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Construction of barley consensus map showing chromosomal regions associated with economically important traits

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In the past, it has been difficult to accurately determine the location of many types of barley molecular markers due to the lack of commonality between international barley linkage maps. In this study, a consensus map of barley was constructed from five different maps (OWB, VxHs, KxM, barley consensus 2 and barley consensus 2003) to produce the consensus AD-2005 map with 1536 markers. The QTL that have been identified in previous barley studies were then incorporated into the integrated consensus map to provide a quick method of aligning and comparing barley linkage maps and to identify markers closely linked to barley traits. The markers placed on this map are consistent with respect to order on the chromosomes with the individual maps and other barley maps with a few minor differences. The consensus AD-2005 was compared with rice Cornell RFLP map to examine the reliability of the constructed map in comparative genomic studies. Unlike previous consensus maps, the purpose of this consensus map (containing QTL) is to provide a tool for scientists to accurately locate molecular markers to chromosome regions responsible for economically important traits. It is estimated that markers placed on the consensus map are located very close to their true positions as determined by the five maps used in this study. It is envisaged that the consensus map will benefit small-grain researchers by providing an efficient means of choosing markers of interest and identifying QTL regions for future genetic or plant breeding studies on a worldwide basis.

Key words: Barley, QTL, genetic linkage mapping, consensus map, comparative genome mapping.

INTRODUCTION

Several different types of DNA markers are currently available for genetic analysis and new marker types are being developed continuously. Markers differ from each other in many respects such as the initial workload and costs for building up the marker system, running costs and ease of use, level of polymorphism, dominance, number of loci analyzed per assay, reproducibility and distribution on the linkage groups of the genetic linkage maps. A genetic linkage map is a fundamental organizational tool for genomic research. The most important applications of genetic maps are towards:

(1) A basic knowledge of genome organization and evolution;
(2) The localization of monogenic and oligogenic traits; and
(3) Studies of genetic diversity.

Therefore, for any given species, individual genetic maps are often constructed with a specific goal in mind, thereby generating multiple maps for a single species that feature novel markers and genetic information. The information contained within these individual maps can be further enhanced when these maps are incorporated into a single consensus map to represent a given species.

Consensus maps have been constructed for a number of plant species such as Arabidopsis thaliana (Hauge et al., 1993), Brassica oleracea (Kianian and Quiros, 1992), Helianthus annus (Gentzbittel et al., 1995), Hordeum

vulgare (Qi et al., 1996) and Zea mays (Beavis and Grant, 1991). Mapping with multiple populations provides several advantages over mapping based on a single population. In particular, a larger number of loci can be placed onto a single map. This is especially important when attempting to map specific genes of interest (e.g., morphological markers or candidate genes for economically important traits) that are unlikely to segregate within a single mapping population. These multi population mapping studies provided evidence for chromosomal rearrangements and gene duplication and have assisted in the assignment of linkage groups to chromosomes. The consensus maps provide the basis for comparative genomic studies among related species and sub species.

Barley (Hordeum vulgare L.) is a model species for genetic and physiological studies and shows a wide range of adaptations to various habitats. It is an annual, diploid self-pollinating species with a relatively short life cycle. Primitive landraces and the wild progenitor of barley (H. spontaneum) exhibit large variations in physiology, morphology and genetics, which might be used to improve cultivated barley (Nevo, 1992; Forster et al., 2000).

QTL mapping has been employed in several areas of biological sciences. In plant breeding; one of the major lines of research is the detection of useful traits in relatives of cultivated species (Fulton et al., 1997; Xiao et al., 1998; Bernacchi et al., 1998). There has been much interest in studying quantitative traits of agronomic importance, disease resistance (Young, 1996), drought tolerance (Teutat et al., 2001; Diab et al., 2004), and many other traits for biotic and abiotic stress tolerance in barley. QTL mapping has led to a vast body of genetic information in public database and provided the scientific community with powerful tools for comparative genomics (Gai et al., 2000; Mekhdov et al., 2000).

In the present study, an integrated consensus map of barley was constructed based on a common set of markers mapped onto the respective linkage groups and the QTL, identified in previous barley studies, were transferred to the integrated consensus map. The main objective of this work is to facilitate comparative mapping studies of cereals and gathering many mapping information to allow scientist to compare genetic information from diploid species such as barley to species with more complex genomic structure that could lead to the identification of highly conserved sequences and regulatory mechanisms by which it is possible to predict function and location of genes in different maps that have been traditionally studied separately.

MATERIALS AND METHODS

Genetic maps

Three Linkage maps and two consensus maps of barley were used in this study to construct the consensus AD-2005 barley map. Rice Cornell RFLP map was used as a test drive comparative model. The major feature of the five barley maps and the rice map are described below.

Hordeum-OWB linkage map

This map was built with a range of markers. These include 11 morphological markers (NEPs), 79 restriction fragment length polymorphisms (RFLPs), 19 intron fragment length polymorphisms (IFLPs) and 50 simple sequence repeats (SSRs). Additional information on the markers in the linkage map is available at http://barleyworld.org.

Hordeum-Graner1VxHs

This map was constructed using 135 individuals of an interspecific F2/F3 progeny (VADA x H. spontaneum). The map consisted of 160 markers with colinear arrangement covers a distance of 1,453 cM and identifies regions of varying map distances.

Hordeum KxM

This map is an RFLP linkage map that was constructed using 120 F2 plants from a cross between Ko A (a Japanese two-rowed malting barley) and Mokusekko 3 (a Chinese six-rowed barley landrace). 188 loci were mapped with an average distance of 6.5 cm between markers for a total of 1389 cM, and included 117 genomic DNA RFLPs, 69 cDNA RFLPs, one isozyme (Est1) and one morphological (vrs1) marker. This map showed three gap regions exceeding 25 cM.

Barley Consensus 2

This consensus map was constructed using four segregation data sets, Proctor x Nudinka, Igri x Franka, Steptoe x Morex, and Harrington x TR306. 22% of the markers were common to at least two of the independent data sets. The integrated map contains 882 markers.

Barley Consensus 2003

This consensus map, combining SSR, RFLP, and AFLP markers has been developed by combining five Australian barley linkage maps, Galleon x Haruna Nijo, Chebec x Harrington, Clipper x Sahara, Alexis x Sloop and Amaji Nijo x W12585. This consensus map consists of 705 markers, with 138 being SSRs.

