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ORIGINAL PAPER

Detection of seed dormancy QTL in multiple mapping populations derived from crosses involving novel barley germplasm

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Abstract Seed dormancy is one of the most important traits in germination process to control malting and pre-harvest sprouting in barley (*Hordeum vulgare* L.). EST based linkage maps were constructed on seven recombinant inbred (RI) and one doubled haploid (DH) populations derived from crosses including eleven cultivated and one wild barley strains showing the wide range of seed dormancy levels. Seed dormancy of each RI and DH line was estimated from the germination percentage at 5 and 10 weeks post-harvest after-ripening periods in 2003 and 2005. Quantitative trait loci (QTLs) controlling seed dormancy were detected by the composite interval mapping procedure on the RI and DH populations. A total of 38 QTLs clustered around 11 regions were identified on the barley chromosomes except 2H among the eight populations. Several QTL regions detected in the present study were reported on similar positions in the previous QTL studies. The QTL on at the centromeric region of long arm of chromosome 5H was identified in all the RI and DH populations with the different degrees of dormancy depth and period. The responsible gene of the QTL might possess a large allelic variation among the cross combinations, or can be multiple genes located on the same region. The various loci and their different effects in dormancy found in the barley germplasm in the present study enable us to control the practical level of seed dormancy in barley breeding programs.

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Introduction

Seed dormancy is defined as an inability of viable mature seeds to germinate under adequate conditions (Simpson 1990). The process of malting barley is one of controlled germination. Too high a level of seed dormancy after harvest requires an extended, and expensive, period of seed storage prior to malting. On the other hand, in areas where sprouting of seeds on the spike can be caused by rains during later ripening, a degree of seed dormancy is desirable. The challenge is to achieve the appropriate balance between germination capacity and tolerance to pre-harvest sprouting.

Seed dormancy shows quantitative inheritance in many species (Foley 2001), leading to reports of dormancy QTL in poplar (Frewen et al. 2000), Arabidopsis (Clerkx et al. 2004), rice (Miura et al. 2002) and wheat (Mori et al. 2005). There are several QTL studies on seed dormancy in barley. Using the Steptoe/Morex doubled haploid (DH) population, Ullrich et al. (1993) reported two major QTLs on chromosome 5H, one near the centromere and one in the telomeric region of the long arm, and multiple minor QTLs on chromosomes 4H and 7H. These four QTLs were designated as SD1–SD4, respectively (Han et al. 1996) and based on alignment of linkage maps, appear to be coincident with QTLs mapped in other studies (Oberthur et al. 1995; Takeda 1996; Romagosa et al. 1999; Prada et al. 2004; Edney and Mather 2004; Zheng et al. 2005). Most of QTL studies on

seed dormancy in barley are based on a very limited sample of germplasm—primarily the cultivars Steptoe, Morex and Harrington. Of the QTLs reported in these varieties, SD1 and SD2 were mapped with high resolution. Han et al. (1999) mapped the SD1 locus to a 4.4 cM marker interval, and Gao et al. (2003) mapped the SD2 locus to a 0.8 cM marker interval using substitution lines developed from crosses between selected Steptoe/Morex DH lines.

We recently extended assessment of dormancy to a more diverse sample of germplasm including 4,365 cultivated and 177 wild barley (*Hordeum vulgare* ssp. *spontaneum*) accessions collected from different regions of the world (Takeda and Hori 2007). From this large screening, eleven accessions with different levels of dormancy were selected and intercrossed using a diallel mating design. Based on the dormancy phenotypes observed in progeny from these matings, we concluded that dormancy is primarily determined by genes with additive effects. Therefore, the goal of a proper balance of germination capacity and tolerance to pre-harvest sprouting may be achieved by identifying dormancy alleles in a broad array of germplasm and subsequently pyramiding target alleles in single genotypes. The objectives of the present study were to integrate and extend prior QTL and germplasm screening work to include seven recombinant inbred (RI) populations and one DH population.

