AN ABSTRACT OF THE THESIS OF

Ergun Ozdemir for the degree of Master of Science in Crop Science presented on May 23, 1994.

Title: Genetic Analysis of Malt Extract and Grain Yield in a Spring Barley (*Hordeum vulgare* L.) Cross.

Abstract approved: Redacted for Privacy

Patrick M. Hayes

Quantitative trait locus (QTL) detection procedures based on medium density genome maps may provide useful information upon which to base offensive, multiple-trait, breeding strategies. QTLs for two complex phenotypes - grain yield and malt extract - provide an ideal model system for genetic analysis. The first objective of this effort was to determine the number, magnitude, and favorable allele status of QTLs for these traits based on various grouping of multiple-environment datasets in order to (i) assess the importance and nature of QTL X environment interaction and (ii) and resolve QTL position. Realization of this objective will allow the selection of molecular markers that can be used to monitor QTL segregation in new populations derived from intermating populations in the reference mapping population. The second objective of this research was to create new test populations that would, respectively, (i) maximize the probability of recovering a genotype with the maximum number of favorable QTL alleles, and (ii) maximize segregation at all possible QTLs. Genotyping of these populations with the markers selected in the course of realizing

the first objective will allow for the identification of genetic stocks that can be phenotyped in extensive field trials. These data can then be employed to compare predicted and realized selection responses. Grain yield and malt extract QTLs were identified through interval mapping procedures based on sixteen environments of yield data and nine environments of malt extract data. Data from these environments were pooled according to agrogeographic and common expression criteria, and the results of these analyses were compared with QTLs revealed across the individual environments and in the analysis of the overall mean. Grain yield QTLs were identified on all chromosomes and malt extract QTLs on six of the seven barley chromosomes. The feed parent (Steptoe) was the largest contributor of yield QTLs and the malting quality parent (Morex) was the largest contributor of malt extract QTLs. Although shifting QTL peaks and overlapping confidence intervals complicate enumeration of QTL effects, there are at least ten yield and malt extract QTLs in this germplasm. However, most of these QTLs were significant in three or fever environments and change in magnitude of response-type QTL X environment interaction are characteristic of these data. Change in rank-type QTL X environment interaction was detected for grain yield on chromosome 2. Steptoe and Morex contributed alternative favorable alleles in Midwestern and Western dryland environments. It will not be possible to accumulate all favorable alleles for both characters in a single genotype, as there are overlapping or coincident QTLs for yield and malt extract with contrasting parents contributing favorable alleles. Segregation at key QTLs will be determined by genotyping the doubled haploid progeny of the two new cross combinations. By

defining target environments, it should be possible to identify subsets of genotypes that will allow for empirical assessment of the worth of key QTL effects.

Genetic Analysis of Malt Extract and Grain Yield in a Spring Barley (*Hordeum vulgare* L.) Cross

by

Ergun Ozdemir

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Completed May 23, 1994

Commencement June 1995

APPROVED:

Redacted for Privacy

Associate Professor of Crop and Soil Science in charge of major

Redacted for Privacy

Head of the Department of Crop and Soil Science

Redacted for Privacy

Dean of Graduate School

Date thesis is presented May 23, 1994

Typed by Ergun Ozdemir for Ergun Ozdemir

Acknowledgment

I would specially like to thank my major professor, Dr. Patrick Hayes, for his collaboration, guidance, patience and support throughout all phases of my study.

I would also like to extend my thanks to members of my committee: Dr. Shawn Mehlenbacher, Dr. Steven Knapp, and Dr. Andrew Hashimoto for their advice and direction throughout the course of this study.

I would like to thank my director, Dr. Fahri Altay for his support of my study; and also all my friends within and outside the barley and wheat group for their encouragement and friendship.

Special thanks to my wife, Hulya, and my son, Batuhan, and to our parents for their patience and understanding.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

To my wife, Hulya, and my son, Batuhan,

and to our parents,

for many years of patience and understanding

Genetic Analysis of Malt Extract and Grain Yield in a Spring Barley (*Hordeum vulgare* L.) Cross

INTRODUCTION

The current enthusiasm for construction of medium density genome maps in virtually every economically important plant species is based, in large part, on the premise that molecular marker assisted selection (MMAS) will lead to greater efficiencies and selection responses than conventional breeding strategies. Medium density linkage maps have been developed in many important crop species, including barley (Graner et al., 1991; Heun et al., 1991; Kleinhofs et al., 1993). Quantitative trait locus (QTL) analyses have been employed to locate genes controlling traits of economic importance in a subset of the crops that have been mapped. For example, in barley, QTLs have been reported for a range of agronomic and malting quality traits (Hayes et al., 1993b); components of winter hardiness (Hayes et al., 1993a); and disease resistance traits (Chen et al., 1994; Heun, 1992). In a further subset of crops, MMAS procedures have been implemented. Typically, these have been targeted at introgressing a limited number of QTLs via marker assisted backcrossing. Again as an example in barley, Chen et al. (1994) mapped QTLs for resistance to barley stripe rust (*Puccinia striiformis* fsp. *hordei*) and implemented a selection effort based on introgressing two chromosome segments via flanking restriction fragment length polymorphism (RFLP) markers. However, there is paucity of information regarding the use of MMAS in the context of an offensive breeding strategy within a relatively narrow germplasm base.