Rice map

This map is an updated version of the Cornell RFLP 1994 map reported by Causse et al. (1994) and revised by Wilson et al. (1999). The mapping population was derived from a backcross between cultivated rice (Oryza sativa) and its wild African relative (Oryza longistaminata).

Construction of the consensus AD-2005 map

Five mapping data sets were downloaded from the publicly available Grain Genes database (http://www.graingenes.org). The consensus map was constructed in three stages with each stage adding a new layer of information. In the first stage, the initial map

Table 1. Quantitative trait loci for traits gathered from different barley studies and placed on barley consensus-AD 2005 map.

Trait	Map	Reference
Relative water content under stress treatment	Tad X ER	Diab et al., 2003
Relative water content under irrigated condition	Tad X ER	Diab et al., 2003
Osmotic potential under irrigated condition	Tad X ER	Diab et al., 2003
Osmotic potential at full turgor	Tad X ER	Diab et al., 2003
Water soluble carbohydrates	Tad X ER	Diab et al., 2003
Fusarium head blight resistance	F x S	Mesfin et al., 2003
		Ma et al., 2000
		Zhu et al., 1999
Flowering time	I x T	Jeremy et al., 1996
Malting quality	H x M	Marquez et al., 2000

was constructed based on common markers (anchor loci) present in the five barley maps. In the second stage, the markers on the five maps were matched according to sequence similarity using the sequence similarity program (http://www.ncbi.nlm.nih.gov/blast/bl2seq/bl2.html) and this information was used to identify additional links between the maps. Finally, the consensus AD-2005 map was constructed as described by Diab (2003).

To construct the consensus AD-2005 map, the consensus map 2 (Qi X et al., 1996) and consensus 2003 (Karakousis et al., 2003) were first integrated to produce the first framework map (AD1). The AD1 framework was then merged with OWB map (Wolfe et al., 1996) to produce a second framework map (AD2), then KXM map (Miyazaki et al., 2000) was incorporated into the AD2 map to produce a third framework map (AD3). Finally, the AD3 framework map was integrated with the VxHs map (Graner et al., 1991) to produce the consensus AD-2005 map with 1536 markers distributed on the seven chromosomes.

Comparative study for rice and barley maps

To examine the reliability of the consensus AD-2005 in comparative studies, the Cornell rice RFLP 2001 map (http://www.gramene.org) was downloaded and compared with the constructed barley consensus AD-2005 map, OWB, KXM and VXHs maps based on common markers (anchor loci).

Incorporation of QTL

The QTL that were previously identified in different barley studies were incorporated into the integrated barley consensus AD-2005 map for QTL comparison purpose. Quantitative trait loci for relative water content under stress condition (RWCs), relative water content under irrigated condition (RWCi), osmotic potential under irrigated condition (OPi), osmotic potential at full turgor (OP100), water soluble carbohydrates (WSC), Fusarium head blight resistance (FHB), flowering time (FT) and malting quality (MQ) were gathered from previous studies and placed on the constructed consensus AD-2005 (Table 1, Figure 1).

RESULTS AND DISCUSSION

Well developed barley genetic maps exist as a result of the efforts of numerous groups worldwide. These maps include RFLPs, amplified fragment length polymorphisms (AFLPs), single sequence repeat or microsatellites (SSRs), isozyme protein markers; and morphological markers (Becker and Heun, 1995; Graner et al., 1991; Heun et al., 1991; Kleinhofs and Graner, 2001). These genetics maps were based on various markers, the most useful being those that are transferable from one mapping population to another. These markers have been incorporated into bin maps (Karakousis et al., 2003; Qi et al., 1996). In the present study, five different barley maps were integrated to produce a consensus map with 1536 markers distributed on the seven linkage groups with 240 common markers between the five maps. The 882 markers of the consensus 2 map were merged with the 705 markers of the consensus 2003 to produce the first framework integrated barley consensus map (AD1) with 1255 markers. The 1255 marker of the AD1 map were then merged with OWB map to produce the second framework integrated barley consensus map (AD2) with 1371 markers. Then the AD2 was incorporated with KxM map to produce the third framework map integrated barley consensus map (AD3) with 1461 marker. Finally, the AD3 map was merged with VXHs map to generate the barley AD-2005 consensus map with 1536 markers.

Description of the barley consensus AD-2005 map

The primary goal for the construction of this consensus map was to place, relative to one another, as many genetic markers as possible onto a single map. Therefore, the concern is raised more towards obtaining a general order and distance among these markers rather than the fine resolution of order and distance. The markers placed on this map are consistent with respect to order on the chromosomes with the barley consensus 2 (Qi et al., 1996), barley consensus 2003 (Karakousis et al., 2003) and with other published or consensus barley maps (Kleinhofs and Graner, 2001; Qi et al., 1996;

Table 2. Comparison between the five individual maps and barley consensus AD-2005 map in respect of number of markers on each chromosome.

Chromosome	Barley consensus 2	Barley consensus 2003	Hordeum-OWB	Hordeum-KxM	Hordeum-Graner VxHs	Barley Consensus - AD 2005
1H	92	87	24	27	19	189
2H	163	160	30	28	28	306
3H	133	54	20	28	28	150
4H	81	59	24	24	18	136
5H	139	137	19	28	28	270
6H	98	81	22	25	20	175
7H	176	127	20	28	19	310
Total	882	705	159	188	160	1536

Miyazaki et al., 2000; Graner et al., 1991; Wolfe et al., 1996; Ramsay et al., 2000) with a few minor differences. This conservative property of the barley genome makes the integrated maps reliable and successful. Based on this integrated map, geneticists and breeders can choose their favorite markers in any region of interest of the barley genome.

For comparable areas, the size of the consensus map constructed in this study (consensus AD-2005) is consistently larger than the consensus map constructed by Qi et al. (1996) and the consensus map constructed by Karakousis et al. (2003) despite the fact that each of those two maps has been constructed using five different maps (Table 2). Obvious explanation is that those two maps were integrated together with another three maps (OWB, VXHs and KXM) beside the step-wise procedure used to integrate the individual maps.

