Theor Appl Genet (1995) 91:921–927

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Mapping of β-glucan content and β-glucanase activity loci in barley grain and malt

Received: 27 March 1995 / Accepted: 21 April 1995

Abstract Genetic study of β-glucan content and β-glucanase activity has been facilitated by recent developments in quantitative trait loci (QTL) analysis. QTL for barley and malt β-glucan content and for green and finished malt β-glucanase activity were mapped using a 123-point molecular marker linkage map from the cross of Steptoe/Morex. Three QTL for barley β-glucan, 6 QTL for malt β-glucan, 3 QTL for β-glucanase in green malt and 5 QTL for β-glucanase in finished malt were detected by interval mapping procedures. The QTL with the largest effects on barley β-glucan, malt β-glucan, green malt β-glucanase and finished malt β-glucanase were identified on chromosomes 2, 1, 4 and 7, respectively. A genome map-based approach allows for dissection of relationships among barley and malt β-glucan content, green and finished malt β-glucanase activity, and other malting quality parameters.

Key words QTL mapping · β-Glucan · β-Glucanase
Malt barley · *Hordeum vulgare*

Communicated by G. Wenzel

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Introduction

Mixed-linked (1-3,1-4)-β-D-glucans are the major components of starchy endosperm and aleurone cell walls in barley grain (termed barley β-glucan). During the malting (germination) of barley grain, β-glucans are partially depolymerized by enzymes synthesized de novo (Bamforth and Martin 1981). The enzymes responsible for this degradation are (1-3,1-4)-β-glucanases [(1-3,1,4)-β-glucan 4-glucanohydrolases], which generally give effective hydrolysis of polymeric barley β-glucans. Undegraded β-glucans remain in malt (termed malt β-glucan). Two (1-3,1-4)-β-glucanase isoenzymes (EI and EII) from germinating barley have been characterized (Woodward and Fincher 1982a,b) and mapped on chromosomes 5 and 1, respectively (Loi et al. 1988).

β-glucans are considered undesirable in feed and malt but desirable for human nutrition. Firstly, higher levels of barley β-glucan make the barley less digestible by non-ruminant animals (Peterson 1972) and may decrease the rate of modification during malting (Martin and Bamforth 1980). Secondly, higher levels of malt β-glucan reflect incomplete endosperm cell-wall degradation and is consequently associated with lowered malt extract values (Fincher 1992). Thirdly, the tendency of β-glucan to form highly viscous aqueous solutions can lead to filtration difficulties at various points in the brewing process (Bamforth and Barclay 1993). On the other hand, β-glucans are considered to have hypocholesterolemic effects in humans (Newman et al. 1989). Therefore, β-glucan content is an important parameter for evaluating food, feed and malt quality.

Powell et al. (1989) reported that barley β-glucan content was controlled by an additive genetic system of three to five "effective factors", but their chromosome locations could not be determined. With the advent of

molecular markers and the construction of comprehensive linkage maps, the systematic mapping and manipulation of QTL are possible. Therefore, the objectives of this study were: (1) to map quantitative trait loci (QTL) associated with β-glucan content in barley and malt, and β-glucanase activity in green malt and finished malt, and (2) to elucidate the relationships among β-glucan content, β-glucanase activity and malting quality traits.

Materials and methods

A population of 150 doubled haploid (DH) lines were derived by a modification of the *Hordeum bulbosum* method (Chen and Hayes 1989) from the F_1 of the cross, Steptoe/Morex. This population was used to construct a 295-point map with an average density of 4 cM (Kleinhofs et al. 1993), and this map has since been expanded to include over 400 markers (Kleinhofs et al. 1994). Current mapping and QTL on-line data sets are available in GrainGenes through the Gopher Server. By selecting relatively evenly spaced markers, we generated a 123-point "skeleton" linkage map with an average marker density of 9.6 cM. This map was produced by GMENDEL (Liu and Knapp 1990) and used for mapping a number of agronomic and malting quality QTL (Hayes et al. 1993). Locus designations were described by Kleinhofs et al. (1993). The relevant known function clones are described below.