Kleinhofs et al. (1993) and Hayes et al. (1993b) published linkage maps and QTL analyses, respectively, based on the progeny of 150 doubled haploid (DH) lines developed from the cross of Steptoe X Morex. Steptoe is a high yielding, broadly adapted six-row feed barley (Muir and Nilan, 1973) and Morex is the U.S. six-row malting quality standard (Rasmusson and Wilcoxson, 1979). This cross combination was chosen as a compromise between the need for adequate DNA-level polymorphism for linkage mapping and the need to generate QTL data within a relatively meaningful germplasm base. Hybridizations between the Coast and Manchurian germplasm pools, represented by Steptoe and Morex, respectively, would generally not be attempted in a breeding effort directed at cultivar development. Segregation and independent assortment would be expected to disrupt the unique assemblage of coupling linkages that defines each of the varieties within the two pools. Thus, in the progeny of this cross, there would be little expectation of recovering a genotype with the yield potential of Steptoe and the malt extract potential of Morex.

Yield and malt extract are "ultimate" phenotypes composed of component characters and represent the cumulative effects of a host of metabolic pathways operating during crop growth and development. Grain yield is considered quantitatively inherited, highly subject to environmental influences, and characterized by genotype x environment interaction (Tapsell and Thomas, 1983). Despite extensive effort directed at developing indirect selection criteria for grain yield based on the components of yield (number of plants per unit area, number of heads per plant, number of kernels per head, and kernel weight) (Rasmusson and Channell, 1970),

selection is typically based on average, long-term performance in replicated multi-environment yield trials. Malt extract is a deceptively simple phenotype, as it is simply the percentage of malted grain that dissolves in warm water. However, the percentage of soluble sugars and proteins is, in turn, a consequence of a host of complex proteolytic pathways. Despite extensive efforts to identify indirect selection criteria for malt extract, this character, like grain yield, is considered quantitatively inherited, highly subject to environmental influences, and characterized by genotype x environment interaction (Burger and LaBerge, 1985). Selection for malt extract, like selection for yield, is therefore typically based on average, long-term performance in replicated multi-environment trials.

Given the inheritance of these characters and the expected genetic structure of the Steptoe X Morex population, grain yield and malt extract represent logical candidates for testing the effectiveness of a marker-based offensive breeding strategy. Principal features of the QTLs for grain yield and malt extract identified in the Steptoe X Morex DH population based on sixteen environments of agronomic trait testing and nine environments of malting quality assessment are variable levels of significance of QTL effects across environments and shifting of QTL position across environments (Hayes and Matthews, 1994). These features are inter-related, but for the purposes of discussion, they can be divided into QTL X environment interaction and QTL resolution.

As outlined by Hayes et al. (1993b), QTL X environment interaction, like genotype X environment interaction, can be of several sorts. The QTL X E interaction

can be the result of (1) significant QTL effects detected only in a subset of the total number of environments, (2) changes in the magnitude of QTL effects across environments, or (3) contrasting favorable alleles at a QTL in different environments. The nature of the interaction is extremely important. Change in rank (crossover) interactions (i.e. item 3, above) would require distinct selection criteria for MMAS for the target environments showing alternative favorable alleles. Based on an assessment of the Steptoe X Morex population in the Western US in 1991, Hayes et al. (1993b) found that all interaction was of the first two types. In 1992, the population was evaluated in a broader range of environments, including locations in the Midwestern US, the Canadian prairies, and two locations in the Eastern US and Canada. Based on this large number of test environments, Hayes and Matthews (1994) detected QTL X E interactions of the third type. These results confirm the need to develop independent MMAS procedures for distinct target environments. The first two types of interaction also pose challenges for MMAS. Paterson et al. (1991) argued that pyramiding environment-specific QTLs could lead to the development of "stable" genotypes. However, population size issues, and the costs of phenotyping and genotypying, favor limiting the number of QTLs that are targets for selection.

QTL X E interaction may, therefore, require prioritization of QTLs as targets for selection, as well as the identification of subsets of target environments with distinct selection targets. To further confound the problem, the precise chromosome position of a QTL is often open to question. With an interval mapping procedure such as MAPMAKER/QTL (Paterson et al., 1988; Lincoln et al., 1992), a maximum LOD

score (peak) indicates the most likely position of the gene or genes determining the QTL effect. Due to linkage, significant, but lower, LOD scores are detected in adjacent intervals. However, as demonstrated by Martinez and Curnow (1992), a single, incorrectly positioned, LOD peak may be seen when there are linked QTLs affecting the same trait. Furthermore when QTL effects for the same phenotype measured in different environments, a host of factors, including errors in both phenotyping and genotyping, may cause the peak to shift one or several intervals. Hayes et al. (1993b) used non-overlapping 90% confidence intervals as evidence for distinct QTL effects. If the distances involved are in the vicinity of 20 cM or less, flanking marker selection will minimize the probability of recovering undesired double crossover genotypes and maximize the probability of recovering the desired genetic effects, even if the QTL peak is incorrectly positioned. However, in the case of adjacent QTLs with contrasting favorable alleles, or in the case of overlapping confidence intervals spanning large intervals, this criterion can be unsatisfactory.

