan plots for the statistical test values of each SNP marker were generated using the R package, considering the genetic position of markers presented by Ubert et al. (2017).

### Comparative mapping

SNP markers with significant effects for heading date and plant height were located in the current consensus map of hexaploid oat (Chaffin et al. 2016). Basic linear alignment sequence tool (BLAST; Altschul et al. 1990) was used to verify the nucleotide similarity of each significant marker identified in this study with genome sequences from grasses species available at GenBank (<https://www.ncbi.nlm.nih.gov/genbank>). Furthermore, grass genome sequences showing high nucleotide similarity to oat markers were located on rice (<http://rapdb.dna.affrc.go.jp/>) and *Brachypodium distachyon* reference genomes (<https://phytozome.jgi.doe.gov/>). Rice and/or *B. distachyon* DNA sequences aligned to the oat markers, and showing conservation higher than 80%, were used to identify chromosome

segments on the physical chromosome maps of these two model grass species. Only chromosomal segments flanked by the conserved sequences were analyzed, because they have a higher probability of containing candidate causal genome regions than any adjacent region (not flanked by markers). The flanked chromosomal segments were meticulously exploited in order to identify possible genes associated with the control of the evaluated traits.

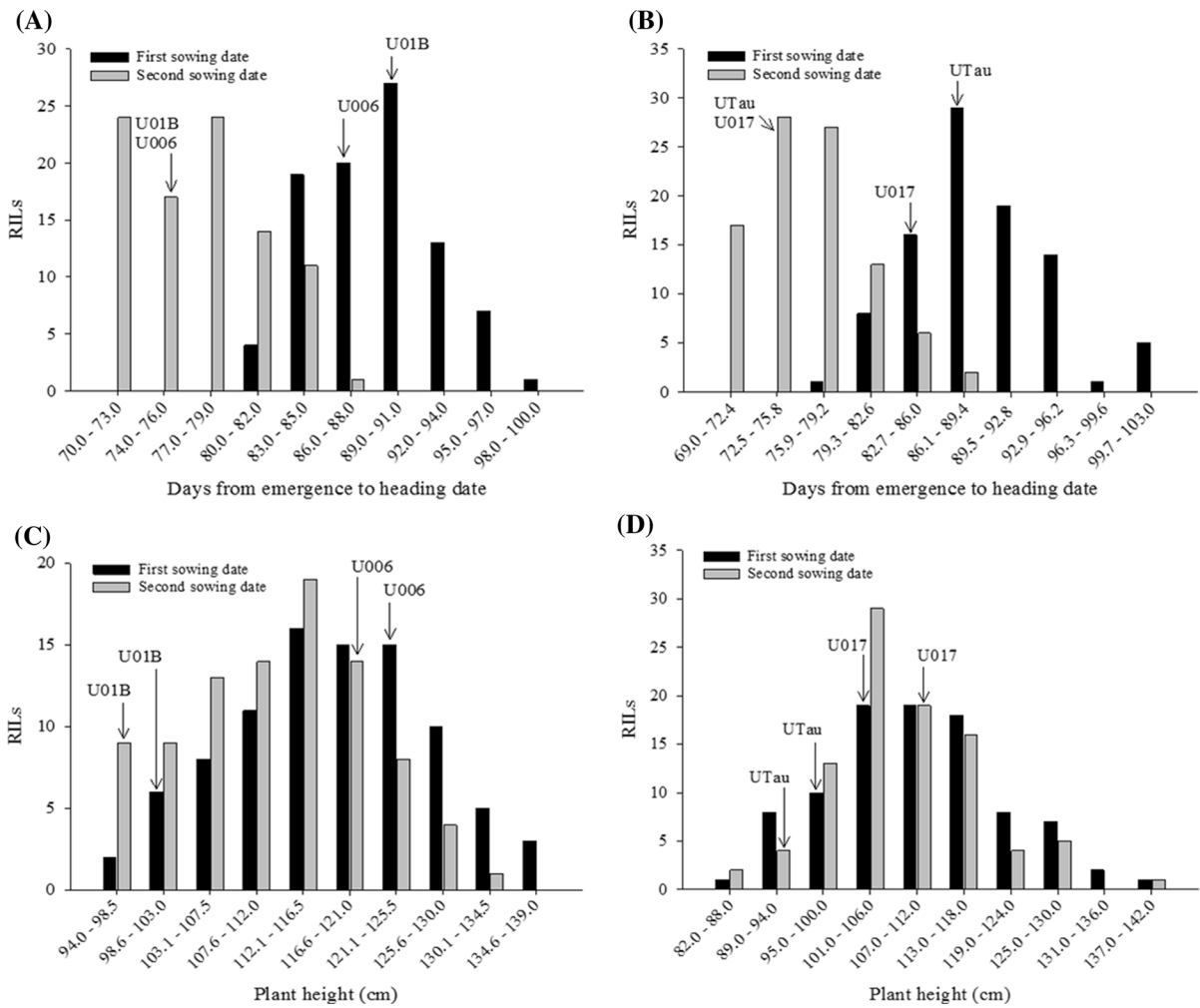
Based on the aligned sequences, comparative maps were generated in order to illustrate the synteny among oat, rice, and *B. distachyon* using the MapChart software (Voorrips 2002). Oat maps refer to linkage association groups from the current oat consensus map and the maps generated by Ubert et al. (2017), therefore they are genetic maps reporting distances in cM between SNP markers. For rice and *B. distachyon*, they are physical maps reporting base pair distances between conserved DNA sequences.

## Results

### Phenotypic assessment for heading date

For the ‘U01B/U006’ population, on the first sowing date, the number of days from emergence to heading ranged from 80 to 100 days among RILs, and averaged as 90 and 87 days for the parental lines ‘UFRGS 01B7114-1-3’ and ‘UFRGS 006013-1’, respectively. On the second sowing date, heading date ranged from 70 to 87 days among RILs, and average as 76 and 74 days for the respective parents (Fig. 1a). For the ‘UTau/U017’ population, days from emergence to heading on the first sowing date varied from 79 to 103 among RILs, and had an average of 86 days for ‘URS Taura’ and 84 days for ‘UFRGS 017004-2’. For the second sowing date, it ranged from 69 to 88 days among RILs, while it was 74 days for ‘URS Taura’ and 75 for ‘UFRGS 017004-2’ (Fig. 1b). These results indicate that the parental lines of each cross showed similar phenotypes for heading date on each sowing date. Despite this phenotypic similarity, a wide variation was observed among the derived RILs.

Significant differences for heading date were identified among RILs and between sowing dates, while no significance was found for the interaction between genotype and sowing date, for both populations (Table 1). RILs of the population ‘U01B/U006’ had a



**Fig. 1** Frequency distribution for heading date and plant height on oat mapping populations ‘U01B/U006’ (a, c) and ‘UTau/U017’ (b, d). The parental lines are indicated by arrows.

U01B = UFRGS 01B7114-1-3; U006 = UFRGS 006013-1; UTau = URS Taura; and U017 = UFRGS 017004-2

reduction of 11 days on the average number of days from emergence to heading, from the first to the second sowing date (Table 1). Similarly, RILs of the ‘UTau/U017’ population presented an average reduction of 13 days from emergence to heading on the second sowing date relative to the first one (Table 1).

Location of QTL for heading date

One and two QTL were detected for heading date on the ‘U01B/U006’ and ‘UTau/U017’ mapping populations, respectively (Fig. 2). For the ‘U01B/U006’ population, eight SNP markers were associated with

the QTL, mapping into the linkage group 21 and covering a genetic region of 9.5 cM (Table 2; Fig. 2a, b). This QTL explained more than 24% of the phenotypic variation observed for heading date, regardless of the sowing date (Table 2). This QTL had a positive effect on heading date of about four to five days (Table 2). Once the allele markers from the parent ‘UFRGS 01B7114-1-3’ were also present in the RILs with later heading dates, this parent must have alleles contributing to increase the number of days from emergence to heading in the population.