The 150 DH lines and the parents were grown at Aberdeen, Idaho; Bozeman, Montana; Klamath Falls, Oregon; and Pullman, Washington in 1991. A randomized complete block design with partial replication was employed at each location as described by Hayes et al. (1993). β-Glucans were measured by standard fluorimetric procedures (Jørgersen and Aastrup 1988) employed by the USDA/ARS Cereal Crops Research Unit, Madison, Wisconsin. The DH lines used for β-glucanase measurement were grown in Toulouse, France in 1992 and in Clermont-Ferrand, France in 1993, in a two replicate randomized complete block design. The malt was obtained with an automatic micromalting system (Phoenix, Australia). The β-glucanase activity in green malt (before kilning) and finished malt (after kilning) was measured using Azo-barley glucan (McCleary and Shameer 1987).

QTL analyses were first conducted separately for each trait/environment combination. As no genotype × environment interaction of a change in favorable allele type was detected, we report QTLs based on multi-environment means. Analyses were performed using MAPMAKER/QTL (Lander et al. 1987; Lincoln et al. 1992). QTL effects were considered significant if they exceeded a LOD score of 2.4 ($P \approx 0.001$) for a sparse map case (Lander and Botstein 1989). The LOD peaks were considered the most likely position of QTL effects, 90% confidence intervals were calculated as described by van Ooijen (1992).

Results and discussion

Phenotypic descriptions

Normal distribution frequencies for barley and malt β-glucan content and for green and finished malt β-glucanase activity were observed for the population of DH lines (Fig. 1). Barley β-glucan content ranged from 3.4% to 5.3% with a mean of 4.3% over the four locations, while the Steptoe and Morex means were 4.3 and 4.7%, respectively. Malt β-glucan content of the DH lines ranged from 0.4 to 2.0% with a mean 1.1% over the four locations, with Steptoe and Morex means of 1.3 and 0.6%, respectively. Green malt β-glucanase activity of the DH lines ranged from 541 to 1116 (U/kg), with a mean of 872 (U/kg); with Steptoe and Morex, the means were 550 and 1100 (U/kg), respectively. Finished malt β-glucanase activity of the DH lines ranged from 226 to 596 (U/kg), with a mean of 410 (U/kg); with Steptoe and Morex, the means were 220 and 530 (U/kg), respectively. Considerable variation in all four traits was apparent among the DH lines. There was phenotypic transgressive segregation for barley β-glucan and possibly for malt β-glucan content.

Map locations of QTL

Three QTL for barley β-glucan (multilocus $r^2 = 34\%$), 6 QTL for malt β-glucan (multilocus $r^2 = 40\%$), 3 QTL for β-glucanase in green malt (multilocus $r^2 = 30\%$) and 5 QTL for β-glucanase in finished malt (multilocus $r^2 = 43\%$) were detected. The map locations, genotype differences and variances explained by identified QTL are presented in Table 1. The QTL with the largest effects on barley β-glucan, malt β-glucan, green malt β-glucanase and finished malt β-glucanase were identified on chromosomes 2 (*Adh8*-ABG019 interval), 1 (*Brz*-ABC156D interval), 4 (ABG484-WG464 interval) and 7 (*Ale*-ABC302 interval), respectively. Within the LOD support interval for the barley β-glucan QTL in the *Adh8*-ABG019 interval on chromosome 2, a second peak was detected in the ABG703-*Chs1B* interval. The chromosome was scanned again with the large effect QTL fixed in the *Adh8*-ABG019 interval. The LOD for the ABG703-*Chs1B* interval was 3.2, thereby providing evidence for two distinct, linked QTLs on chromosome 2.

Overlapping QTL and trait relationship implications

Two QTLs for finished malt β-glucanase are coincident with 2 QTLs having the largest effects on malt β-glucan on chromosome 1 (Table 1). It is likely that coincident QTLs for malt β-glucan and finished malt β-glucanase are really the consequence of one gene, as the level of malt β-glucan is dependent largely on β-glucanase activity during germination. The phenotypic correlation coefficient for malt β-glucan versus finished malt β-glucanase in this study was -0.34 ($P < 0.01$). There may be some relationship between the malt β-glucan/finished malt β-glucanase QTL that mapped to the ABG011-ABC455 interval in the centromere region on chromosome 1 and the (1-3, 1-4)-β-glucanase isoenzyme EII gene that has been previously mapped to the long arm of chromosome 1 (Loi et al. 1988; Slakeski et al. 1990). The EII isoenzyme is transcribed in the aleurone and classified as "germination specific" (Fincher 1992). Depending upon the accuracy of the respective mapping efforts, the ABG011-ABC455 gene may be the EII gene or associated with the EII gene.