With a QTL estimation procedure such as MAPMAKER/QTL that is only capable of utilizing single point estimates of phenotype for each genotype, a degree of improved QTL resolution may be achieved by averaging effects over a number of test environments. However, arbitrarily pooling data across locations may lead to cancellation of effects and a corresponding loss of QTL information. As pointed out by Knapp (1991), in MMAS, as in conventional breeding, a sound breeding strategy is based on careful characterization of test and target environments.

With these considerations in mind, we designed a long-term strategy to validate QTL effects in the Steptoe X Morex germplasm and to assess the utility of MMAS as a tool for an offensive breeding strategy designed to simultaneously improve grain yield and malt extract. Our rationale was that if we developed new arrays of doubled haploid genotypes with defined chromosome intervals contributed by the Steptoe and Morex parents, we could determine their QTL composition and validate the effects of these QTLs in field tests. There were two principal objectives to the first phase of this research. The first objective was to address the issues of QTL X environment interaction, environment-specificity, and QTL resolution in the context of developing a set of molecular markers that could be used to characterize new test populations for defined grain yield and malt extract QTLs. The second objective was to develop two new DH populations from cross combinations within the mapping population that would, respectively, (i) maximize the probability of obtaining all possible positive QTL alleles for the two traits, and (ii) maximize the probability of segregation at all possible QTL loci. Genotyping the test populations and comparing their predicted and realized performance will be the subject of future investigations.

MATERIALS AND METHODS

The development of the mapping population, linkage map construction, and initial QTL analyses were reported by Kleinhofs et al. (1993) and Hayes et al. (1993b). Briefly, the 150 DH lines that are the basis of this report were derived from the F_1 of the cross of Steptoe X Morex by the *Hordeum bulbosum* technique, as described by Chen and Hayes (1989). A 295-point medium density linkage map was developed in the population, using on the following markers: 152 cDNA RFLPs, 114 genomic RFLPs, 14 RAPDs, five isozymes, two morphological loci, one disease resistance locus, and five SAP markers (Kleinhofs et al., 1993). Hayes et al. (1993b) used a subset of 123 of these markers to construct a linkage map upon which to base QTL analyses. These analyses were based on assessment of the population at locations in the western US in 1991. The population was evaluated at additional locations in the US and Canada in 1992. QTL analyses of the additional data are available as online data files (Hayes and Matthews, 1994). In total, agronomic data is available from 16 environments and malting quality data from 9 environments. A list of the test environments and participating investigators is provided in Table 1. Cumulatively, these test environments represent a spectrum of typical U.S. and Canadian barley production areas. A randomized complete block design with partial replication was employed at each location in 1991. In 1992, the number of replications varied with each location. Plot size and management were in accordance with recommended practices for each location. Malt extract was measured on a 400 g sample of each of the 150 DH lines and two parents, following the standart procedure employed by the

Table 1. Parameters defining each of the sixteen environments where the Steptoe X Morex DH mapping population was evaluated in field trials in 1991 and 1992.

Environment	Year	Location	Cooperator	Traits	
				Yield	Extract
1	1992	Crookston, Minnesota USA	D. Rasmusson	+	+
2	1992	Ithaca, New York USA	M. Sorrells	+	-
3	1992	Guelph, Ontario Canada	D. Falk	+	-
4	1992	Pullman, Washington USA	S. Ullrich	+	+
5	1992	Brandon, Manitoba Canada	W. Legge	+	-
6	1992	Outlook, Saskatchewan Canada	R. Irvine	+	-
7	1992	Goodale, Saskatchewan Canada	B. Rossnagel	+	-
8	1992	Saskatoon, Saskatchewan Canada	B. Rossnagel	+	-
9	1992	Tetonia, Idaho USA	D. Wesenberg	+	+
10	1992	Bozeman, Montana (irrigated) USA	T. Blake	+	+
11	1992	Bozeman, Montana (dryland) USA	T. Blake	+	+
12	1991	Aberdeen, Idaho USA	D. Wesenberg	+	+
13	1991	Klamath Falls, Oregon USA	P. Hayes	+	+
14	1991	Pullman, Washington USA	S. Ullrich	+	+
15	1991	Bozeman, Montana (irrigated) USA	T. Blake	+	+
16	1991	Bozeman, Montana (dryland) USA	T. Blake	+	-

USDA/ARS Cereal Crops Research Unit, Madison, Wisconsin. Complete protocols are available upon request.