For the ‘UTau/U017’ mapping population two QTL affecting heading date were detected on both sowing

**Table 1** Summary of variance analyses for heading date and plant height in two oat mapping populations

Cause of variation	DF	Mean square	
		Heading date	Plant height
'U01B/U006' population			
Block/sowing date	2	15.96	56.07
Genotype (G)	90	63.95**	317.31**
Sowing date (SD)	1	12289.08**	2971.43**
G × SD	90	2.86 <sup>ns</sup>	22.00 <sup>ns</sup>
Experimental error	180	4.66	34.79
Average 1st SD	–	88	117
Average 2nd SD	–	77	112
CV 1st SD (%)	–	2.89	5.25
CV 2nd SD (%)	–	2.18	5.04
'UTau/U017' population			
Block/sowing date	2	3.60	18.22
Genotype (G)	92	83.02**	388.04**
Sowing date (SD)	1	14731.94**	325.55 <sup>ns</sup>
G × SD	92	3.04 <sup>ns</sup>	32.24 <sup>ns</sup>
Experimental error	184	2.77	33.75
$\bar{X}$ 1st SD	–	89	109
$\bar{X}$ 2nd SD	–	76	107
CV 1st SD (%)	–	2.07	6.59
CV 2nd SD (%)	–	1.93	3.66

DF degrees of freedom; CV coefficient of variation

\*Significant at 5% probability of error by the F test ( $p \leq 0.05$ ); \*\*significant at 1% probability of error by the F test ( $p \leq 0.01$ ); <sup>ns</sup> not significant ( $p > 0.05$ )

dates. QTL-1 was present on the linkage group 10, while QTL-2 was detected on linkage group 30. QTL-1 was associated with six SNP markers in the first sowing date (Fig. 2c), covering 16.2 cM, and explaining from 17 to 22% of the phenotypic variation (Table 2), while just one marker maintained its significance on the second sowing date (Fig. 2d). QTL-2 showed the same five associated SNP markers on both sowing dates (Table 2; Fig. 2c, d), covering 5.2 cM, and explaining from 18 up to 21% of the phenotypic variation, on the first sowing date, and from 22 up to 25%, on the second one (Table 2). These QTL had opposing effects on heading date of about four to five days. QTL-1 had a positive effect, while QTL-2 showed a negative effect (Table 2). Allele markers associated with these effects came from the parent 'URS Taura'.

### Comparative mapping for heading date

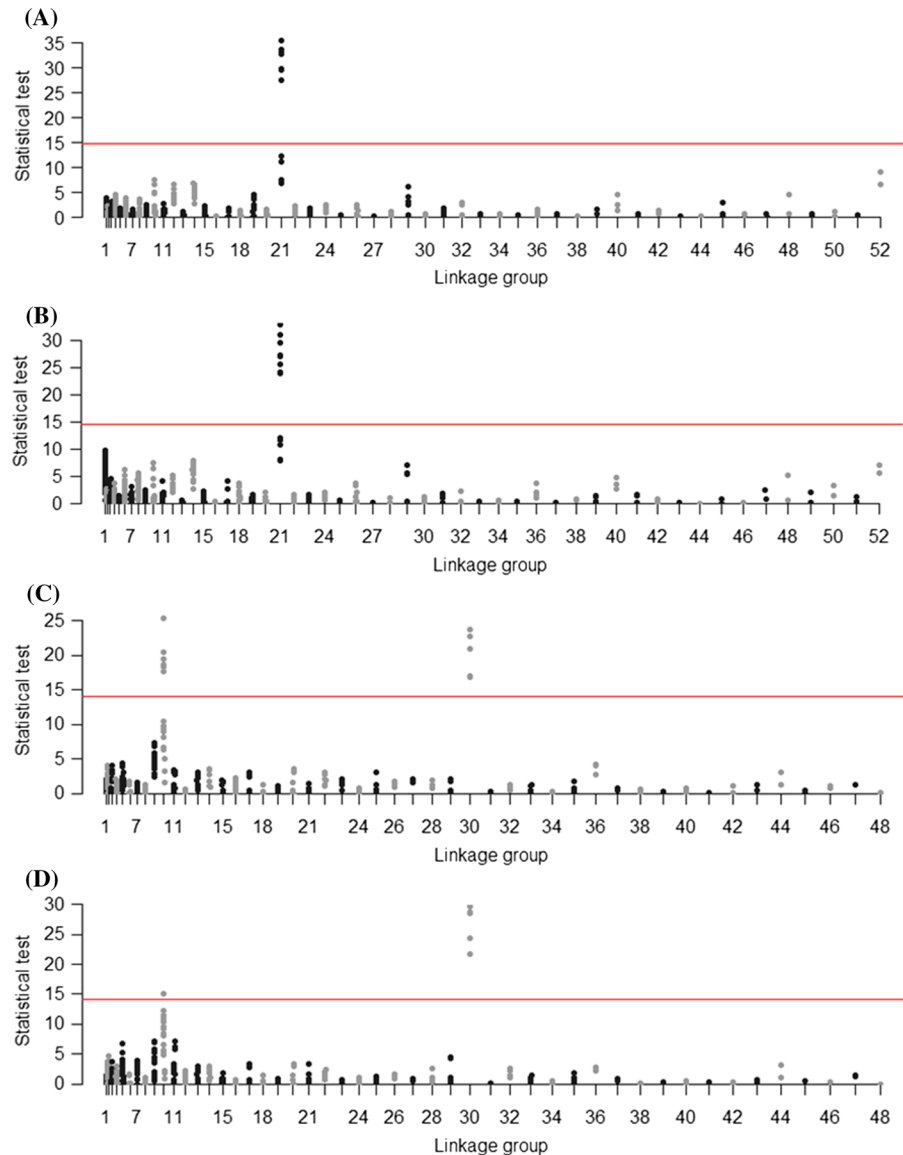
Comparative mapping was carried out to locate specific positions of SNP markers associated with heading date in our study on the current oat consensus map (Chaffin et al. 2016) and on the rice and *B. distachyon* genomes. For population 'U01B/U006', four SNP markers located on the linkage group 21, GMI\_ES14\_c18564\_370, GMI\_ES14\_c8262\_683, GMI\_ES01\_c9256\_320, and GMI\_GBS\_1769, were located into the linkage group 'Mrg33' from the oat consensus map. The other four significant SNP markers were not included on the oat consensus map (Table 2; Fig. 3).

Three significant SNP markers for heading date, on 'U01B/U006' population, were conserved in the rice chromosome 4, one of which was also conserved in the *B. distachyon* chromosome 5. Although the marker GMI\_ES\_LB\_8325 did not map on the current oat consensus map, it showed a nucleotide similarity of 80% to the Os04t0349500-01 rice locus (Fig. 3; Supplemental Table 1). The marker GMI\_ES14\_c8262\_683, located on 'Mrg33' of the oat consensus map, revealed 86% nucleotide similarity to the Os04t0379300-01 rice locus (Fig. 3; Supplemental Table 1). The third SNP marker, GMI\_ES01\_c9256\_320, also mapped on oat consensus linkage group 'Mrg33', exhibited 83% nucleotide similarity to the rice locus Os04t0431100-01 and to the *B. distachyon* locus Bradi5g10250 (Fig. 3).

On the rice chromosome 4, the region flanked by loci Os04t0379300-01 and Os04t0431100-01 carries two important genetic factors associated with heading date control: a photoperiod responsive protein and the SET DOMAIN GROUP 708 (SDG708) protein, a histone H3 lysine 36-specific methyltransferase (Supplemental Table 1). This methyltransferase is also present at the *B. distachyon* chromosome 5 (Bradi5g10110), located very close (0.1 Mbp) to the Bradi5g10250 locus, which showed nucleotide similarity to the oat SNP marker GMI\_ES01\_c9256\_320 (Fig. 3).