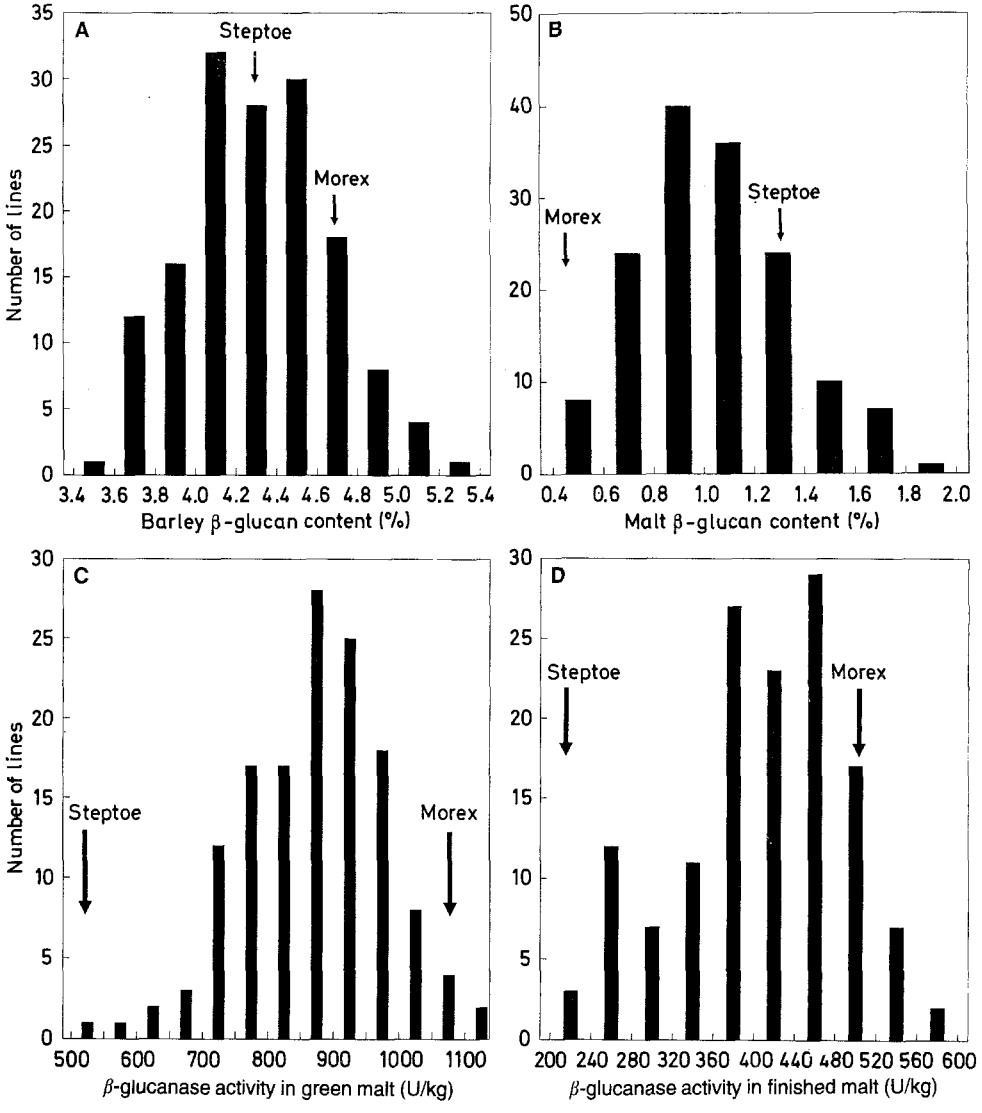

Fig. 1 A–D Frequency distribution of barley β-glucan content (**A**), malt β-glucan content (**B**), β-glucanase activity in green malt (**C**) and β-glucanase activity in finished malt (**D**) among DH lines with the Steptoe and Morex parents β-glucan content indicated

The results for the long arm of chromosome 5 are interesting, as QTLs for all four traits measured are coincident or have overlapping support intervals. Additionally the EI isoenzyme gene of β-glucanase (*Glb1*) maps to the same chromosome region (Slakeski et al. 1990; Kleinhofs et al. 1994). Possible explanations for the overlap of these β-glucan and β-glucanase QTLs in the vicinity of *Glb1* on chromosome 5 are :(1) the QTLs are attributable to *Glb 1*, or (2) there is a cluster of associated genes for these related traits, such as the hordein protein multigene families on chromosome 5 (Kreis and Shewry 1992).