The utility of the constructed consensus map is enhanced with the availability of the SSR, RFLP, and AFLP markers integrated from the barley consensus map 2003 (Karakousis et al. 2003). The integrated map removes many large gaps present in the individual maps and in other consensus maps except a gap on chromosome 4H. The poor coverage in this region might be due to a lack of polymorphism for the markers screened in this region.

Incorporation of QTL

QTL analysis can be done in relation to mapped genetic markers and provide data on genome location and the relative effects both positive and negative of loci and alleles. The next step is the identification of the genes, alleles and physiological processes that are biologically important. Numerous studies identifying QTL for relative water content (RWC), osmotic potential (OP), water soluble carbohydrates (WSC), Fusarium head blight resistance (FHB), flowering time (FT) and malting quality (MQ) have been conducted in barley (Teulat et al., 2001; Diab et al., 2004; Mesfin et al., 2003; Ma et al., 2000; Zhu et al., 1999; Jeremy et al., 1996; Marquez et al., 2000; Hayes et al., 1993; Tinker et al., 1996). Presently, 143 QTL were gathered from previous barley studies and placed on the consensus AD-2005 map. Seventy seven QTL for Fusarium head blight resistance, 32 for malting quality, 24 for flowering time, 1 for relative water content under stress condition, 1 for relative water content under irrigated condition, 2 for osmotic potential at full turgor, 1 for osmotic potential under irrigated condition and 5 for water soluble carbohydrates (Figure 1).

For Fusarium head blight resistance trait, 7 QTL were located on chromosome 1H, 12 on chromosome 2H, 9 on 3H, 8 on 4H, 13 on 5H, 12 on 6H and 16 on chromosome 7H (Figure 1). Mesfin et al. (2003) reported the presence of QTL for FHB on all chromosomes except chromosome 6H, and Zhu et al. (1999) found QTL for FHB resistance on all barley chromosomes except chromosome 5H, while Ma et al. (2000) reported QTL for FHB resistance located on chromosomes 2H, 3H, 5H, 6H and 7H. Taken together, these studies indicate that resistance is conditioned by many loci and that the low resolution of the mapping populations has resulted in a limited assessment of the FHB. Integrating these QTL from different studies on a single consensus map gives the opportunity for scientist to compare between QTL and might solve the problem of low resolution maps hence detecting false negative QTL during trait analysis. Two markers (ABG317 and ABC153) on chromosome 2H were found to be associated with QTL for Fusarium head blight resistance. Those two markers were located on the same chromosomal region on the consensus barley AD-2005 (Figure 1). This indicates the reliability of placing QTL on consensus maps.

For flowering time trait, 6 QTL were placed on chromosome 1H, 4 on 2H, 1 on 4H, 7 on 5H, 3 on 6H and 7H each, while no QTL were found on chromosome 3H (Figure 1). This result agrees with the finding of Jeremy

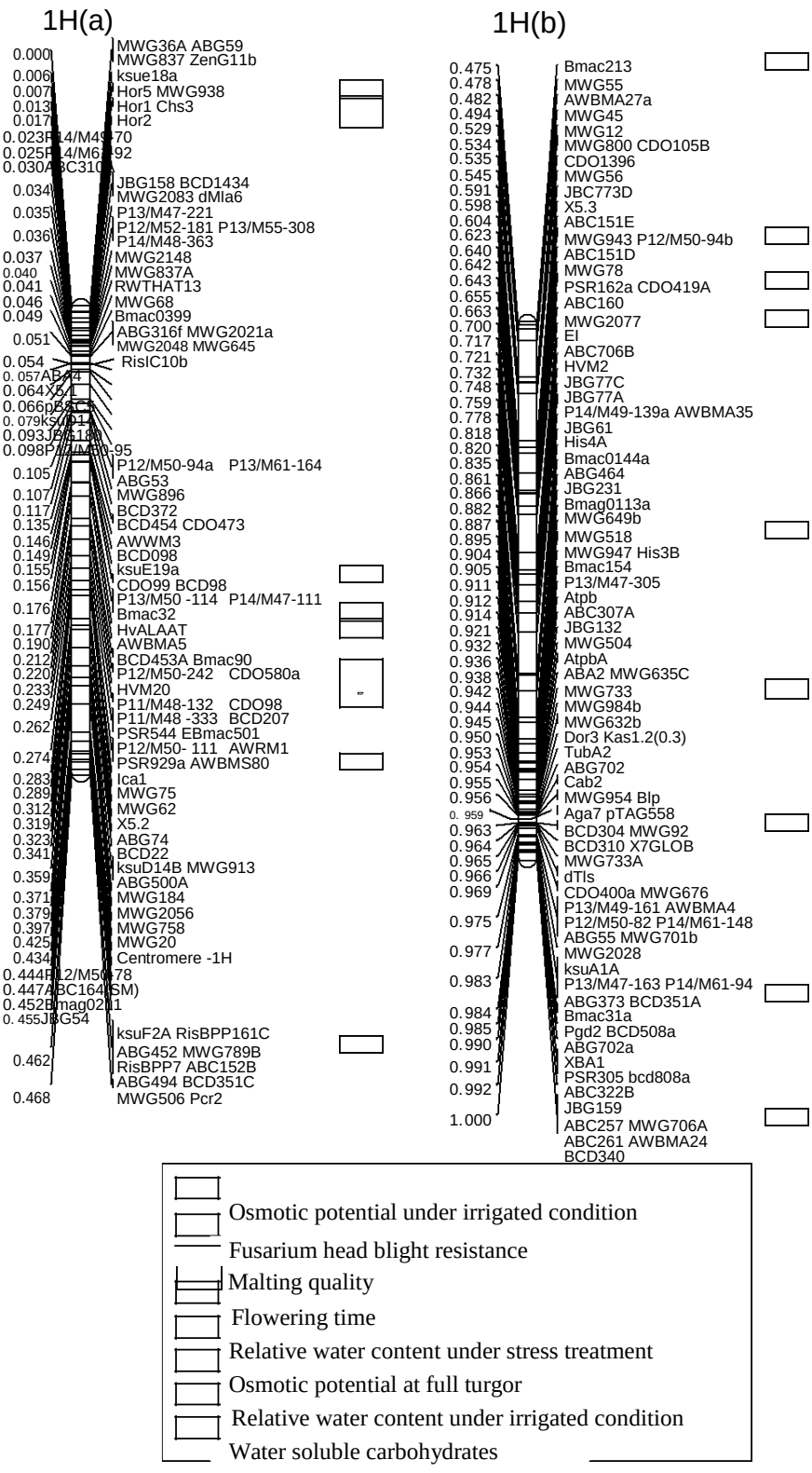

Figure (1). Integrated barley Consensus AD-2005 map with QTL for some biotic and abiotic traits.