Materials and methods

Plant materials

Seven recombinant inbred (RI) populations were derived from single crosses between cultivated barley accessions. The crosses, and abbreviations used to describe the resulting populations are as follows: Russia 6 × H.E.S. 4 (RHI); Mokusekko 3 × Ko A (RIA); Harbin 2-row × Khanaqin 7 (RI1); Harbin 2-row × Turkey 6 (RI2); Harbin 2-row × Turkey 45 (RI3); Harbin 2-row × Katana 1 (RI4); and Harbin 2-row × Khanaqin 1 (RI5). These RI populations were advanced to F_{10} (RIA) or F_{12} (all others) via single seed descent. A doubled haploid population (DHHS) was developed from the cross of Haruna Nijo × H602. H602 is an accession of wild barley (*H. vulgare* ssp. *spontaneum*). All RI populations consist of 94 lines and the DHHS population consists of 93 lines. The 12 parental accessions (Russia 6, H.E.S. 4, Mokusekko 3, Ko A, Harbin 2-row, Khanaqin 7, Turkey 6, Turkey 45, Katana 1, Khanaqin 1, Haruna Nijo and H602) all have hulled caryopsis, various country of origin (Table 1). They show a wide range of seed dormancy (Table 1) and/or different rate of loss of dormancy (Takeda and Hori 2007).

Phenotype evaluation

All populations were grown under field conditions at the Research Institute for Bioresources, Okayama University, Kurashiki, Japan (34°35′N and 133°46′E). All nurseries were fall-sown in 2002 and 2004; dormancy was scored on grain samples harvested in the spring of the following year (2003 and 2005). Twenty plants of each parental accession and line were grown in a single row. Rows were 90 cm apart. Within-row spacing was 4 cm. Row type, lemma color, aleurone-layer color and rachilla-hair length were scored and mapped as morphological markers. Phenotypes for the four morphological traits of the 12 parental accessions are shown in Table 1.

Table 1 Phenotypes of twelve parental accessions for four morphological traits and germination percentages at 5 and 10 weeks post-harvest afterripening periods in 2003 and 2005

Accession	Origin	Row type	Lemma color	Aleurone-layer color	Rachilla-hair length	Germination in 2003 (%)		Germination in 2005 (%)	
						5 weeks	10 weeks	5 weeks	10 weeks
Harbin 2-row	China	Two	Normal	Normal	Long	100	100	100	100
Haruna Nijo	Japan	Two	Normal	Normal	Long	94	100	100	100
Russia 6	Russia	Two	Normal	Normal	Long	80	100	93	–
Ko A	Japan	Two	Normal	Normal	Long	–[a]	–	91	–
H.E.S. 4	Afghanistan	Six	Normal	Normal	Long	24	78	27	–
Katana 1	Syria	Two	Normal	Normal	Short	18	29	12	24
Mokusekko 3	China	Six	Normal	Blue	Long	–	–	4	–
Turkey 45	Turkey	Two	Normal	Blue	Long	0	7	0	0
Turkey 6	Turkey	Two	Black	Blue	Short	0	2	0	0
Khanaqin 1	Iraq	Two	Black	Blue	Short	–	–	0	1
Khanaqin 7	Iraq	Two	Black	Blue	Short	–	–	0	0
H602	ssp. *spontaneum*	Two	Black	Blue	Long	0	0	0	0

[a] Missing data

Seed germination percentage was used to score the level of seed dormancy. The protocol for scoring seed dormancy was described by Takeda and Hori (2007). In brief, spikes of each line were harvested at physiological maturity (when all green color was lost from the spike and the internode below the spike). After drying 2 days at 30°C at 10% relative humidity, spikes were hand-threshed and the seed was stored at −20°C. Upon removal from the freezer, seeds were after-ripened at 25°C for two time periods: 5 and 10 weeks. Fifty seeds of each accession from each after ripening date (with exceptions described below) were germinated for 4 days on moistened filter paper in Petri dishes at 25°C. Each germination test was replicated twice. The donors of lower level dormancy in each cross have certain level of dormancy, which was common in Japanese two-row malting barleys (Haruna Nijo and Ko A) and their derived accessions (Harbin 2-row). The data of germination percentage after 0 week in Takeda and Hori (2007) were Haruna Nijo: 2%, Ko A: 4% and Harbin 2-row 12%. Russia 6 also showed lower germination of 16%. Thus, the means of the two-replicate germination tests conducted at 5 and 10 weeks post-harvest were used to calculate the dormancy phenotypic score for each of the lines tested. Both 5- and 10-week dormancy were scored on DHHS, RHI, RI2, RI3 and RI4 in 2003. In 2005, both 5- and 10-week dormancy were scored on DHHS, RI1, RI2, RI3, RI4 and RI5 but only at 5-week dormancy was scored on RHI and RIA, due to the low level of dormancy observed for the parents and progeny in 2003.