The SNP markers associated with heading date on 'UTau/U017' population, which mapped on linkage group 10 and 30, were located into linkage groups 'Mrg02' and 'Mrg24' from the oat consensus map, respectively. The SNP markers on 'Mrg02' covered a region of 10.9 cM, while on 'Mrg24' the markers covered a region of 6.9 cM (Fig. 4). From the six

**Fig. 2** Manhattan plots for heading date on the mapping populations ‘U01B/U006’ (‘a’ and ‘b’) and ‘UTau/U017’ (‘c’ and ‘d’). ‘a’ and ‘c’ corresponds to the first sowing date, while ‘b’ and ‘d’ represents the second one. Markers’ position is relative to the genetic maps developed by Ubert et al. (2017). SNP markers are indicated by points. Linkage groups are shown alternately in black and grey in order to facilitate the visualization of significant SNPs in different linkage groups. The red horizontal line represents the significance threshold. (Color figure online)



markers located on ‘Mrg02’, one SNP marker, GMI\_DS\_LB\_7722, showed 80% nucleotide similarity to a rice sequence, at position 2,515,235–2,515,367 of rice chromosome 6, and 88% sequence similarity to a genome region of *B. distachyon* chromosome 1, at position 49,573,619–49,573,728 (Fig. 4). Another SNP marker, GMI\_ES\_LB\_11316, exhibited 86% nucleotide similarity to the locus Os06t0168600-01, also on rice chromosome 6, and 90% similarity to the locus Bradi1g48170.1, on *B. distachyon* chromosome 1 (Fig. 4). On the rice genomic region flanked by the conserved loci, which covered a physical distance of

934 Kbp, three important genes for heading date were identified: *HEADING DATE 3B (Hd3b)/RICE FLOWERING LOCUS T1 (RFT1)*; *HEADING DATE 3A (Hd3a)*; and the MADS-box gene *OsMADS5* (Fig. 4; Supplemental Table 1). As verified in rice, the MADS-box gene *MADS5* was also identified in the conserved region of *B. distachyon* chromosome 1 (Supplemental Table 1).

From the five SNP markers mapped on linkage group 30 of population ‘UTau/U017’ and located on consensus group ‘Mrg24’, two markers, GMI\_ES14\_c15338\_376 and GMI\_ES17\_c18602\_497, showed 76

**Table 2** Summary of QTL affecting heading date on the ‘U01B/U006’ and UTau/U017’ mapping populations

SNP marker <sup>‡</sup>	Consensus group <sup>†</sup>	Linkage group	Map position (cM)	LOD score	Main effect	P. variation SNP (%)
<i>U01B/U006 (first sowing date)</i>						
GMI_ES_CC9561_343	–	21	0.0	6.45	4.59	22.95
GMI_ES14_c18564_370	Mrg33	21	1.6	7.27	4.78	23.90
QTL peak	Mrg33	21	–	–	–	–
GMI_ES15_c15940_121	–	21	3.1	7.66	4.84	24.20
GMI_ES_CC16664_207	–	21	4.9	7.19	4.76	23.80
GMI_ES_LB_8325	–	21	5.9	6.38	4.59	22.95
GMI_ES14_c8262_683	Mrg33	21	6.5	5.95	4.40	22.00
GMI_ES01_c9256_320	Mrg33	21	8.1	7.08	4.67	23.35
GMI_GBS_17697	Mrg33	21	9.5	5.97	4.24	21.20
<i>U01B/U006 (second sowing date)</i>						
GMI_ES_CC9561_343	–	21	0.0	5.88	4.59	27.00
GMI_ES14_c18564_370	Mrg33	21	1.6	6.71	4.80	28.24
QTL peak	Mrg33	21	–	–	–	–
GMI_ES15_c15940_121	–	21	3.1	7.14	4.88	28.71
GMI_ES_CC16664_207	–	21	4.9	6.38	4.71	27.71
GMI_ES_LB_8325	–	21	5.9	5.54	4.49	26.41
GMI_ES14_c8262_683	Mrg33	21	6.5	5.23	4.33	25.47
GMI_ES01_c9256_320	Mrg33	21	8.1	5.91	4.49	26.41
GMI_GBS_17697	Mrg33	21	9.5	5.19	4.15	24.41
<i>UTau/U017 (first sowing date)</i>						
GMI_GBS_29651	Mrg02	10	24.1	3.97	4.55	18.96
GMI_GBS_22030	Mrg02	10	25.3	4.21	4.65	19.38
GMI_GBS_85630	Mrg02	10	29.7	3.84	4.12	17.17
GMI_DS_LB_7722	Mrg02	10	30.9	4.06	4.23	17.63
GMI_ES01_c11287_335	Mrg02	10	35.7	4.43	4.80	20.00
QTL-1 peak	Mrg02	10	–	–	–	–
GMI_ES_LB_11316	Mrg02	10	40.3	5.51	5.37	22.38
GMI_ES17_c18602_497	Mrg24	30	0.0	3.69	– 4.35	18.13
GMI_GBS_2049	Mrg24	30	1.3	3.65	– 4.39	18.29
GMI_ES03_c5706_921	Mrg24	30	2.9	4.95	– 4.94	20.58
GMI_ES14_c6751_372	Mrg24	30	3.9	4.56	– 4.87	20.29
QTL-2 peak	Mrg24	30	–	–	–	–
GMI_ES14_c15338_376	Mrg 24	30	5.2	5.15	– 5.10	21.25
<i>UTau/U017 (second sowing date)</i>						
QTL-1 peak	Mrg02	10	–	–	–	–
GMI_ES_LB_11316	Mrg02	10	40.3	3.26	3.71	19.53
GMI_ES17_c18602_497	Mrg24	30	0.0	5.28	– 4.45	23.42
GMI_GBS_2049	Mrg24	30	1.3	4.71	– 4.30	22.63
GMI_ES03_c5706_921	Mrg24	30	2.9	6.43	– 4.83	25.42
GMI_ES14_c6751_372	Mrg24	30	3.9	6.19	– 4.86	25.58
QTL-2 peak	Mrg24	30	–	–	–	–

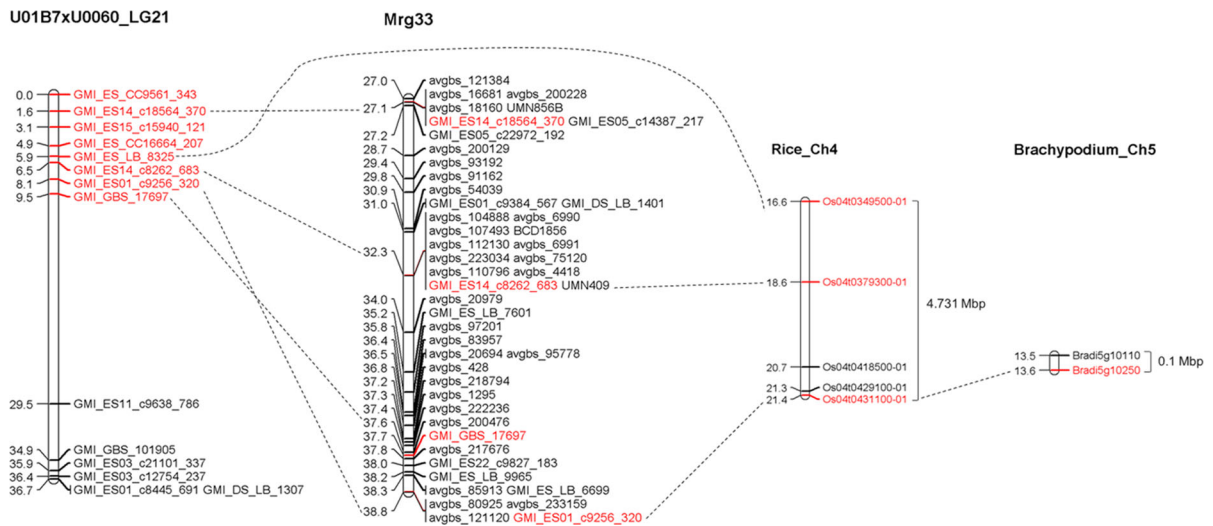


**Table 2** continued

SNP marker <sup>‡</sup>	Consensus group <sup>†</sup>	Linkage group	Map position (cM)	LOD score	Main effect	P. variation SNP (%)
GMI_ES14_c15338_376	Mrg33	30	5.2	6.25	– 4.85	25.53

<sup>‡</sup>Nucleotide sequences of each SNP maker is available at <https://triticeaetoolbox.org/oat/>

<sup>†</sup>Consensus group based on Chaffin et al. (2016)



**Fig. 3** Comparative mapping of the oat SNP markers associated with heading date on the ‘U01B/U006’ mapping population. Dotted lines show the SNP markers’ position relative to the

oat consensus group ‘Mrg33’ or rice loci located on chromosome four (Rice Ch4) and *B. distachyon* loci located on chromosome five (Brachypodium\_Ch5)