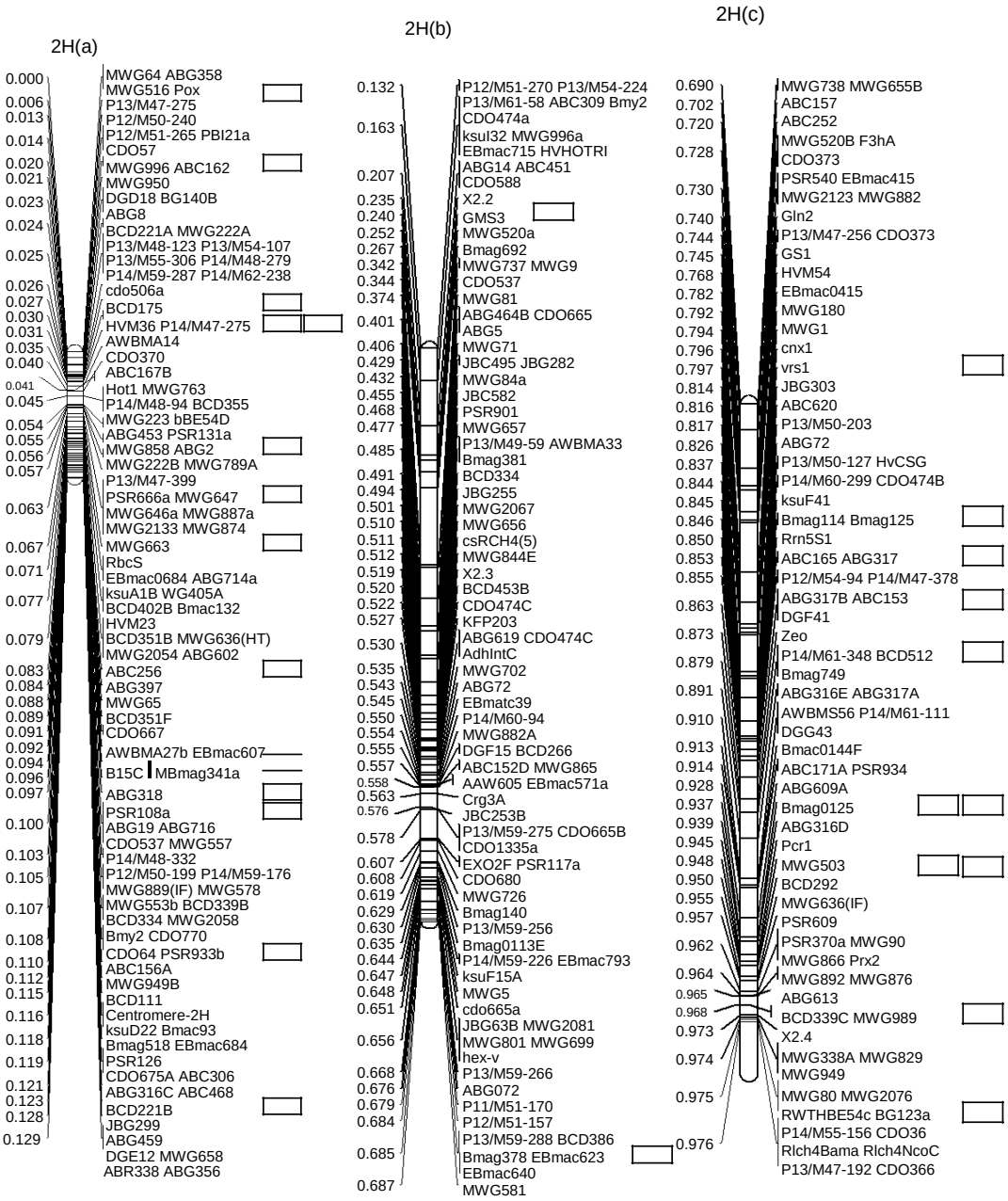

Figure 1. contd.