Linkage map construction

We have previously reported high density linkage maps for RHI (1,172 loci; Hori et al. 2003), RI2 (383 loci; Hori et al. 2006) and DHHS (1,114 loci; Sato et al. 2004). The published RHI and RI2 linkage maps were constructed primarily with AFLP markers. In order to facilitate alignment of maps and QTL between populations, 384 EST markers distributed throughout the genome were selected from the DHHS linkage map. EST markers showing polymorphisms between the parental accessions were mapped in RHI and RI2. The same 384 EST markers were used to construct linkage maps for RIA, RI1, RI3, RI4 and RI5. Locus names, chromosome assignments, linkage positions, and primer sequences of consensus EST markers are shown in Supplemental Table 1. SSR markers were assayed as described by Ramsay et al. (2000). EST markers were amplified and scored as described by Hori et al. (2005). Four morphological loci segregating in the mapping parents including row type (*vrs1*; 2H), lemma color (*Blp*; 1H), aleurone-layer color (*Blx*; 4H) and rachilla-hair length (*srh*; 5H) were scored. Linkage maps were constructed using MAPMAKER/EXP ver. 3.0 (Lander et al. 1987). SSR markers were used as anchors to assign other markers to the seven barley linkage groups at LOD = 3.0. The Kosambi mapping function (Kosambi 1944) was used to estimate distances between marker loci.

QTL detection

Mean germination values for the 5- and 10-week data were transformed to arcsine. Composite interval mapping was performed using QTL Cartographer ver. 2.5 (Wang et al. 2005). LOD thresholds were determined by 1,000 permutation tests. The LOD peaks at significant QTL intervals were used as QTL locations on the linkage maps.

Results

Seed dormancy

A phenotypic frequency distribution showing germination percentages of RI and DH lines and their parents in 2005 is shown in Fig. 1. Germination percentages of the RI and DH lines ranged from 0% (dormancy) to 100% (non-dormancy) in both years. The average 5- and 10-week dormancy germination percentages of two seasons were 27.2 and 45.7 in DHHS, 23.8 and 42.2 in RI1, 22.5 and 48.0 in RI2, 21.8 and 50.0 in RI3, 45.7 and 76.6 in RI4, and 19.2 and 52.2 in RI5. These results reveal quantitative variation for dormancy at each after-ripening period and a loss of dormancy over time. All the correlation coefficients for germination percentages between years were significant and ranged 0.54–0.74 (5 weeks) and 0.42–0.86 (10 weeks) in the mapping populations. There were higher average germination percentages at 5 weeks in RHI (52.7), RIA (57.0) and RI4 (45.7) in 2005.

Construction of linkage maps using barley EST markers

Seventy-five of the 384 EST markers derived from the linkage map of DHHS (Sato et al. 2004) showed polymorphisms between the parents of RHI and were integrated into the AFLP-based linkage map constructed by Hori et al. (2003). Twenty-nine of the 384 EST markers showed polymorphisms between the parents of RI2 and were integrated into the AFLP-based linkage map of Hori et al. (2006). Polymorphisms for the 384 EST markers were also determined for each remaining parental combination, and used to construct linkage maps in RIA, RI1, RI3, RI4 and RI5. These linkage maps consist of 82–110 loci with the total map lengths of 1,078.3–1,233.5 cM (Table 2). The polymorphic barley EST markers located on the multiple populations were integrated into the consensus linkage map. Positions of the polymorphic barley EST markers on the consensus linkage map are shown in Supplemental Table 1.