We hypothesize that the 2 β-glucan QTL (closest to the centromere) and 2 β-glucanase QTL effects are attributed to the *Glb 1* gene or gene family on chromosome 5. The EI isoenzyme of (1-3, 1-4)-β-glucanase of *Glb 1* has been shown to be active in vegetative tissues during growth as well as in germinating grain from scutellum and aleurone tissue (Slakeski et al. 1990) and appears to be subject to a more complex control mechanism than the EII isoenzyme, which is exclusively from aleurone and is germination-specific (Fincher 1992). Morex contributed higher malt β-glucanase activity alleles and the lower barley and malt β-glucan content alleles on chromosome 5. The higher malt β-glucanase activity in Morex germinating grain may also correspond to higher EI β-glucanase activity during seed development and thus lower β-glucan accumulation in seed (from the *Glb 1*-ABC160 QTL). The higher overall barley grain β-glucan content of Morex relative to Steptoe (Fig. 1) would thus be attributed to the chromosome 2 QTL.

Although the effects of the two previously characterized and mapped isoenzymes of endo-(1-3, 1-4)-β-glucanase, EI (chromosome 5) and EII (chromosome 1) (Loi et al. 1988; Slakeski et al. 1990) may account for some of the detected QTL, additional QTL were identified for both traits. Other enzymes implicated in (1-3,

Table 1 QTL genotype difference (Diff.) and variance (%Var) explained where LOD score ⩾ 2.4. Value in bold type indicates LOD peak. Adjacent values indicate the support interval. The letter suffix indicates the parent contributing the larger value allele. Marker intervals in bold type indicate centromere location (*S* Steptoe, *M* Morex)

Marker interval		Recombination frequency (%)	β-glucan						β-glucanase					
			Barley			Malt			Green malt			Finished malt		
			Diff.	% Var	LOD	Diff.	% Var	LOD	Diff.	% Var	LOD	Diff.	% Var	LOD
Chromosome 1														
ABA301	Plc	3.4												
Plc	BCD129	7.5												
BCD129	Glx	8.3												
Glx	WG789A	5.5												
WG789A	ABG380	4.9												
ABG380	ABC158	7.7												
ABC158	KsuA1A	6.1				0.18S	8.5	2.6				46.0M	8.0	2.5
KsuA1A	ABC154A	3.4				0.19S	9.6	3.2				45.8M	8.0	2.4
ABC154A	Brz	7.3				0.24S	16.1	5.7				45.6M	7.9	2.5
Brz	ABC156D	5.8				**0.26S**	**17.9**	**5.9**				**51.2M**	**10.0**	**3.0**
ABC156D	ABG022A	12.8				0.22S	13.6	4.7				50.6M	9.8	3.0
ABG022A	ABG701	3.9				0.18S	8.7	2.9						
ABG701	ABG011	4.4				0.17S	8.0	2.6				47.7M	8.6	2.5
ABG011	ABC455	5.6				**0.22S**	**12.8**	**4.4**				**52.2M**	**10.2**	**3.2**
ABC455	**Amy2**	6.9				0.22S	12.6	4.3				52.2M	10.2	3.1
Amy2	Ubil	16.1				0.20S	10.6	3.0						
Ubil	ABC310B	4.0												
ABC310B	ABC305	6.7												
ABC305	PSR129	4.9												
PSR129	ABG461	13.0												
ABG461	Cat3	19.7												
Chromosome 2														
ABG313A	ABG703	7.9												
ABG703	Chs1B	11.0	**0.23M**	**10.5**	**3.2**									
Chs1B	ABG008	7.2	0.22M	9.9	3.1									
ABG008	Rbcs	4.6	0.22M	9.1	3.0									
Rbcs	ABG002	11.5	0.26M	13.1	4.0									
ABG002	ABG459	9.0	0.26M	12.8	4.1									
ABG459	Pox	6.8	0.27M	14.4	5.0									
Pox	Adh8	5.5	0.28M	15.2	5.2									
Adh8	ABG019	11.7	**0.32M**	**19.2**	**5.8**									
ABG019	**ABC162**	6.6	0.28M	15.2	5.1									
ABC162	ABG014	8.3	0.22M	9.7	3.3									
ABG014	His3C	10.3												
His3C	KsuF15	11.9												
KsuF15	Crg3A	22.1												
Crg3A	Gln2	16.4												
Gln2	ABC157	7.4												
ABC157	ABC165	7.4												
ABC165	Pcr1	7.5												
Pcr1	ABA005	8.6												
Chromosome 3														
ABA303	ABC171	23.0												
ABC171	ABG057	13.5												
ABG057	ABG471	3.6												
ABG471	Dor4A	19.8				**0.16S**	**7.3**	**2.4**						
Dor4A	ABG396	6.4				0.16S	7.3	2.4						
ABG396	**ABG703A**	9.4												
ABG703A	PSR156	9.3												
PSR156	ABG377	7.6												
ABG377	ABG453	10.5												
ABG453	ABC307B	10.2												
ABC307B	CDO113B	12.3												
CDO113B	His4B	16.9												
His4B	ABG004	14.1												
ABG004	mPub	7.3												
mPub	ABC174	13.4												
ABC174	ABC166	11.6												
ABC166	ABC172	11.0												