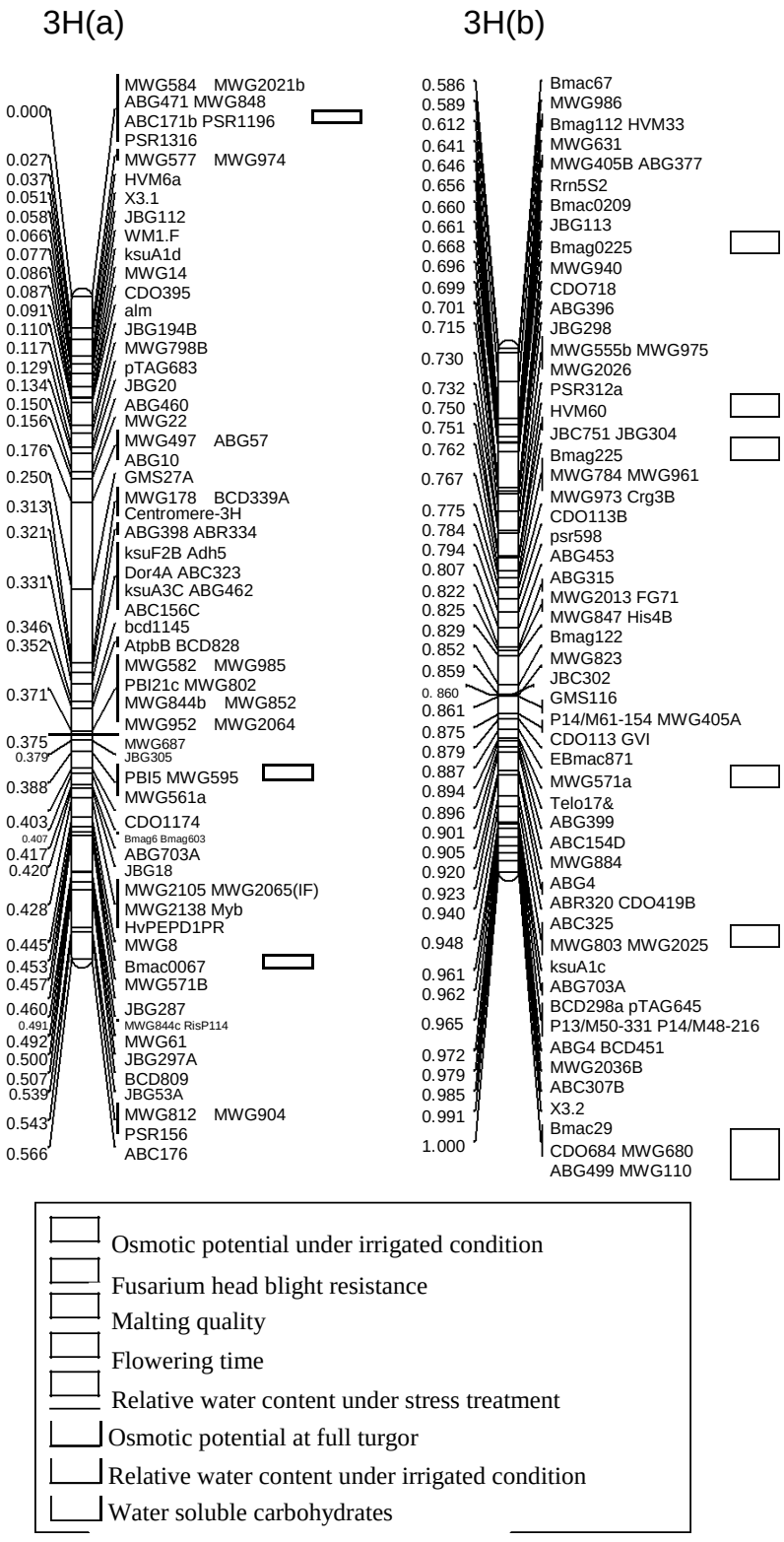

Figure 1. contd.

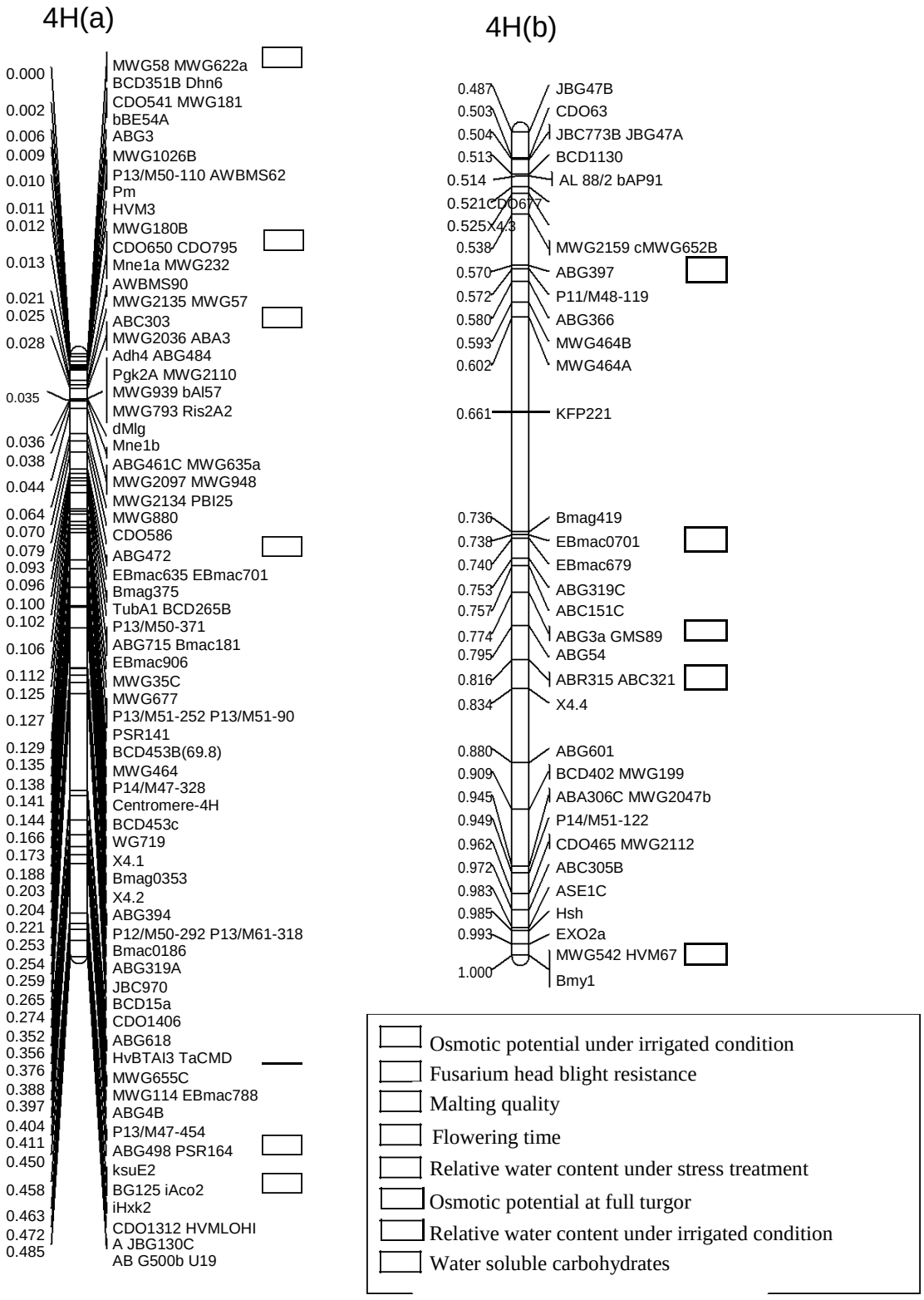

Figure 1. contd.