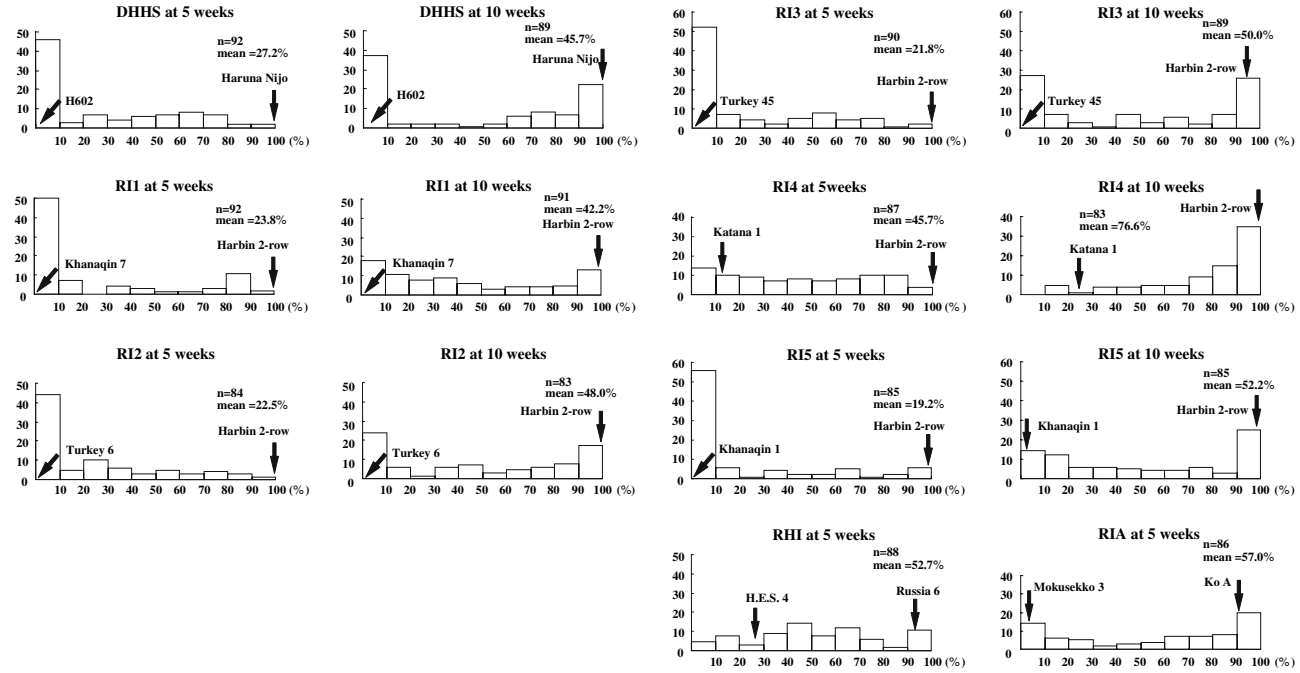

Fig. 1 Frequency distributions of germination percentages at 5 and 10 weeks post-harvest after-ripening periods (5- and 10-week dormancy scores) on eight mapping populations in 2005. Germination percentages of their parental accessions are indicated by *arrows*

Table 2 Summary of linkage map information including the numbers of barley EST, SSR, RFLP, morphological markers, and total linkage map length of each RI and DH population

Population	Numbers of markers						Total map length (cM)
	Morphological	EST	SSR	RFLP	AFLP	Total	
DHHS	4	1,055	35	16		1,114[a]	1,362.7
RHI	3	75	34	3	1,134	1,249	1,595.7
RIA	2	102		1		105	1,233.5
RI1	4	81				85	1,217.0
RI2	4	29	45	1	328	407	1,377.1
RI3	2	80				82	1,103.8
RI4	4	90				94	1,208.2
RI5	2	76	32			110	1,078.3

[a] After Sato et al. (2004)

Seed dormancy QTLs

QTL chromosome locations, anchor marker intervals on the consensus linkage map, peak LOD scores, the percentages of variance explained, and estimated additive effects are shown in Table 3. Seed dormancy QTLs were detected in every population. In total, across populations, 38 QTLs were detected that clustered in 11 chromosome regions (Fig. 2). QTLs were detected on all chromosomes except 2H. The non-dormant parent contributed alleles for greater dormancy on chromosome 1H in RI3, chromosome 6H in RI1 and on chromosome 7H in RHI. As already mentioned, the donors of lower level dormancy in each cross have certain level of dormancy. These dormancy alleles might result negative values of QTL weights. Large-effect QTLs were found near the centromere on the long arm on chromosome 5H in all of the populations. However, the effects of this QTL varied. There was considerable variation for all QTL parameters—ranges for these were LOD scores (3.0–29.8), explained variances (15–77%) and estimated additive effects (9.1–46.2). Since marker resolutions were not quite high in several populations, some of the QTLs might be undetected due to lower statistical significance.