Table 1 (Continued)

Marker interval	Recombination frequency (%)		β-glucan						β-glucanase					
			Barley			Malt			Green malt			Finished malt		
			Diff.	% Var	LOD	Diff.	% Var	LOD	Diff.	% Var	LOD	Diff.	% Var	LOD
Chromosome 4														
WG622	ABG313B	10.5				**0.20S**	**10.4**	**3.3**						
ABG313B	CDO669	4.6				0.19S	9.2	3.0						
CDO669	BCD402B	14.0				0.20S	10.7	3.0						
BCD402B	TubA1	10.3							64.9M	8.6	2.4			
TubA1	ABG003	4.8							64.1M	8.4	2.4			
ABG003	**ABG484**	5.4							70.4M	10.1	3.2			
ABG484	WG464	10.4							**79.5M**	**12.6**	**3.6**			
WG464	ABG472	15.8							77.5M	12.3	3.3			
ABG472	ABG500B	16.1							63.8M	8.3	2.5			
ABG500B	ABG397	7.0												
ABG397	Bmy1	25.4												
Bmy1	KsuH11	3.3												
Chromosome 5														
AGA006	Hor2	2.5												
Hor2	Hor1	10.5												
Hor1	ABA004	6.6												
ABA004	CDO99	8.0												
CDO99	Ica1	11.2	0.23S	9.8	3.3									
Ica1	ABG500A	7.9	0.25S	11.7	3.8									
ABG500A	ABG494	9.9	0.27S	13.8	4.4									
ABG494	**Glb1**	7.6	0.27S	14.4	4.9									
Glb1	ABC160	8.8	**0.28S**	**15.0**	**4.9**				**67.7M**	**9.3**	**2.7**			
ABC160	ABG464	14.7	0.27S	13.8	4.0				**71.5M**	**10.5**	**3.0**	**50.5M**	**11.2**	**3.0**
ABG464	His3B	9.6	0.22S	9.5	2.8	0.17S	8.0	2.5	73.5M	11.0	3.1	**56.7M**	**12.3**	**3.6**
His3B	iPgd2	16.6	0.21S	9.0	2.6	**0.18S**	**8.7**	**2.5**	**77.6M**	**12.3**	**3.2**	55.8M	11.9	3.5
iPgd2	ABG702	12.6												
ABG702	ABA002	6.4				**0.17S**	**7.9**	**2.7**						
ABA002	ABG373	8.3				0.17S	7.9	2.7						
ABG373	ABG387A	5.3												
Chromosome 6														
PSR167	Nar1	6.3												
Nar1	ABG378	5.2												
ABG378	Cxp3	9.0												
Cxp3	PSR106	16.7												
PSR106	ABG387B	4.5												
ABG387B	ABG458	14.5												
ABG458	Rrn1	6.3												
Rrn1	ABG474	7.1												
ABG474	**KsuD17**	4.1												
KsuD17	KsuA3D	7.3												
KsuA3D	Nar7	8.7												
Nar7	Nir	5.5												
Nir	PSR154	12.3												
Chromosome 7														
ABC483	ABG705	27.6												
ABG705	ABG395	7.9												
ABG395	Rrn2	3.6												
Rrn2	**Ltp1**	**4.5**												
Ltp1	ABC706	5.8										48.6M	8.8	2.7
ABC706	Ale	5.4										55.5M	11.6	3.6
Ale	ABC302	10.1							**73.1M**	**10.8**	**3.4**	**63.5M**	**15.3**	**4.6**
ABC302	CDO57B	13.0							72.7M	10.7	3.3	60.5M	13.9	4.4
CDO57B	mSrh	5.4												
mSrh	ABG473	6.5												
ABG473	CDO504	31.3												
CDO504	WG908	7.7												
WG908	ABG495A	8.8												
ABG495A	ABG496	6.2												
ABG496	ABC482	7.4												
ABC482	ABG707	7.2										44.9M	7.7	2.4
ABG707	ABG463	9.1										**49.1M**	**9.2**	**2.6**
ABG463	ABA304	8.6										45.7M	7.9	2.4