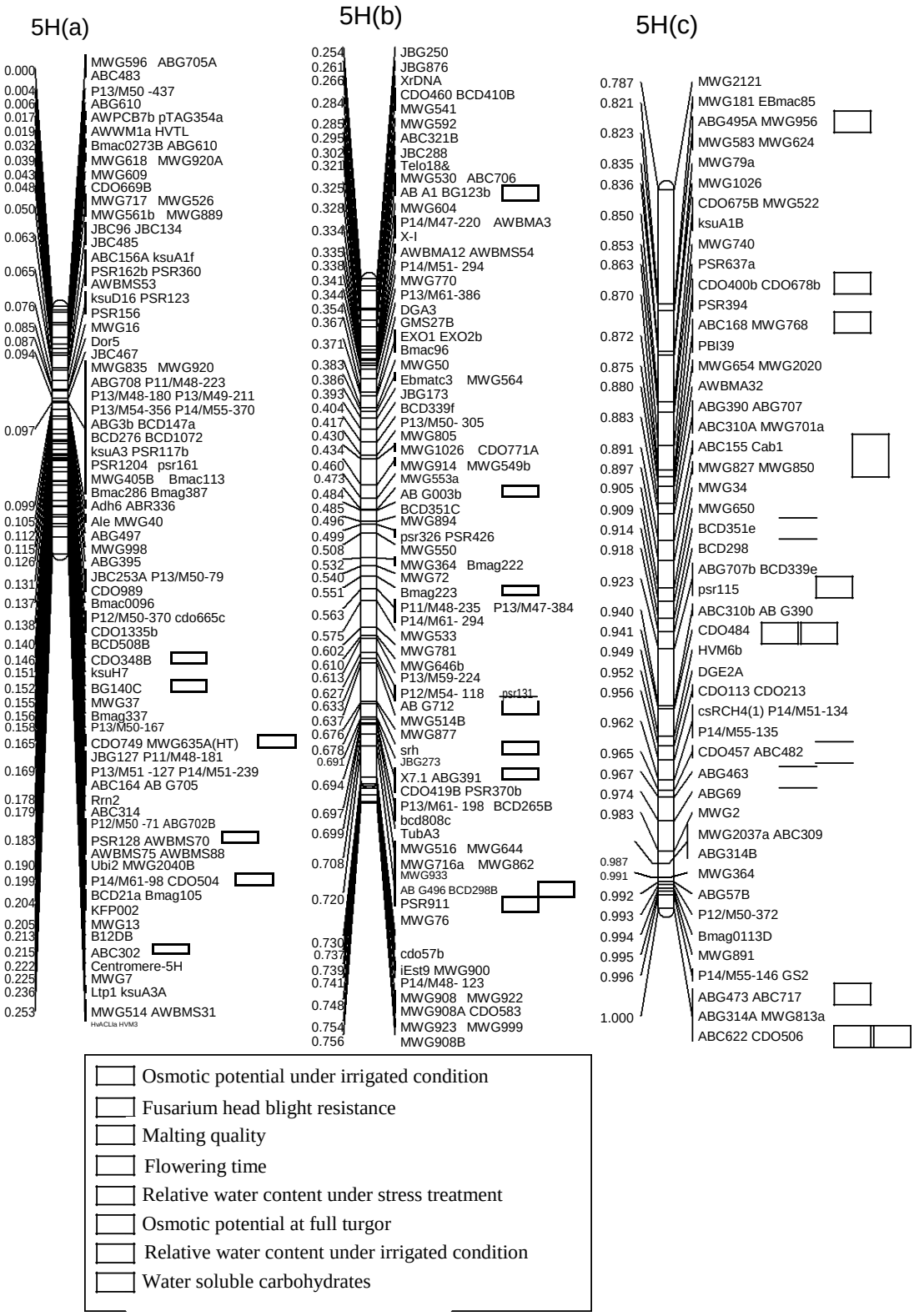

Figure 1. contd.