Discussion

A set of 384 barley EST markers was used as a resource for integrating all the linkage maps developed in the multiple populations. This integration of common framework markers facilitates alignment of QTL positions detected in different populations. Across populations, the QTL clustered in

Table 3 QTLs associated with seed dormancy detected by composite interval mapping on a consensus linkage map among RI and DH populations

Population	Year	After-ripening period (weeks)	Chromosome	Consensus marker interval	LOD[a]	Var.[b] (%)	Weight[c]
DHHS	2003	5	5H	k04703–k00950	24.0	77.3	29.1
		10	1H	k03878–k03006	3.6	3.6	6.5
			5H	k04703–k00950	29.1	72.8	28.8
	2005	5	1H	k03878–k03006	3.6	5.5	5.8
			5H	k04703–k00950	17.8	72.3	15.8
			5H	k04431–	4.7	8.0	6.7
		10	4H	k05053–k00136	4.7	5.1	8.8
			5H	k04703–k00950	22.9	51.8	26.5
			5H	k04431–	3.1	3.2	6.6
RHI	2003	5	5H	k04703–k05217	13.3	38.8	14.4
		10	7H	k03540–k09456	3.1	12.8	−6.4
	2005	5	5H	k04703–k05217	9.4	32.3	11.4
			7H	k03540–k09456	6.0	18.2	−9.0
RIA	2005	5	5H	k03390–k00584	5.4	20.4	27.5
			6H	k06764–k08181	3.2	11.4	18.5
RI1	2005	5	3H	k03264–k03870	5.2	5.4	12.4
			5H	k00950–k00584	29.8	68.0	46.2
			6H	k07387–k00930	3.5	3.6	−10.0
		10	1H	k10026–k09230	4.0	4.8	11.3
			5H	k00950–k00584	27.5	59.5	42.5
			7H	k06732–k06507	6.1	6.5	13.4
RI2	2003	5	5H	k04703–k03993	15.5	39.5	30.4
		10	5H	k04703–k03993	17.4	48.0	24.6
	2005	5	3H	k03870–k03533	3.5	7.4	12.0
			5H	k04703–k03993	17.4	55.7	32.3
		10	3H	k03870–k03533	5.9	11.6	20.3
			5H	k04703–k03993	20.5	64.7	44.9
RI3	2003	5	5H	k04703–k00584	21.1	51.9	47.9
		10	1H	k03006–k00304	3.4	11.5	−15.9
			5H	k04703–k00584	6.9	27.1	23.2
	2005	5	5H	k04703–k00584	13.6	32.5	29.8
		10	5H	k04703–k00584	17.5	44.4	45.7
RI4	2003	5	5H	k00950–k06860	6.4	26.4	9.6
		10	5H	k00950–k06860	6.3	35.7	9.1
	2005	5	5H	k04703–k00950	7.8	40.6	13.1
		10	5H	k00950–k06860	6.5	28.8	10.6
RI5	2005	5	5H	k00584–k03993	6.5	46.0	48.1
		10	5H	k00584–k03993	3.0	15.3	23.6

[a] Peak LOD score

[b] Explained variance

[c] Estimated additive effect of alleles of non-dormant parental accessions in each population; Haruna Nijo (DHHS), Russia 6 (RHI), Ko A (RIA) and Harbin 2-row (RI1, RI2, RI3, RI4 and RI5)

11 regions and these clusters were found on all chromosomes except 2H (Fig. 2). One QTL, on the long arm of chromosome 5H, was detected in every population. Other QTLs were specific to populations, years and/or after-ripening times. In the germplasm sampled in this study, the primary determinant of dormancy is on 5H and that alleles at other loci show genotype-, year- and/or after ripening- specific effects. Several morphological trait loci including row type (*vrs1*), rachilla hair type (*srh*), black lemma (*Blp*) and blue aleurone layer color (*Blx*) mapped on the linkage maps. The QTL on chromosome 1H has a linkage with *Blp* and another QTL on chromosome 5H has a linkage with *srh*. Consequently, RI lines with black lemma (1H) were significantly more dormant than those of normal lemma in RI2 at 10 weeks in 2003 and in RI1 and RI5 at 10 weeks (2005) and RI lines with long rachilla-hair (5H) were significantly more dormant than those with short rachilla-hair in RI2, RI4 and RI5 at 5 and 10 weeks in 2003 and 2005.