1-4)-β-glucan hydrolysis include (1-3)-β-glucanases, cellulases and exo-β-glucanases (Fincher 1992). If it is assumed that the β-glucanase assay used in this study was nearly 100% specific for endo-(1-3, 1-4)-β-glucanases, then additional isoenzymes may account for these QTLs.

Several relationships between the β-glucan and β-glucanase traits and other malting quality traits can be explored or verified from our QTL analyses. Malt β-glucan content was correlated with malt extract percentage ($r = -0.44$, $P < 0.01$), diastatic power ($r = -0.51$, $P < 0.01$) and α-amylase activity ($r = -0.63$, $P < 0.01$). Stuart et al. (1988) reported $r = -0.74$ ($P < 0.01$) for malt β-glucan versus malt extract. A comparison of our QTL analyses with those reported by Hayes et al. (1993) and Hayes and Iyambo (1994) for malting quality traits indicate that the 2 QTLs for malt β-glucan and finished malt β-glucanase activity mapped in the *Brz-Amy2* interval on chromosome 1 are coincident with 2 QTL regions for malt extract, α-amylase and diastatic power. A QTL for malt β-glucan and 1 for green malt β-glucanase also overlap with 2 malt extract QTL in the CDO669-BCD402B and ABG484-WG464 intervals, respectively, on chromosome 4. These phenomena seem logical in terms of the relationships among these traits. High β-glucanase activity not only results in low malt β-glucan content, but also due to its role in cell-wall degradation allows amylases to efficiently enter starchy endosperm to hydrolyze starch. Well-modified endosperm will give rise to high malt extract percentage as well as low malt β-glucan. The major QTL for green and finished malt β-glucanase activity is coincident with the major seed dormancy QTL in the Ale-ABC302 interval on chromosome 7 (Ullrich et al. 1993). The correlation coefficients between dormancy and green and finished malt β-glucanse are 0.51 ($P < 0.01$) and 0.57 ($P < 0.01$), respectively. Seed dormancy or the lack thereof is related to the early germination stage of β-glucanase activity and endosperm cell-wall breakdown, and the case may be made for a single genetic determinant in this region of chromosome 7.

Barley β-glucan QTL were found to overlap with α-amylase and diastatic power in the *Pox*-ABG019 interval on chromosome 2, and with malt extract in the ABG494-ABC160 interval on chromosome 5, but no significant phenotypic correlations were found among these traits (data not shown). QTL analysis revealed a genetic relationship not seen in the phenotypic correlations. Whether these QTLs are a consequence of linked genes, a gene cluster or single gene pleiotropism is yet to be determined.

The mapping of QTL associated with β-glucan content and β-glucanase activity provides an alternative selection approach via linked markers. The advantages of using molecular marker assisted selection (MMAS) over phenotype-based selection for β-glucan content or β-glucanase activity are: (1) MMAS can identify genotypes with the potential of low β-glucan content or high β-glucanase activity in the F_2; (2) it doesn't require grain for β-glucan and β-glucanase analysis, which is always limited in early generations; and (3) fewer β-glucan and β-glucanase analyses will be needed. Unlike the loci for qualitative traits, precise location of a QTL on the linkage map is not determined by present QTL analysis technology. Therefore, the use of flanking markers 10–20 cM apart and the bracketing of target QTL should suffice for MMAS with a minimum of double crossovers. The flanking markers for the peak interval of each QTL shown in Table 1 should be suitable for MMAS, because most of them are linked within 10 cM and the rest within 20 cM. The most suitable flanking markers may best be identified from an up-to-date full map (e.g. consult GrainGenes).

Acknowledgments Department of Crop and Soil Sciences Scientific Paper Number 9503-13, College of Agriculture and Home Economics Research Center, Washington State University, Pullman, Wash., USA, Project 1006. This work is part of the North American Barley Genome Mapping Project. We are grateful for the financial support of American barley growers, the malting and brewing industry, and USDA-CSRS Special Grant Agreement 94-34213-0030.

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