QTL analyses were performed using the 123-point "skeleton" linkage map developed by Hayes et al. (1993b) and the interval mapping procedures of MAPMAKER/QTL (Paterson et al., 1988; Lincoln et al., 1992; Lander et al., 1987). The LOD scores for each putative QTL, together with the weight (average effect of an allele substitution), and the proportion of phenotypic variance accounted for by individual and multiple QTLs (r^2) were output for each effect exceeding a LOD threshold of 2.5. A number of datasets were employed for the QTL analyses: (i) the overall mean, representing the average of all environments; (ii) the subset of the 9 Western environments (Pullman, WA. 1991; Pullman, WA. 1992; Tetonia, ID. 1992; Bozeman, MT. 1991 dryland; Bozeman, MT. 1991 irrigated; Bozeman, MT. 1992 dryland; Bozeman, MT. 1992 irrigated; Aberdeen, ID. 1991; and Klamath Falls, OR. 1991); (iii) the subset of 4 Western irrigated environments (Aberdeen, ID. 1991; Klamath Falls, OR. 1991; Bozeman, MT. 1991 irrigated; and Bozeman, MT. 1992 irrigated); (iv) the subset of 5 Western dryland environments (Pullman, WA. in 1991 and 1992, Bozeman, MT. dryland in 1991 and 1992, and Tetonia, ID. 1992); (iv) the subset of 5 Midwest environments (Brandon, MAN. 1992; Outlook, SASK. 1992; Goodale, SASK. 1992; Saskatoon, SASK. 1992; and Crookston, MN. 1992); (v) the subset of 2 Eastern environments (Guelph, ONT. 1992; and Ithaca, NY. 1992); and (vi) various subsets of environments based on common patterns of QTL expression. The environments in the group (vi) subsets are defined in the text. For these analyses,

data were pooled from all locations showing a significant QTL effect, with the same favorable allele, in a common region of the genome.

Based on QTL data from the 1991 data set, we established the breeding goal of fixing all favorable alleles for malt extract and grain yield. The entire QTL dataset was searched and as no individual line was found that met this goal, it was apparent that at least an additional round of mating was required. Using the procedures described by Liu and Hayes (1993), a Genome Map Assisted Plant Breeding (GMAPB) program was developed that, based on genotype and QTL information, determined the probability of recovering the desired genotype in the progeny of each of the possible 11,475 intermatings and backcrosses. The same procedures were then used to identify the mating that would maximize segregation at all possible QTLs. The "ideal genotype" (IG) cross was SM73 X SM145, while the "maximum difference" (MD) cross was SM80 X SM145. One hundred DH lines were derived, using the *Hordeum bulbosum* technique (Chen and Hayes, 1989), from the F_1 of each cross combination. The genotyping of these new DH populations and their assessment under field conditions will be the subject of future investigations.

RESULTS

Chromosome 1

Yield QTL effects were detected in three of the sixteen environments (Table 2.1). There were no significant effects in the overall analysis. On the short arm, a peak was detected at the *Plc - BCD129* interval in the Klamath Falls, Oregon dataset, with Steptoe contributing the favorable allele. Steptoe also contributed the favorable allele at a poorly resolved QTL region on the long arm of the chromosome in two very distinct environments: Guelph, Ontario and Pullman, Washington, 1992. When data from these two environments were averaged, the peak shifted to the terminal interval defined by *ABG461 - Cat3* (Table 2.2). Alleles at the short arm QTL are at positive fixation in both the IG and MD crosses (Figure 1). No significant effects were detected in any agrogeographic groupings. The situation with the long arm is not so clear, due to the shifting of peaks in the three datasets. If the *ABG461 - Cat3* position is indeed the site of the effect, then QTL alleles are at positive fixation in both crosses. If, however, the individual environment peaks are used as the criteria for locus location, then the negative (Morex) QTL allele is fixed in the IG cross for the Pullman effect and the Guelph, Ontario effect is positively fixed. The Guelph effect would likewise be fixed in the MD cross. Segregation would be expected for the Pullman effect.

As shown in Table 2.3, malt extract effects were detected in seven of the nine environments and in the overall analysis. In all cases Morex contributed the favorable allele. In the overall analysis, the peak interval was adjacent to the interval bordered

Table 2.1. QTL genotype differences for grain yield (kg/ha) on chromosome 1, where LOD≥2.5. The letter suffix indicates the parent contributing the larger value allele (M=Morex; S=Steptoe). The value in bold indicates the QTL peak. Adjacent values indicate the 90% confidence interval. Marker intervals in bold type indicate the centromere location.