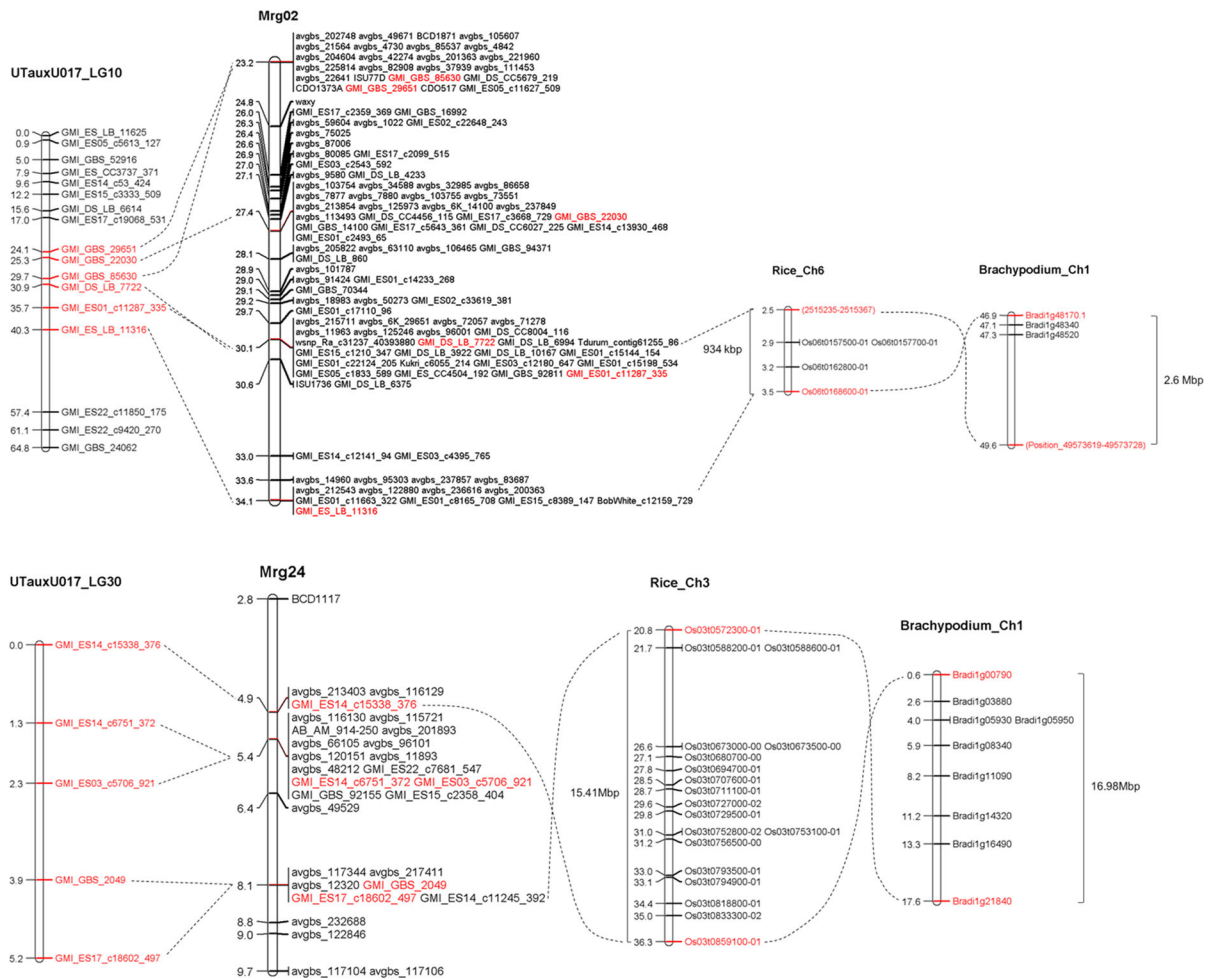
and 86% nucleotide similarity with the rice loci Os03t0859100-01 and Os03t0572300-01, located on chromosome 3, respectively (Fig. 4). The rice chromosomal segment between conserved loci, relative to oat, covered a 15.41 Mbp physical distance (Fig. 4) and harbors a large number of genes affecting heading date, including: *SLENDER1 (SLN1)*; *CONSTANS-like 10*; *APETALA1 (API)/FRUITFULL (FUL)*-like genes; MADS-box transcription factor *OsMADS34*; *EARLY FLOWERING1 (ELF1)*; and *SQUAMOSA-PROMOTER BINDING PROTEIN-LIKE8 (SPL8)* (Supplemental Table 1).

The same two SNP markers mentioned right above, GMI\_ES14\_c15338\_376 and GMI\_ES17\_c18602\_497 also showed 88 and 86% of nucleotide similarity with the *B. distachyon* loci Bradi1g00790 and Bradi1g21840, respectively. These two *B. distachyon* loci were located on chromosome 1

and covered a physical distance of 16.98 Mbp (Fig. 4). Some genes affecting heading date were also identified between them, such as: genes encoding CASEIN KINASES1 proteins; MADS-box transcription factor *OsMADS14*, which is a homologue to *API* gene; and a gene encoding the DELLA protein *SLN1* (Supplemental Table 1).

#### Phenotypic assessment for plant height

RILs of the ‘U01B/U006’ population presented a plant height average of 117 cm, varying from 94 to 139 cm, on the first sowing date, and had an average of 112 cm on the second sowing date, ranging from 95 to 131 cm (Table 1; Fig. 1c). The parental line ‘UFRGS 01B7114-1-3’ showed average plant height of 100 and 93 cm, on the first and the second sowing dates, respectively. The other parental line, ‘UFRGS



**Fig. 4** Comparative mapping of the oat SNP markers associated with heading date on the ‘UTau/U017’ mapping population. Dotted lines show the SNP markers’ position relative to the oat consensus groups ‘Mrg02’ and ‘Mrg24’, rice loci located on

chromosomes three and six (Rice\_Ch3 and Rice\_Ch6), and *B. distachyon* loci located on chromosome one (Brachypodium\_Ch1)

006013-1’, was taller than ‘UFRGS 01B7114-1-1’ on both sowing dates, with an average of 123 and 120 cm, on the first and the second sowing dates, respectively (Fig. 1c). In this population, the genotype and sowing date main effects were significant, while the interaction between them was not (Table 1).

RILs from the ‘UTau/U017’ population presented similar plant height averages between the first (109 cm) and second (107 cm) sowing dates (Table 1). For the first sowing date plant height among RILs ranged from 82 to 142 cm, and from 85 to 137 cm on the second one (Fig. 1d). The parent ‘URS Taura’ showed an average plant height of 99 cm

on the first sowing date, and 92 cm on the second one, while ‘UFRGS 017004-2’ presented an average plant height of 106 and 108 cm, on the first and second sowing dates, respectively (Fig. 1d). This population presented a higher phenotypic variation for plant height than the ‘U01B/U006’ population, regardless of the sowing date (Fig. 1c, d). In addition, only the genotype main effect was significant for the ‘UTau/U017’ population, indicating that neither sowing date nor genotype by sowing date interaction influenced the plant height in this population (Table 1).

## Location of QTL for plant height

Genomic regions associated with plant height were identified on both oat populations. For population ‘U01B/U006’ three major QTL were found associated with the trait. The QTL-1 was detected on both sowing dates, while the other two were identified on either one or the other sowing date (Table 3; Fig. 5a, b). The QTL-1 was significant on both sowing dates and mapped on linkage group 8, being associated with 14 SNP markers on the first sowing date, covering a total genetic region of 22.9 cM (Table 3 and Fig. 5a). All 14 SNP markers significantly associated with plant height on linkage group 8, on the first sowing date, were also detected on the second one, plus other three SNP markers, covering a total of 46 cM (Table 3; Fig. 5b). QTL-1 had a negative effect on plant height about 8–10 cm on the first sowing date, explaining between 18 and 21% of the phenotypic variation. On the second sowing date, this same QTL explained about 19–24% of the variation, with a negative effect between 7 and 9 cm on plant height (Table 3). Allele markers associated with these negative effects came from the hulled parent ‘UFRGS 01B7114-1-3’. The second QTL for plant height, named QTL-2, was detected only on the first sowing date on population ‘U01B/U006’. QTL-2 was associated with only two SNP markers and located on linkage group 21, covering a region of 1.8 cM. This QTL had a positive effect of about 8 cm on plant height and explained about 18% of the phenotypic variation (Table 3; Fig. 5b). The third QTL for the trait, named as QTL-3, was located on linkage group 3 and detected only on the second sowing date, associated with three SNP markers, covering 2.9 cM. This QTL, as observed for QTL-1, also had a negative effect on plant height of about 7 cm, and explained 20–21% of the phenotypic variation (Table 3; Fig. 5b). Both QTL-2 and QTL-3 effects are associated with allele markers coming from the hulled parent ‘UFRGS 01B7114-1-3’.