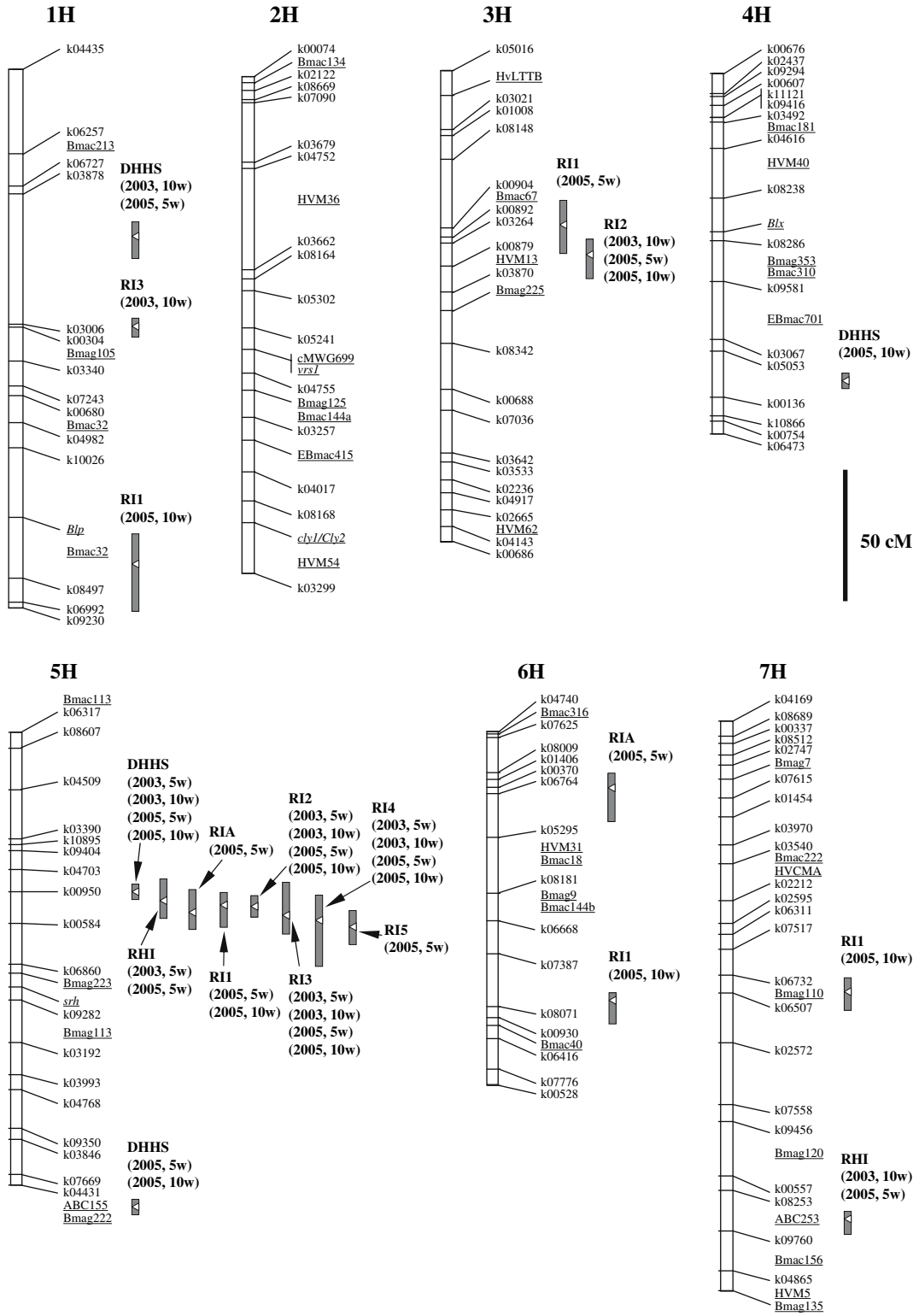

Fig. 2 A consensus linkage map based on eight mapping populations and positions of QTLs for seed dormancy at 5 and 10 weeks after-ripening periods in 2003 and 2005. Linkage groups are orientated with *short arms* from the top. Marker names are shown on the right side of each chromosome. The anchor loci including SSR, RFLP and morphological markers are indicated with *under line*. QTL positions are indicated by *gray boxes* on the right side of each chromosome. Peaks of the significant marker intervals are indicated by *triangles* in boxes

These results agreed with the reports that some morphological traits were associated with seed dormancy in barley (Stanca et al. 2003; Prada et al. 2004).