Chromosome marker interval		% Recomb.	Guelph ONT.,92	Pullman WA.,92	K. Falls OR.,91
ABA301	*Plc*	3.4			
Plc	*BCD129*	7.5			**813S**
BCD129	*Glx*	8.3			809S
Glx	*WG789*	5.5			749S
WG789A	*ABG380*	4.9			740S
ABG380	*ABC158*	7.7			
ABC158	*ksuA1A*	6.1			
ksuA1A	*ABC154A*	3.4			
ABC154A	*Brz*	7.3			
Brz	*ABC156D*	5.8			
ABC156D	*ABG22A*	12.8			
ABG22A	*ABG701*	3.9			
ABG701	*ABG11*	4.4			
ABG11	*ABC455*	5.6			
ABC455	***Amy2***	6.9			
Amy2	*Ubi1*	16.1		293S	
Ubi1	*ABC310B*	4.0		306S	
ABC310B	*ABC305*	6.7		**307S**	
ABC305	*PSR129*	4.9		285S	
PSR129	*ABG461*	13.0		272S	
ABG461	*Cat3*	19.7	**330S**		

Table 2.2. QTL genotype differences for based on pooling data from two environments grain yield (kg/ha) on chromosome 1, where LOD≥2.5. The letter suffix indicates the parent contributing the larger value allele (M=Morex; S=Steptoe). The value in bold indicates the QTL peak. Adjacent values indicate the 90% confidence interval. Marker intervals in bold type indicate the centromere location.

Chromosome Marker	interval	% Recomb.	Group[†]
ABA301	*Plc*	3.4	
Plc	*BCD129*	7.5	
BCD129	*Glx*	8.3	
Glx	*WG789*	5.5	
WG789A	*ABG380*	4.9	
ABG380	*ABC158*	7.7	
ABC158	*ksuA1A*	6.1	
ksuA1A	*ABC154A*	3.4	
ABC154A	*Brz*	7.3	
Brz	*ABC156D*	5.8	
ABC156D	*ABG22A*	12.8	
ABG22A	*ABG701*	3.9	
ABG701	*ABG11*	4.4	
ABG11	*ABC455*	5.6	
ABC455	***Amy2***	6.9	
Amy2	*Ubi1*	16.1	
Ubi1	*ABC310B*	4.0	
ABC310B	*ABC305*	6.7	
ABC305	*PSR129*	4.9	175S
PSR129	*ABG461*	13.0	233S
ABG461	*Cat3*	19.7	**316S**

[†]Group=mean of environments Guelph, ONT. 1992 and Pullman, WA. 1992.

Table 2.3. QTL genotype differences for malt extract (%) on chromosome 1, where LOD≥2.5. The letter suffix indicates the parent contributing the larger value allele (M=Morex; S=Steptoe). The value in bold indicates the QTL peak. Adjacent values indicate the 90% confidence interval. Marker intervals in bold type indicate the centromere location.

Chromosome marker interval		% Recomb.	Crookston MN.,1992	Pullman WA.,1992	Tetonia ID.,1992	Bozeman (irrigated) MT., 92	Klamath Falls OR.,1991	Pullman WA.,1991	Bozeman (irrigated) MT.,1991	Overall mean
ABA301	*Plc*	3.4								
Plc	*BCD129*	7.5								
BCD129	*Glx*	8.3								
Glx	*WG789*	5.5								
WG789A	*ABG380*	4.9								
ABG380	*ABC158*	7.7								
ABC158	*ksuA1A*	6.1								
ksuA1A	*ABC154A*	3.4								
ABC154A	*Brz*	7.3		0.72M	0.74M	0.97M		0.95M		
Brz	*ABC156D*	5.8		0.81M	**0.75M**	**1.05M**		**0.96M**		
ABC156D	*ABG22A*	12.8	1.18M	**0.89M**	0.71M	1.17M		0.94M		
ABG22A	*ABG701*	3.9	**1.19M**	0.83M	0.66M	1.08M		0.85M		0.79M
ABG701	*ABG11*	4.4	1.17M	0.86M	0.74M	1.21M		0.83M	0.92M	0.83M
ABG11	*ABC455*	5.6	1.14M	**0.96M**	**0.79M**	**1.37M**	**0.95M**	0.99M	**1.04M**	**0.94M**
ABC455	***Amy2***	6.9	1.17M	0.96M	0.77M	1.33M	0.94M	**1.00M**	1.03M	0.90M
Amy2	*Ubi1*	16.1	**1.22M**	0.79M	0.74M	1.18M		0.93M	0.72M	0.81M
Ubi1	*ABC310B*	4.0								
ABC310B	*ABC305*	6.7								
ABC305	*PSR129*	4.9								
PSR129	*ABG461*	13.0								
ABG461	*Cat3*	19.7								

Table 2.4. QTL genotype differences for group environments malt extract (%) on chromosome 1, where LOD≥2.5. The letter suffix indicates the parent contributing the larger value allele (M=Morex; S=Steptoe). The value in bold indicates the QTL peak. Adjacent values indicate the 90% confidence interval. Marker intervals in bold type indicate the centromere location.