For population ‘UTau/U017’ only one QTL was detected for plant height, on the linkage group 5, associated with 18 SNP markers on the first sowing date, and 19 SNP markers on the second one, covering a region of 38.1 cM on both sowing dates (Table 4; Fig. 5c, d). This QTL had negative effect of 8–11 cm on plant height, on both sowing dates, which is associated with allele markers from the hulled parent ‘URS Taura’. The phenotypic variation explained by

each associated SNP marker varied from 15 to 19% on the first sowing date, and from 16 to 21% on the second one (Table 4).

## Comparative mapping for plant height

Six SNP markers were consistently associated with plant height on both populations, regardless of sowing date, mapping on linkage groups 8 on ‘U01B/U006’ population and linkage group 5 on ‘UTau/U017’ population (Tables 3, 4). From these six SNP, five were located on the current oat consensus map (Chaffin et al. 2016), on ‘Mrg09’, ‘Mrg20’, and ‘Mrg21’ (Tables 3, 4; Fig. 6), as well as on the rice and *B. distachyon* genomes. A syntenic chromosome region among oat, rice, and *B. distachyon* was identified for plant height. The oat SNP markers GMI\_ES01\_c27869\_512 and GMI\_ES05\_c5597\_803 mapped on consensus linkage groups ‘Mrg20’ and ‘Mrg9’, respectively. These markers presented nucleotide similarity of 85% to locus Os03t0719900-02 and 82% to locus Os03t0815200-01, located on rice chromosome 3, covering a region of about 5 Mbp (Fig. 7). Important genes affecting plant height are located on the rice chromosomal fragment flanked by these loci, such as: *SCARECROW-LIKE7* (*SCR7*), which plays an important role on gibberellin signaling; auxin responsive genes; other genes acting on plant hormones; and MYB gene family members (Fig. 7 and Supplemental Table 2). The same oat SNP markers, GMI\_ES01\_c27869\_512 and GMI\_ES05\_c5597\_803, present 87 and 84% of nucleotide similarity with the loci Bradi1g10490 and Bradi1g04140 from *B. distachyon*, respectively (Fig. 7). These loci are located on Brachypodium chromosome 1 and they are flanking important genetic factors for plant height, such as: an auxin transcriptional regulator protein; an auxin transporter protein; an auxin responsive gene; and MYB gene family members (Fig. 7; Supplemental Table 2).

## Discussion

### Heading date

Even though the parental lines of the two studied oat populations were not contrasting for heading date, a wide phenotypic variation was seen for the trait among

**Table 3** Summary of QTL affecting plant height on the ‘U01B/U 006’ mapping population

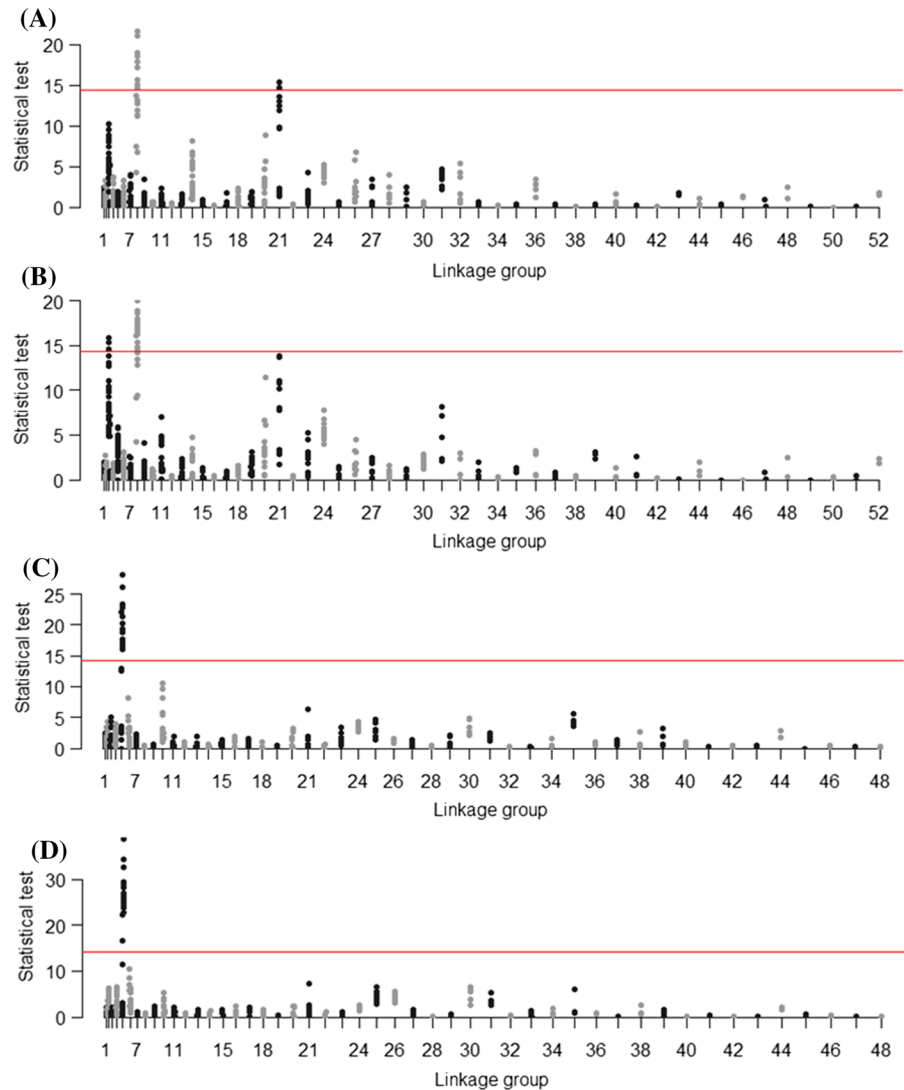
SNP marker <sup>‡</sup>	Consensus group <sup>†</sup>	Linkage group	Map position (cM)	LOD score	Main effect	P. variation SNP (%)
<i>Plant height (first sowing date)</i>						
<b>GMI_GBS_4508</b>	Mrg21	8	11.7	3.17	– 8.33	18.51
GMI_GBS_96826	Mrg20	8	14.5	3.28	– 8.28	18.40
GMI_ES_LB_11633	Mrg20	8	14.8	3.39	– 8.44	18.76
GMI_ES03_c9122_309	Mrg20	8	15.7	3.39	– 8.43	18.73
GMI_ES01_c2436_405	Mrg20	8	18.1	3.41	– 8.45	18.78
GMI_ES21_c6485_431	Mrg20	8	18.4	4.02	– 9.17	20.38
GMI_ES15_c8569_380	Mrg20	8	18.4	4.02	– 9.17	20.38
<b>GMI_GBS_100319</b>	Mrg20	8	19.7	3.86	– 8.95	19.89
<b>GMI_ES05_c5597_803</b>	Mrg09	8	21.4	3.39	– 8.43	18.73
<b>GMI_ES15_c8938_386</b>	Mrg21	8	26.9	3.73	– 8.01	17.80
<b>GMI_DS_LB_10411</b>	–	8	28.7	4.69	– 8.87	19.71
GMI_ES17_c7110_570	Mrg20	8	33.5	3.71	– 8.76	19.47
GMI_GBS_25081	Mrg20	8	33.9	4.12	– 9.26	20.58
QTL-1 peak	Mrg20	8	–	–	–	–
<b>GMI_ES01_c27869_512</b>	Mrg20	8	34.6	4.56	– 9.64	21.42
GMI_ES15_c15940_121	–	21	3.1	3.19	7.98	17.73
QTL-2 peak	–	21	–	–	–	–
GMI_ES_CC16664_207	–	21	4.9	3.32	8.21	18.24
<i>Plant height (second sowing date)</i>						
GMI_ES02_c1838_173	Mrg04	3	32.3	3.34	– 7.20	20.00
QTL-3 peak	Mrg04	3	–	–	–	–
GMI_GBS_13021	Mrg04	3	33.5	3.45	– 7.41	20.58
GMI_ES14_c2341_405	Mrg04	3	35.2	3.17	– 7.22	20.06
GMI_ES05_c3954_482	Mrg21	8	9.8	3.50	– 7.76	21.56
<b>GMI_GBS_4508</b>	Mrg21	8	11.7	3.71	– 8.03	22.31
GMI_GBS_96826	Mrg20	8	14.5	3.60	– 7.77	21.58
GMI_ES_LB_11633	Mrg20	8	14.8	3.60	– 7.78	21.61
GMI_ES03_c9122_309	Mrg20	8	15.7	3.82	– 7.99	22.19
GMI_ES01_c2436_405	Mrg20	8	18.1	3.65	– 7.83	21.75
GMI_ES21_c6485_431	Mrg20	8	18.4	4.10	– 8.30	23.06
GMI_ES15_c8569_380	Mrg20	8	18.4	4.10	– 8.30	23.06
<b>GMI_GBS_100319</b>	Mrg20	8	19.7	4.04	– 8.20	22.78
<b>GMI_ES05_c5597_803</b>	Mrg09	8	21.4	3.80	– 7.98	22.17
<b>GMI_ES15_c8938_386</b>	Mrg21	8	26.9	3.52	– 7.00	19.44
<b>GMI_DS_LB_10411</b>	–	8	28.7	3.91	– 7.34	20.39
GMI_ES17_c7110_570	Mrg20	8	33.5	3.32	– 7.45	20.69
GMI_GBS_25081	Mrg20	8	33.9	3.86	– 8.08	22.44
QTL-1 peak	Mrg20	8	–	–	–	–
<b>GMI_ES01_c27869_512</b>	Mrg20	8	34.6	4.34	– 8.48	23.56
GMI_ES17_c3050_316	Mrg20	8	37.9	3.23	– 7.34	20.39
GMI_ES02_c20190_105	Mrg20	8	55.8	3.23	– 7.27	20.19