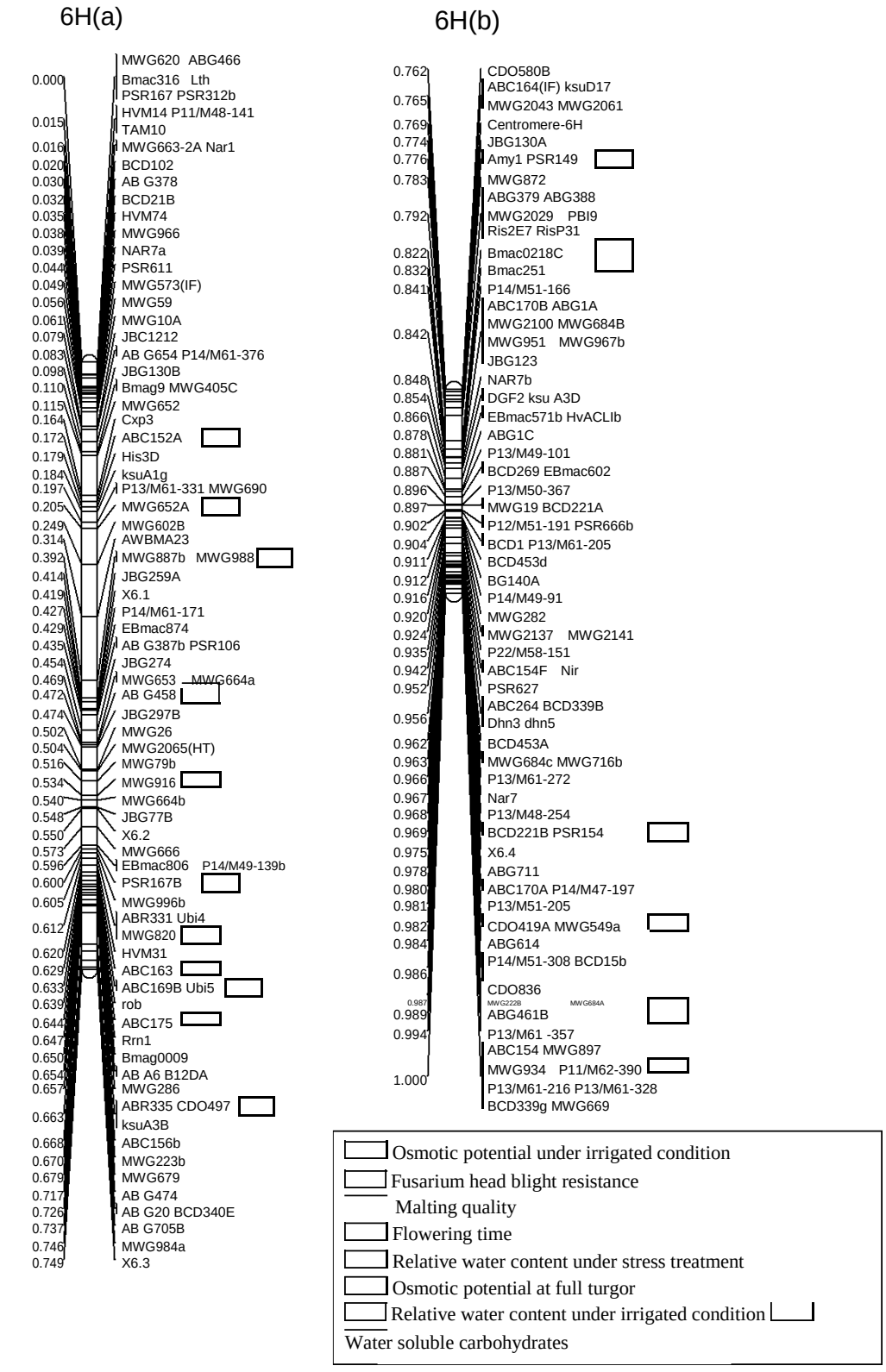

Figure 1. contd.

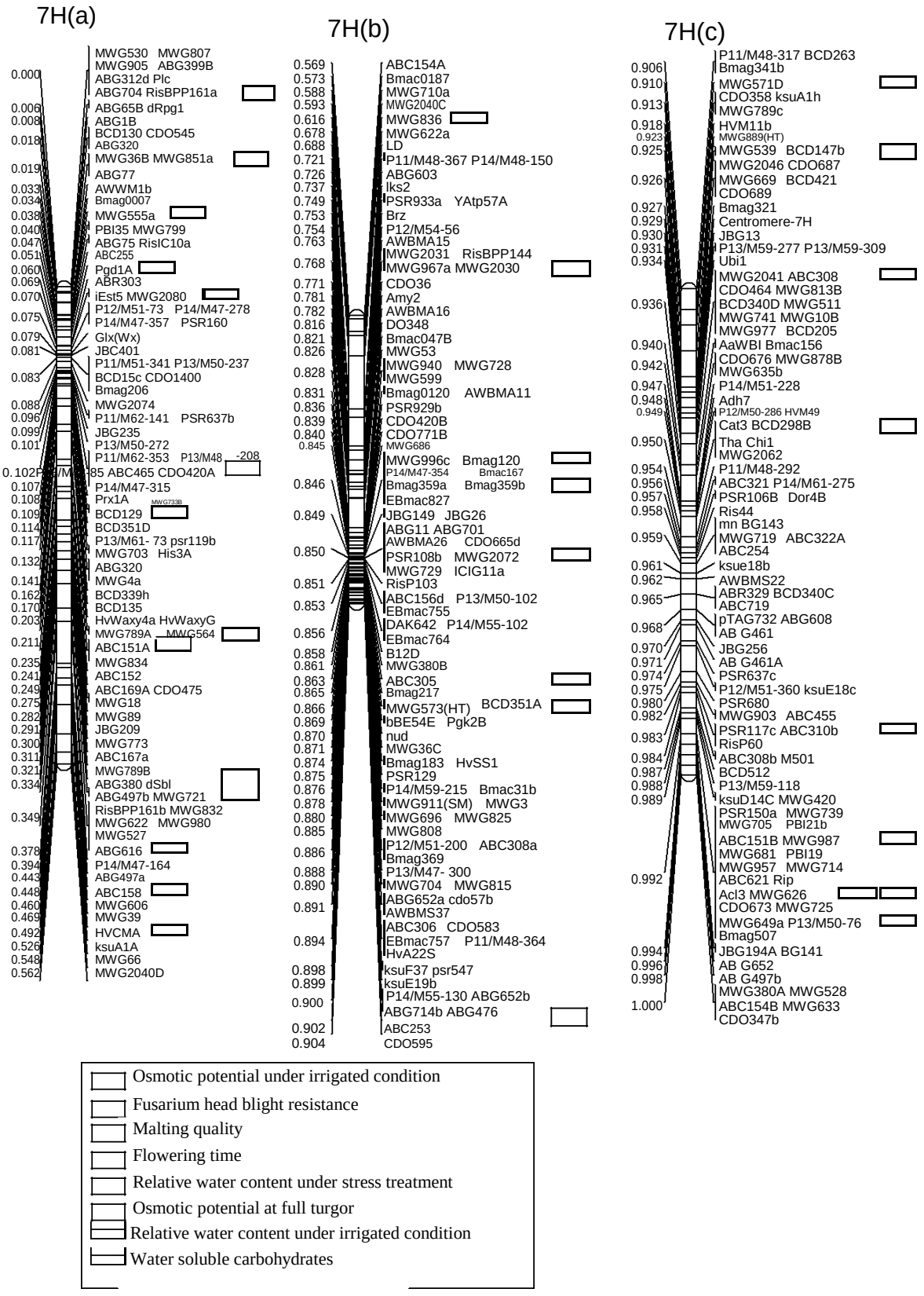

Figure 1. contd.

et al. (1996) as they identified QTL for flowering time on all chromosomes except the chromosome 3H. This indicates that the constructed consensus map is consistent with other barley maps used in QTL studies. In some genomic regions of the consensus map, markers associated with flowering time and Fusarium head blight resistance were co-located on the same place. Jeremy et al. (1996) reported a correlation between heading date and plant height but there is no reports for a correlation between heading date and Fusarium head blight resistance. This might reflect a possible correlation between the two traits. However, more studies and investigations are needed to be done in this area to verify this possibility.

Malting quality traits such as percentage of plump kernels, test weight, grain protein percentage, soluble/total protein ratio, -amylase activity, diastatic power and malt-extract percentage are highly correlated and controlled by almost the same loci (Marquez et al., 2000). In the present study 32 QTL for malting quality were placed on the integrated map. Six of them were on chromosome 1H, 8 on 2H, 2 on 4H, 5 on 5H, 4 on 6H and 7 on 7H (Figure 1). In the progeny of Steptoe (feed) x More (malt), malting quality QTL were mapped to all seven chromosomes (Hayes et al., 1993). In the progeny of Harrington (malt) x TR306 (feed), malting quality QTL mapped to all chromosomes except 2H (Mather et al., 1997).