Chromosome marker interval		% Recomb.	Group[†]	Western	Western (irrigated)	Western (dryland)	Midwest
ABA301	*Plc*	3.4					
Plc	*BCD129*	7.5					
BCD129	*Glx*	8.3					
Glx	*WG789*	5.5					
WG789A	*ABG380*	4.9					
ABG380	*ABC158*	7.7					
ABC158	*ksuA1A*	6.1					
ksuA1A	*ABC154A*	3.4					
ABC154A	*Brz*	7.3	0.80M	0.68M		0.77M	
Brz	*ABC156D*	5.8	0.84M	0.73M	0.63M	0.83M	
ABC156D	*ABG22A*	12.8	**0.92M**	**0.83M**	**0.66M**	0.98M	1.18M
ABG22A	*ABG701*	3.9	0.91M	0.81M		0.98M	**1.19M**
ABG701	*ABG11*	4.4	0.91M	0.83M	0.67M	0.98M	1.17M
ABG11	*ABC455*	5.6	**1.03M**	**0.94M**	**0.76M**	**1.10M**	1.14M
ABC455	***Amy2***	6.9	1.00M	0.90M	0.74M	1.07M	1.17M
Amy2	*Ubi1*	16.1	0.88M	0.82M	0.70M	0.93M	**1.22M**
Ubi1	*ABC310B*	4.0					
ABC310B	*ABC305*	6.7					
ABC305	*PSR129*	4.9					
PSR129	*ABG461*	13.0					
ABG461	*Cat3*	19.7					

[†]Group=mean of environments Crookston MN. 1992, Pullman WA. 1992, Tetonia ID. 1992, Bozeman (irrigated) MT. 1992, Klamath Falls OR. 1991, and Pullman WA. 1991.

by *Amy2*. The *Amy2* locus was mapped with a clone specific to the α-amylase multi-gene family located on chromosome 1 (Khursheed and Rogers, 1988). As α-amylase is involved in the breakdown of starch, it would be reasonable to expect a coincident malt extract effect. However, the malt extract peaks were consistently upstream from the *Amy2* locus. The same peak was identified in five of the seven environments. In five of the seven data sets, but not the overall average, an additional peak was detected further upstream, with peaks ranging from *Brz* to *ABG701*. The *ABC156D* - *ABG22A* interval defined the peak in the West, irrigated West, Midwest, and common expression (mean of Crookston MN.; Pullman WA. 1992; Tetonia ID.; Bozeman MT irrigated 1992; Klamath Falls OR.; and Pullman WA. 1991) datasets (Table 2.4). Peaks in the Midwest data set did not directly coincide with those identified in the other pooled analyses. Thus, there are at least two malt extract QTLs on chromosome 1, and one of them may be related to the *Amy2* locus. As shown in Figure 1, the positive Morex alleles are fixed in the IG cross. There are opportunities for recovery of lines with either or both QTLs in the MD cross.

As shown in Figure 1, three markers will be used to genotype the progeny of the MD cross for the extract effects. The total interval length is 37.7 cM. The two intervals are 13.4 and 24.3 cM, respectively. Two markers will be used to identify recombinants for the Pullman yield effect. The interval length is 12.2 cM.