SNP markers in bold are significant in both mapping populations, regardless of sowing date

<sup>‡</sup>Nucleotide sequences of each molecular maker is available at <https://triticeatoolbox.org/oat/>

<sup>†</sup>Consensus group based on Chaffin et al. (2016)

**Fig. 5** Manhattan plots for plant height on the mapping populations ‘U01B/U006’ (‘a’ and ‘b’) and ‘UTau/U017’ (‘c’ and ‘d’). ‘a’ and ‘c’ corresponds to the first sowing date, while ‘b’ and ‘d’ represents the second one. Markers’ position is relative to the genetic maps developed by Ubert et al. (2017). SNP markers are indicated by points. Linkage groups are shown alternately in black and grey in order to facilitate the visualization of significant SNPs in different linkage groups. The red horizontal line represents the significance threshold. (Color figure online)



RILs (Fig. 1), indicating that hulled and naked parents have distinct genetic mechanisms acting on heading date. The naked parental lines ‘UFRGS 006013-1’ and ‘UFRGS 017004-2’ share the same pedigree, ‘Coker 492/Starter-1/UFRGS 8’. In contrast, the hulled parents come from different crosses, although they are relatives, once both carry ‘Pc68/5\*Starter (F<sub>4</sub>)’ in their pedigree. Therefore, it is expected that genetic differences between mapping populations come from the hulled parents ‘UFRGS 01B7114-1-3’ and ‘URS Taura’.

In Southern Brazil there are, at least, two crops a year, one spring–summer crop and one winter–spring crop. The major spring–summer crop is soybeans and

all winter–spring crops must have adequate cycle, allowing soybeans to be sown at the best sowing window. For that, winter–spring crops must have early cycle. Hexaploid oats varieties adopted by Southern Brazilian farmers, cropped for grain, are usually sown at late fall to early winter (May to June), but are spring types. These varieties do not have vernalization or long day-length requirements to head, even though they are not completely insensitive to both environmental stimuli. Therefore, the expansion of oat cultivation in this region is associated to the development of varieties combining early flowering and high grain yield, leading to higher profitability for the oat crop per se and for the summer crop.

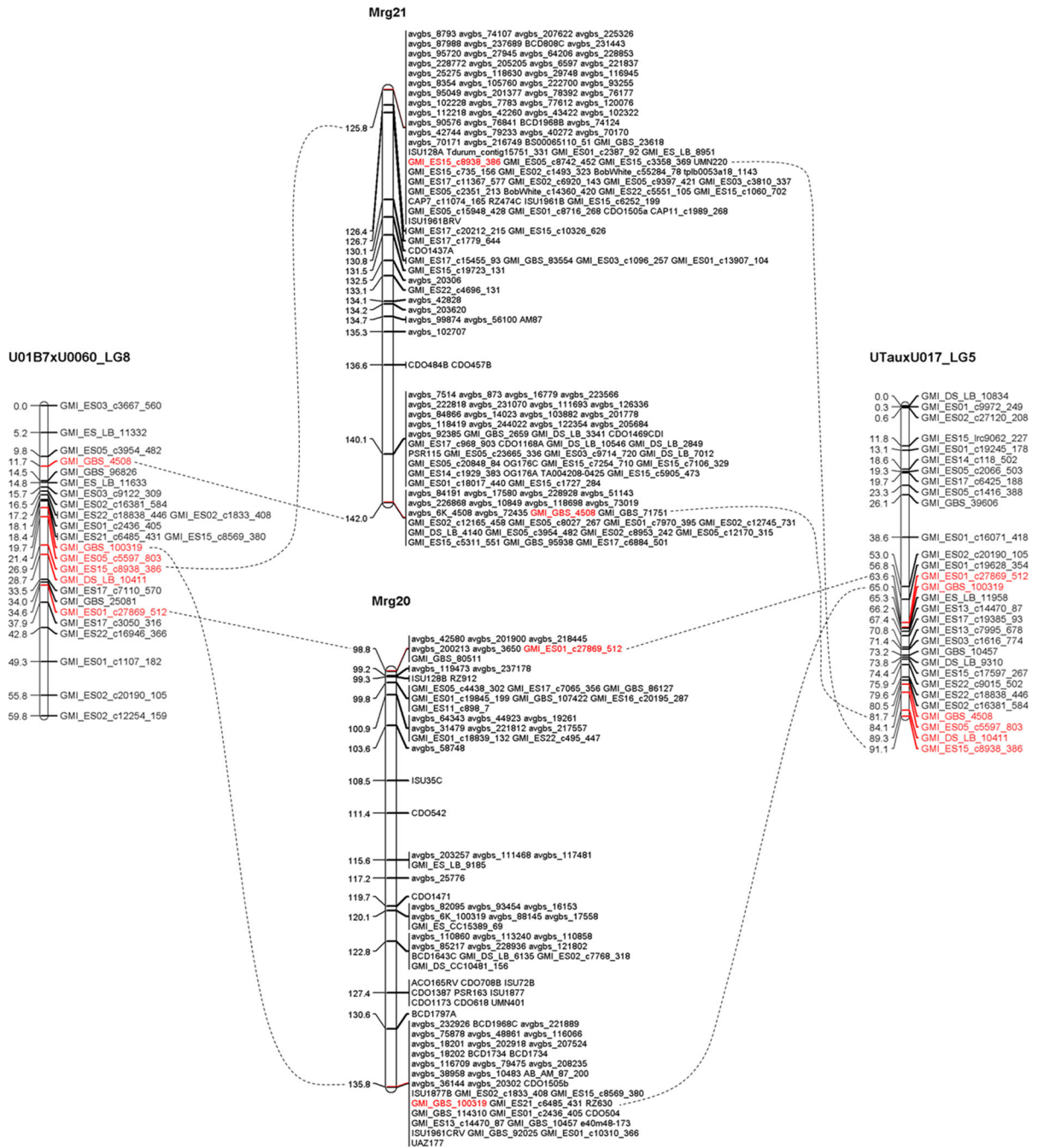
**Table 4** Summary of QTL affecting plant height on the ‘UTau/U17’ mapping population