Ten QTL related to drought tolerance were incorporated into the consensus AD-2005 map. One for osmotic potential under irrigated condition on chromosome 2H, 1 for relative water content under stress condition on chromosome 7H, and one QTL for relative water content under irrigated condition on chromosome 5H. Two QTL for osmotic potential at full turgor were placed, one on chromosome 4H and one on 3H. While 5 QTL for water soluble carbohydrates were placed, two of them on chromo-some 7H and 5H each and one on chromosome 2H. This result agrees with Diab et al. (2004) and Teulat et al. (2001). QTL for water soluble carbohydrates and relative water content were found to be associated with the marker MWG626 and the marker Acl3 respectively on chromosome 7H. These traits are components of drought tolerance; therefore, the co-localization of these QTL is most likely due to pleiotropic effects of the same gene(s). The correlation between the 2 traits has been reported by Teulat et al. (2001) and Diab et al. (2004).

Markers associated with more than one trait

Markers on the consensus AD-2005 that was found to be associated with more than one trait should receive more attention, as it could be of a great use to correlate traits that were not reported to be correlated or to support a correlation between traits that was suspected or need more investigation. For example, the marker HVM36 on chromosome 2H was found to be associated with a QTL for Fusarium head blight resistance (Mesfin et al., 2003) and a QTL for osmotic potential (Diab et al., 2004). Also the marker (Bmag0125) on the same chromosome was found to be associated with a QTL for Fusarium head blight resistance (Mesfin et al., 2003) and a QTL for water soluble carbohydrates (Diab et al., 2004). Another case of one marker associated with 2 different traits is the locus MWG503 on the same chromosome (2H) that was reported to be associated with a QTL for Fusarium head blight resistance (Mesfin et al., 2003) and a QTL for malting quality (Marquez et al., 2000). There are no reports supporting the correlation between these traits, however, the association of these traits with the same marker suggests a sort of correlation between these traits.

The marker CDO484 on chromosome 5 was found to be associated with QTL for relative water content and water soluble carbohydrates (Diab et al., 2004). The co-location of water soluble carbohydrates and relative water content in this region suggests that the accumulation of water soluble carbohydrates may be important for plants to maintain their relative water content. Teulate et al. (2001) reported a correlation between these two traits as a part of the drought tolerance mechanism in barley.

This study reports the first barley consensus map gathering QTL for Fusarium head blight resistance, malting quality, flowering date and QTL related to drought stress. Gathering QTL for agronomic traits and biotic and abiotic stress on the same map provides new tools to align QTL traits between gramenea species and determine the most important regions for saturated mapping. The comparative genome mapping of such QTL may provide new information on shared genetic variation for those traits among cereals, which in turn might be useful for identifying potential candidate genes.

Proof of reliability of the consensus AD-2005 map

Comparative genomic studies of maps between cereal species have shown conservation of genome structure (Devos and Gale,1993 and 1997; Van Deynze et al., 1995a,b,c). More extensive analysis of genome organization has revealed that the genome of rice can be subdivided into 19 linkage segments, which can be aligned with the genomes of wheat and barley (Moore et al., 1995). Based on previous comparative linkage mapping studies, the rice linkage groups 5 and 10 are known to be syntenic with at least parts of the linkage group 1(1H), while the rice chromosome 1 is syntenic with chromosome 3(3H). Similarly, rice non homologous chromosomes (4 and 7), (3 and 10) and (6 and 8) are syntenic with chromosomes 2H, 4H, and 7H, respectively. Accordingly, the Cornell rice RFLP 2001 map (http://www. gramene. org) was downloaded and

Table 3. Comparison of the common markers (anchor loci) found in comparative study between rice and consensus AD-2005, OWB, KXM, and VXHs barley maps.

	Marker	Position	Marker	Position	Marker	Position	Marker	Position
Map	OWB - 1H		KXM - 1H		VXHs - 1H		Consensus AD-2005 -1H	
Rice 5	0	-	CDO105B	102.8	MWG68	46.5	BCD454 CDO580a CDO105B	0.16 0.244 0.519
Rice 10	0	-	0	-	0	-	CDO98 BCD207	0.26 0.28
	OWB - 2H		KXM - 2H		VXHs - 2H		Consensus AD-2005 - 2H	
Rice 4	0	-	JBG282	113.7	0	-	CDO680 CDO36	0.608 0.97
	OWB - 3H		KXM - 3H		VXHs - 3H		Consensus AD-2005 - 3H	
Rice 1	0	-	MWG110	113.3	0	-	CDO395 BCD828 MWG110	0.087 0.35 1.0
	OWB - 4H		KXM - 4H		VXHs - 4H		Consensus AD-2005 - 4H	
Rice 3	CDO542 CDO122	31.2 32.3	0	-	0	-	CDO795	0.013
	OWB - 7H		KXM - 7H		VXHs - 7H		Consensus AD-2005 - 7H	
Rice 6	0	-	0	-	0	-	Glx(Wx) CDO475 Amy2	0.175 0.295 0.67
Total	2		3		1		14	

compared with the constructed barley consensus AD-2005, OWB, KXM and VXHs maps based on common markers (anchor loci). The results obtained from this comparative study are showed in Table 3. The total number of shared markers between rice and barley maps increased from two with OWB map, three with KXM and one with VXHs to 14 when the consensus AD-2005 map was used. These results meet the main objective of constructing an integrated barley consensus map to increase the chance of finding anchor loci between durum wheat, barley and rice.

The construction of consensus map allows scientists to easily compare genetic information from diploid species such as barley to species with more complex genomic structure, such as wheat, and increases the efficiency of molecular marker and gene isolation technologies applied to crop improvement. The objective of this work was to construct a consensus map for barley to be used in molecular breeding, QTL analysis and comparative genome mapping, which in turn will help plant breeders to combine QTL traits with other traits desired by farmers. Although more data are desperately needed, we can now conclude that this consensus map will serve as a useful tool for more precise mapping of cereals, molecular breeding studies in barley and related species, gene isolation based on map-based cloning and a basis for studies of genome organization and evolution.

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