We used novel and diverse germplasm to develop the populations used for this study and yet we found striking coincidence with QTL detected in unrelated germplasm. Ullrich et al. (1993) detected a total of 27 seed dormancy QTL in the Steptoe × Morex population. Han et al. (1996) assigned locus names to four of these QTLs: SD1 and SD2 near the centromere and telomere, respectively, of chromosome 5HL, SD3 on 7H, and SD4 on 4H. According to the positions of anchor markers, the QTLs we detected on 5H appear to be coincident with SD1 and SD2. The QTL detected at 10 weeks after-ripening (2005) on chromosome 7H in RI1 may be coincident with SD3. There are other reports of seed dormancy QTLs coincident with SD1–SD4 in subsequent studies involving Steptoe × Morex (Oberthur et al. 1995; Romagosa et al. 1999) or in populations derived from crosses of other genotypes with Morex: Triumph/Morex (Prada et al. 2004) and Harrington/Morex (Edney and Mather 2004). Takeda (1996) also reported QTL coincident with the SD2 loci in Harrington/TR306. Based on these commonalities of QTL detected in a range of germplasm, and the additive inheritance of dormancy (Takeda and Hori 2007), we conclude that we have contributed to the development of a reasonably comprehensive catalog of the determinants of grain dormancy in barley, the principal determinants of which are on chromosome 5H.

There was considerable variation in the estimates of QTL parameters (LOD scores, additive variances and estimated additive effects) for the major-effect QTL near the centromere on 5HL (Table 3). For example, RHI, RIA and RI4 had lower QTL values than all other populations. The average germination percentages after 5 weeks of after-ripening were also markedly higher than for the other populations in 2005 (Fig. 1). This may indicate allelic variation at the same locus or the effects of alleles at multiple, tightly linked loci. In either case, this locus (or complex locus) may be a principal determinant of the differences in degree of dormancy observed between wild and cultivated barley, and within cultivated barley. Zheng et al. (2005) detected QTLs at the corresponding region in *H. vulgare* ssp. *spontaneum* strain 23–39, although Vanhala and Stam (2006) did not detect QTL in this region using two *H. vulgare* ssp. *spontaneum* strains (Ashkelon and Mehola). This finding could be explained by a lack of allelic variation at a locus with tremendous adaptive importance for a wild species.

Understanding additive epistatic interactions between these loci will be important in applying this information to barley improvement. Han et al. (1996), Oberthur et al. (1995) and Romagosa et al. (1999) concur that the SD1 locus regulates the expression of the SD2 and SD3 loci in the Steptoe/Morex population. Likewise, understanding the role of environment in seed dormancy will be important. Prada et al. (2004) reported that SD1 and SD2 loci show QTL × E. The large number of populations used in this study, the replication across years, and the sampling at two after-ripening dates provides a rich data source that we are currently using to characterize seed dormancy QTL × QTL and QTL × E interactions. In addition to providing new insights into QTL interaction, future in-depth analyses our data on QTLs at different after-ripening periods may be warranted. For example, Takeda and Hori (2007) showed how barley germplasm accessions could have the same degree of dormancy without after-ripening, but very different degrees of dormancy after 5, 10, or 15 weeks of after-ripening. This indicates that different factors control the initial degree of seed dormancy and the rate of loss of dormancy. Romagosa et al. (1999) and Prada et al. (2004) reported that the SD1 locus determined the initial degree of seed dormancy and that the SD2 locus is associated with the rapidity with which dormancy is lost during after-ripening.

Han et al. (1996), Romagosa et al. (1999) and Gao et al. (2003) suggested that replacing the dormancy allele at SD1 with the non-dormant allele and replacing the dormant allele at SD2 with a non-dormant allele would lead to an optimum level of seed dormancy in the Steptoe/Morex background. However, we found degrees of variation in the effects of SD1 alleles that could be of immediate practical benefit. These benefits will be greatest when based on an understanding of gene structure and function. Han et al. (1999) used substitution lines derived from the Steptoe/Morex DH lines to achieve a higher resolution map of the SD1 region. We are developing a truly high-resolution map of the region using the recombinant chromosome substitution lines derived from the cross between Haruna Nijo and H602 (Hori et al. 2005). QTL cloning and characterization of the SD1 locus should prove useful information for understanding and manipulating the genetics of seed dormancy in barley.

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