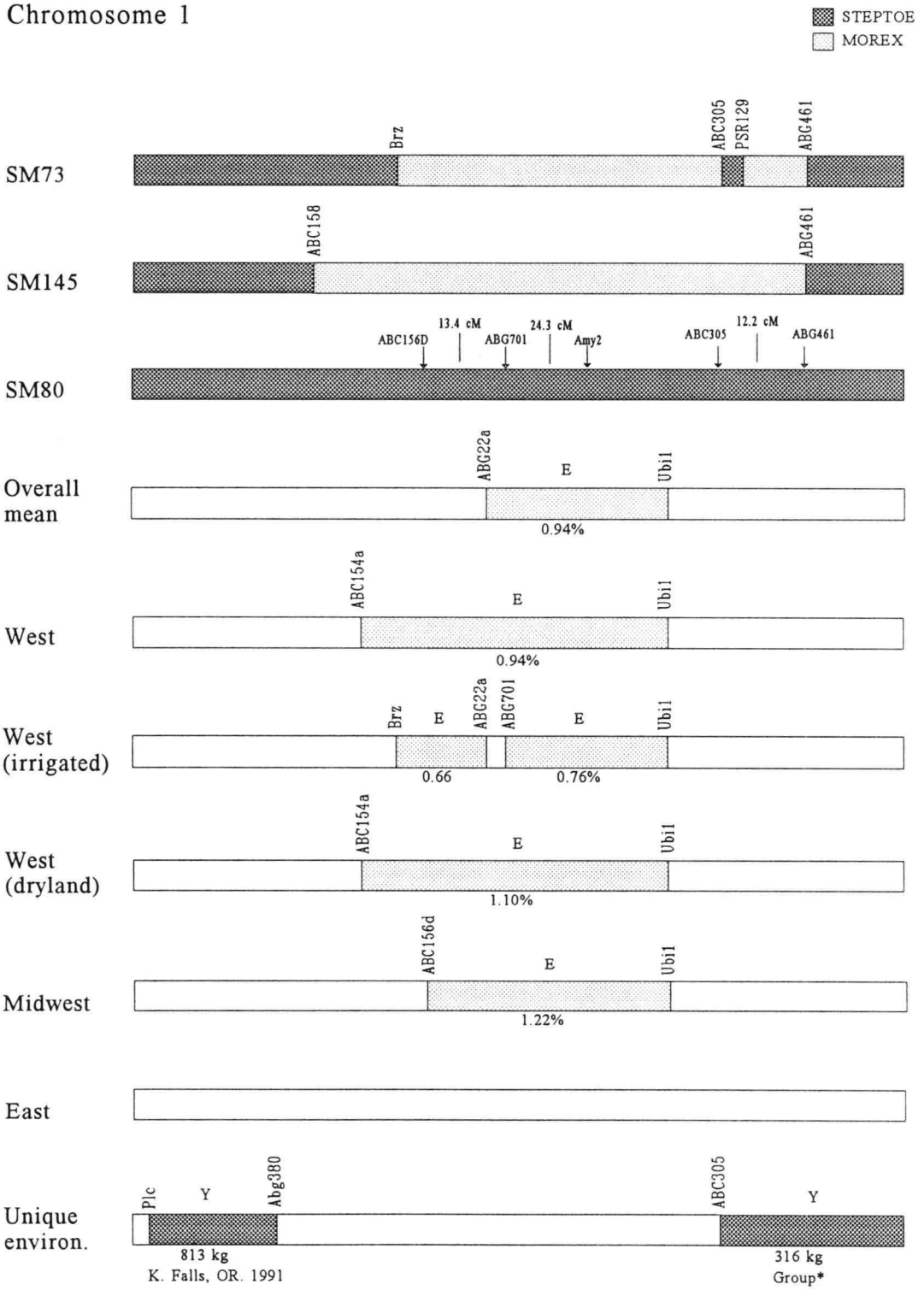
Chromosome 2

QTL effects for yield were detected in eleven of sixteen individual environments datasets, in the overall mean dataset, and in various grouped analyses

Figure 1
Genome structure of the parents of the IG (SM73 X SM145) and MD (SM80 X SM145) crosses and positions of QTL effects detected in various datasets on chromosome 1. QTL effects are shown with 90% confidence intervals. "E" indicates a malt extract QTL and "Y" a yield QTL. The parent contributing the favorable allele is indicated with the shading pattern described by the legend. Marker designations perpendicular to the chromosomes indicate breakpoints. Markers parallel to the chromosomes are those that will be used to genotype cross progeny. Distances between these markers are indicated in cM.

Figure 1, continued

Chromosome 1



*Group=mean of Guelph, ONT. and Pullman, WA. 1992

(Table 3.1 and 3.2), but not in the overall analysis. Looking across the individual environment data (Table 3.1), there appear to be three principal regions of QTL effects. The grouped analyses resolved these QTLs to peaks at the *Rbcs - ABG2, Adh8 - ABG19* and *ksuF15 - Crg3a* intervals. As described by Hayes et al. (1993b), the *Rbcs - ABG2* interval was the site of a significant QTL for heading date, which may reflect the effects of the *Ea* locus (Nilan, 1964). In an example of contrasting favorable alleles determined by genes conferring adaption to specific agrogeographic conditions, Morex contributed the favorable yield allele in the Canadian environments and Steptoe the favorable allele in the three Western U.S. environments where significant effects were detected. In all environments, Morex contributed the higher value allele for heading date at this locus, with effects of allele substitutions ranging from 3.1 - 9.7 days (Hayes et al., 1994). The alternative favorable alleles for yield presumably led to cancellation of effects and consequently a lack of significance in the overall analysis.

In the individual environments, the positions of the two QTLs were poorly resolved. There were alternative favorable alleles in two environments for a QTL with a peak at the *ABC162 - ABG14* interval, with Morex contributing the favorable allele at Guelph, Ontario and Steptoe the favorable allele at Ithaca, New York. When data from these various environments were pooled (Table 3.2), Steptoe contributed the favorable allele at QTLs with peaks at *Adh8 - ABC19* (in the pooled analysis of data from three common expression datasets) and *ksuF15 - Crg3a* (in the pooled analysis of three common expression data sets and in the Western dryland subset).

Table 3.1. QTL genotype differences for grain yield (kg/ha) on chromosome 2, where LOD≥2.5. The letter suffix indicates the parent contributing the larger value allele (M=Morex; S=Steptoe). The value in bold indicates the QTL peak. Adjacent values indicate the 90% confidence interval. Marker intervals in bold type indicate the centromere location.

Chromosome marker interval		% Recomb.	Ithaca NY.1992	Guelph ONT.1992	Pullman WA.1992	Brandon MAN. 1992	Outlook SASK. 1992	Goodale SASK. 1992	Saskatoon SASK. 1992	Tetonia ID.1992	Bozeman (irrigated) MT.1992	Pullman WA.1991	Bozeman (dryland) MT.1991
ABG313A	*ABG703*	7.9											357S
ABG703	*Chs1B*	11.0					676M		390M	462S			401S
Chs1B	*ABG8*	7.2					706M	458M	406M	576S			442S
ABG8	*Rbcs*	4.6				511M	710M	486M	434M	618S			484S
Rbcs	*ABG2*	11.5				**593M**	**743M**	**607M**	**503M**	**874S**		**415S**	**626S**
ABG2	*ABG459*	9.0				565M	657M	568M	485M	870S		407S	619S
ABG459	*Pox*	6.8	416S			492M		454M	377M	708S			480S
Pox	*Adh8*	5.5	415S			340M				659S			395S
Adh8	*ABG19*	11.7	**428S**	339M	386S					544S	**546S**		345S
ABG19	***ABC162***	6.6	414S	377M	**439S**						524S		
ABC162	*ABG14*	8.3	**456S**	**386M**	438S						396S		
ABG14	*His3C*	10.3	379S	342M	366S						**520S**		
His3C	*ksuF15*	11.9			270S						492S		
ksuF15	*Crg3a*	22.1									472S	503S	
Crg3a	*Gln2*	16.4										**543S**	
Gln2	*ABC157*	7.4										430S	
ABC157	*ABC165*	7.4										351S	
ABC165	*Pcr1*	7.5											
Pcr1	*ABA5*	8.6											