SNP marker <sup>‡</sup>	Consensus group <sup>†</sup>	Linkage group	Map position (cM)	LOD score	Main effect	P. variation SNP (%)
<i>Plant height (first sowing date)</i>						
GMI_ES02_c20190_105	Mrg20	5	53.0	4.80	– 11.17	18.62
<b>GMI_ES01_c27869_512</b>	Mrg20	5	63.6	5.08	– 10.99	18.32
<b>GMI_GBS_100319</b>	Mrg20	5	65.0	3.84	– 9.62	16.03
GMI_ES_LB_11958	Mrg20	5	65.3	3.80	– 9.53	15.88
GMI_ES13_c14470_87	Mrg20	5	66.2	4.19	– 10.01	16.68
GMI_ES17_c19385_93	Mrg20	5	67.4	4.97	– 10.93	18.22
GMI_ES13_c7995_678	Mrg20	5	70.8	5.67	– 11.00	18.33
QTL-1 peak	Mrg20	5	–	–	–	–
GMI_ES03_c1616_774	Mrg20	5	71.4	6.12	– 11.42	19.03
GMI_GBS_10457	Mrg20	5	73.2	4.39	– 9.77	16.28
GMI_DS_LB_9310	Mrg20	5	73.8	4.06	– 9.46	15.77
GMI_ES15_c17597_267	Mrg20	5	74.4	4.08	– 9.47	15.78
GMI_ES22_c9015_502	Mrg20	5	75.9	3.56	– 9.22	15.37
GMI_ES22_c18838_446	Mrg20	5	79.6	3.67	– 9.33	15.55
GMI_ES02_c16381_584	Mrg20	5	80.5	4.19	– 9.74	16.23
<b>GMI_GBS_4508</b>	Mrg21	5	81.7	4.15	– 9.91	16.52
<b>GMI_ES05_c5597_803</b>	Mrg09	5	84.1	4.65	– 10.54	17.57
<b>GMI_DS_LB_10411</b>	–	5	89.3	3.50	– 8.78	14.63
<b>GMI_ES15_c8938_386</b>	Mrg21	5	91.1	3.60	– 8.88	14.80
<i>Plant height (second sowing date)</i>						
GMI_ES02_c20190_105	Mrg20	5	53.0	4.86	– 9.62	18.50
GMI_ES01_c19628_354	Mrg20	5	56.8	3.63	– 8.38	16.12
<b>GMI_ES01_c27869_512</b>	Mrg20	5	63.6	7.47	– 11.08	21.31
<b>GMI_GBS_100319</b>	Mrg20	5	65.0	5.49	– 9.66	18.58
GMI_ES_LB_11958	Mrg20	5	65.3	5.51	– 9.62	18.50
GMI_ES13_c14470_87	Mrg20	5	66.2	6.38	– 10.29	19.79
GMI_ES17_c19385_93	Mrg20	5	67.4	7.08	– 10.90	20.96
GMI_ES13_c7995_678	Mrg20	5	70.8	8.47	– 11.15	21.44
QTL-1 peak	Mrg20	5	–	–	–	–
GMI_ES03_c1616_774	Mrg20	5	71.4	8.42	– 11.16	21.46
GMI_GBS_10457	Mrg20	5	73.2	6.23	– 9.75	18.75
GMI_DS_LB_9310	Mrg20	5	73.8	5.43	– 9.21	17.71
GMI_ES15_c17597_267	Mrg20	5	74.4	5.60	– 9.31	17.90
GMI_ES22_c9015_502	Mrg20	5	75.9	5.25	– 9.39	18.06
GMI_ES22_c18838_446	Mrg20	5	79.6	5.69	– 9.71	18.67
GMI_ES02_c16381_584	Mrg20	5	80.5	6.17	– 9.88	19.00
<b>GMI_GBS_4508</b>	Mrg21	5	81.7	5.88	– 9.90	19.04
<b>GMI_ES05_c5597_803</b>	Mrg09	5	84.1	6.10	– 10.16	19.54
<b>GMI_DS_LB_10411</b>	–	5	89.3	5.15	– 8.92	17.15
<b>GMI_ES15_c8938_386</b>	Mrg21	5	91.1	4.93	– 8.75	16.83

SNP markers in bold are significant in both mapping populations, regardless of sowing date

<sup>‡</sup>Nucleotide sequences of each SNP maker is available at <https://triticaeatoolbox.org/oat/>

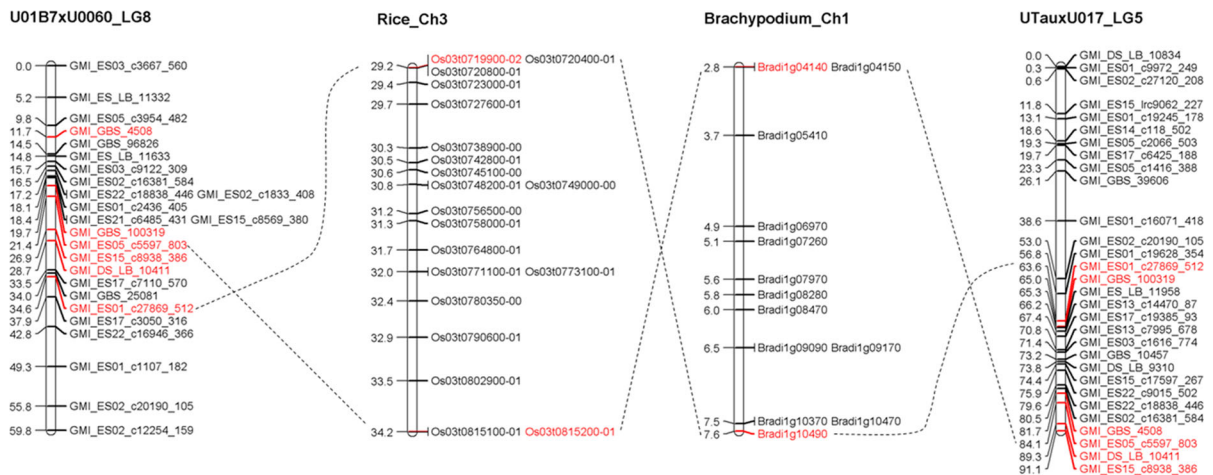
<sup>†</sup>Consensus group based on Chaffin et al. (2016)



**Fig. 6** Comparative mapping of the oat SNP markers associated with plant height on the ‘U01B/U006’ and ‘UTau/U006’ mapping populations. Dotted lines shows the SNP markers’ position relative to ‘Mrg20’ and ‘Mrg21’ groups from the oat consensus map

The transition from vegetative to reproductive stage is a well-coordinated genetic/biochemical event and is influenced by different regulatory pathways, such as photoperiod, environmental temperature, vernalization, circadian clock, gibberellin, and autonomous

pathway (Blümel et al. 2015). The Brazilian oat genotypes were divided into two main genetic systems affecting heading earliness, both being dominant for early flowering. One of these genetic system is controlled by one major locus *Ma-2*, identified in the



**Fig. 7** Comparative mapping of the oat SNP markers associated with plant height on the ‘U01B/U006’ and ‘UTau/U017’ mapping populations relative to rice and *B. distachyon*. Dotted

lines show the oat SNP markers’ position relative to rice loci located on chromosome three (Rice\_Ch3) and *B. distachyon* loci located on chromosome one (Brachypodium\_Ch1)

variety UFRGS 8, which is a genitor of the naked parents used in our study. The other one is controlled by the two major loci *Ma-3* and *Ma-4*, which show smaller effects than *Ma-2*, and were identified in five other oat varieties, including UFRGS 10 (Federizzi et al. 1996), which is a genitor of the hulled parent ‘UFRGS 01B7114-1-3’. There is strong evidence that the locus *Ma-2* corresponds to the *Dil* locus identified by Locatelli et al. (2006) in two mapping populations involving UFRGS 8. *Dil* was mapped into a region syntenic with linkage group 17 of the ‘Kanota x Ogle’ (KO) oat mapping population (O’Donoghue et al. 1995). Using searching tools available at the ‘GrainGenes’ platform (<https://wheat.pw.usda.gov/GG3/>), it was possible to verify that the molecular markers associated with *Dil* locus are located on the linkage group ‘Mrg02’ of the current consensus oat map (Chaffin et al. 2016). On ‘Mrg02’ we identified the QTL-1 for heading date on the mapping population ‘UTau/U017’, which is associated with the SNP marker GMI\_ES\_LB\_11316 in both sowing dates. For QTL-1 we found that alleles from the hulled parent ‘URS Taura’ are associated with a decrease in the number of days to heading.

The detection of three QTL associated to heading, one for ‘U01B/U006’ population and two for ‘UTau/U017’ population, on both sowing dates, indicate their strong association with the trait, which can affect heading date on about five days (Table 2). This effect on the phenotype is also seen in the analysis of

variance, where no interaction between heading and sowing date was observed (Table 1). Our study is the first report of a genomic region controlling heading date on linkage group ‘Mrg33’ from the oat consensus map (Fig. 3). The rice protein SDG708, encoded by genes located in a syntenic region between rice and oat (Fig. 3), is involved in flowering time through its histone H3 lysine 36 methylation activity, which modulates the chromatin structure of key flowering regulatory genes such as *Hd3a*, *RFT1*, and *Early heading date 1 (Ehd1)* (Liu et al. 2016).

The QTL located on ‘Mrg02’ of the current oat consensus map, which presents the peak near to the SNP marker GMI\_ES\_LB\_11316 (Table 2), acts delaying heading date by approximately 5 days in the ‘UTau/U017’ population. This QTL is located exactly at the same region detected by Esvelt Klos et al. (2016) controlling heading date on the ‘Mrg02’. In their work, the SNP marker GMI\_ES\_LB\_11316, among others, was highly associated with heading date in a genome-wide association study, including 682 oat lines and performed across 15 locations-years in USA, Canada, and United Kingdom. This SNP marker explained 18% of the phenotypic variation on average, ranging from 12 to 28% (Esvelt Klos et al. 2016), similar values to those found in our study (Table 2). Esvelt Klos et al. (2016) suggested as candidate genes controlling heading date located on ‘Mrg02’ of the oat consensus map to be *Vernalization3 (Vrn3)* and the linked regulatory gene *CONSTANS (CO)*. In this



sense, most likely *Vrn3* alleles from ‘URS Taura’ are increasing the number of days to flowering (about 5 days) on the ‘UTau/U017’ population (Table 2).

The QTL-2 for heading date, detected on linkage group 30 of the ‘UTau/U017’ population, which is located on ‘Mrg24’ linkage group of the current oat consensus map, presented the significance peak near to the SNP marker GMI\_ES14\_c15338\_376 (Table 2), which is located at the position 4.9 cM in the consensus map (Chaffin et al. 2016). On ‘Mrg24’ Esvelt Klos et al. (2016) also found a significant QTL for heading date, at the position 64.6 cM, therefore the QTL detected in our study probably correspond to a different one than that identified by these authors. The QTL-2 controlling heading date corresponds to a conserved haplotype in rice and *B. distachyon*, identified through comparative mapping with molecular markers from the ‘UTau/U017’ genetic map (Fig. 4). This syntenic region represents a large chromosomal fragment in each species, of 15.41 and 16.98 Mbp, for rice and *B. distachyon*, respectively (Supplemental Table 1). The large number of genes controlling flowering in rice (15 genes) and in *B. distachyon* (seven genes) found in the syntenic region is a strong indication that the QTL-2 represents a very important chromosomal region controlling flowering in oats. Moreover, it may contain several genes controlling the trait in oats, as already indicated by the presence of another QTL in a distant region of the same linkage group (Esvelt Klos et al. 2016).

### Plant height

We found three QTL controlling plant height, one of them was found in common for both mapping populations, being located on the ‘Mrg20’ of the oat consensus map. Some molecular markers associated with this QTL were located on the linkage groups ‘Mrg09’ and ‘Mrg21’ of the consensus map (Tables 3, 4). The consensus linkage groups contain SNP markers mapped on the same linkage groups in our mapping population, linkage group 8 on ‘U01B/U006’ population (Table 3) and linkage group 5 on ‘UTau/U017’ population (Table 4). ‘Mrg 20’ and ‘Mrg 21’ were described as oat homeologues chromosomes by Chaffin et al. (2016). Therefore, it is possible that they correspond to genomic regions that were translocated and are localized on the same chromosome in

our populations. The evidence for translocation between ‘Mrg09’ and ‘Mrg21’ was recently reported by Esvelt Klos et al. (2016) on the oat mapping populations ‘IL86-1156 × Clintland 64’ and ‘AC Assiniboia x MN841801’. These results may explain the fact that SNP markers on the same linkage groups in our mapping populations were found as linked to these two consensus linkage groups.

A QTL for plant height linked to the SNP marker GMI\_GBS\_77286 was found in a genome-wide association study involving a European oat collection (Tumino et al. 2017). This SNP marker is located at 67.5 cM on consensus group ‘Mrg09’, a position far away from the SNP marker GMI\_ES05\_c5597\_803 (Tables 3, 4) that is associated with one of the QTL identified in our study at 111.4 cM in this same consensus group (Chaffin et al. 2016). Therefore, there is no evidence that the associated regions represent the same QTL for plant height.

All SNP markers that were significant for plant height in our mapping populations, and mapped on ‘Mrg20’, were located between positions 98.8 (marker GMI\_ES01\_c27869\_512) and 135.8 cM (marker GMI\_GBS\_100319), being 37 cM apart in this consensus linkage group (Chaffin et al. 2016). In contrast, the same SNP markers were located 14.9 cM apart on the mapping population ‘U01B/U006’ (Table 3) and only 1.4 cM apart on population ‘UTau/U017’ (Table 4). The major QTL associated with plant height in this region was syntenic to a region of the chromosome 3 of rice and chromosome 1 of *B. distachyon* (Fig. 7). On both species a genomic region of about 5 Mbp was noticed between conserved flanking markers, where a great set of genes are annotated. These genes are involved in different biochemical pathways, such as stress responses and hormone synthesis, transport and signaling. In rice, genes affecting auxin, gibberellin, ethylene, cytokinin, and abscisic acid metabolism were found, while in *B. distachyon* genes involved basically on auxin metabolism were present at the conserved region (Supplemental Table 2). Therefore, these genes are involved directly or indirectly in plant growth and development, thus affecting plant height.

The QTL-2 and QTL-3 associated with plant height on the population ‘U01B/U006’ were not consistently significant across sowing dates (Table 3). Thus, they may represent regions showing genotype by environment interaction for the trait. QTL-2 was associated

with SNP markers on linkage group 21 of this mapping population cannot be compared to any other published work on the theme, once it was not anchored on the current consensus oat map, as well as did not show synteny either to rice or *B. distachyon* (Table 3). The SNP marker associated with QTL-3, in the same mapping population, are located on consensus linkage group 'Mrg04'. There are not studies showing plant height QTL on 'Mrg04' in the literature. Also, no conservation among oat, rice and *B. distachyon* was found for the SNP markers associated to the oat QTL-3.

QTL mapping studies combining heading date and plant height traits have been carried out in crop species, such as rice (Lee et al. 2014), wheat (Heidari et al. 2012), soybean (Cao et al. 2017), and oats (De Koeper et al. 2004). The present study was performed in a single growing season, what may imply some limitations to produce solid QTL mapping. Nevertheless, the results are consistent between sowing dates, which showed different environmental conditions during plants' development, as well as between mapping populations. Two biparental populations involving one naked and one hulled oat parent were assessed. Naked oats represent the subspecies *Avena sativa* subsp. *nudisativa*, which developed as an isolated germplasm in Mongolia and Northern China regions (Loskutov and Rines 2011). Consequently, naked oats represent a repository of alleles to be exploited in *A. sativa* breeding programs, especially for traits such as heading date and plant height, which were the aim of our study. Naked oats present lower yields compared to hulled oats, even if the weight of hull adhered to the oat grains are discounted. The main reason for the lower yields in naked oats is its high floret infertility, mainly at terminal florets of each spikelet (Valentine 1995). In this direction, the development of molecular markers nearby useful QTL regions for heading date and plant height may facilitate the transference of desirable alleles either from naked to hulled oat genotypes or from hulled to naked ones.

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