Table 3.2. QTL genotype differences for group environments grain yield (kg/ha) on chromosome 2, where LOD≥2.5. The letter suffix indicates the parent contributing the larger value allele (M=Morex; S=Steptoe). The value in bold indicates the QTL peak. Adjacent values indicate the 90% confidence interval. Marker intervals in bold type indicate the centromere location.

Chromosome marker interval		% Recomb.	Group†	Group††	Group‡	Western (dryland)	Midwest
ABG313A	*ABG703*	7.9					327M
ABG703	*Chs1B*	11.0	508M		353S		399M
Chs1B	*ABG8*	7.2	517M		414S		403M
ABG8	*Rbcs*	4.6	532M		466S		407M
Rbcs	*ABG2*	11.5	**595M**		**643S**	**399S**	**439M**
ABG2	*ABG459*	9.0	555M		632S	399S	413M
ABG459	*Pox*	6.8	454M	301S	502S	373S	345M
Pox	*Adh8*	5.5		308S		368S	
Adh8	*ABG19*	11.7		**358S**		342S	
ABG19	***ABC162***	6.6		330S		262S	
ABC162	*ABG14*	8.3		310S			
ABG14	*His3C*	10.3				312S	
His3C	*ksuF15*	11.9		352S		323S	
ksuF15	*Crg3a*	22.1		**367S**		**346S**	
Crg3a	*Gln2*	16.4		273S		297S	
Gln2	*ABC157*	7.4					
ABC157	*ABC165*	7.4					
ABC165	*Pcr1*	7.5					
Pcr1	*ABA5*	8.6					

†Group=mean of environments Brandon MAN. 1992, Outlook SASK. 1992, Goodale SASK. 1992, and Saskatoon SASK. 1992.

††Group=mean of environments Ithaca NY. 1992, Pullman WA. 1992, Bozeman (dryland) MT. 1992, and Pullman WA. 1991.

‡Group=mean of environments Tetonia ID. 1992, Pullman WA. 1991, and Bozeman (dryland) MT. 1991.

QTLs for malt extract was detected in three environments and in the overall mean dataset (Table 3 .3) Morex contributed the favorable allele. The grouped analyses positioned the peak at the same interval as that revealed in the overall analysis: *Rbcs - ABG2* (Table 3.4). This is the same interval where significant yield effects were detected.

As shown in Figure 2, both the IG and MD crosses are segregating for the QTL effects with peaks at *Rbcs - AGB2 and Adh8 - ABG19.* Four markers, spanning a total length of 46.3 cM, will be used to genotype the progeny of both crosses. Intervals between flanking markers range from 7.9 to 19.6 cM. The target genotype will be a function of target environments, with Morex contributing the favorable allele for yield in the Midwest environments and Steptoe the favorable allele for yield in the Western dryland environments. As Morex contributes a positive allele for extract in this same interval, both favorable alleles can be fixed for the Midwestern environments, but QTLs for only of the two traits can be fixed for the Western environments. Both crosses are segregating for the second QTL effect, with the peak at *Adh8 - ABC162.* Assuming the *ksuF15 - Crg3a* peak is indeed the true position of the QTL, this effect is positively fixed in both crosses.

Chromosome 3

A yield QTL was detected in ten of sixteen environments and in the overall analysis (Table 4.1). In all cases, Steptoe contributed the favorable allele. The peak interval was defined by *ABG396 - AB703A* in five of the environments, the overall dataset, in the grouped data, and in all Western datasets (Tables 4.1 and 4.2). The

Table 3.3. QTL genotype differences for malt extract (%) on chromosome 2, where LOD≥2.5. The letter suffix indicates the parent contributing the larger value allele (M=Morex; S=Steptoe). The value in bold indicates the QTL peak. Adjacent values indicate the 90% confidence interval. Marker intervals in bold type indicate the centromere location.

Chromosome marker interval		% Recomb.	Pullman WA.1992	Aberdeen ID.1992	Pullman WA.1991	Overall mean
ABG313A	*ABG703*	7.9		**0.96M**		
ABG703	*Chs1B*	11.0	0.74M	0.87M		
Chs1B	*ABG8*	7.2	**0.81M**	**0.90M**	0.85M	
ABG8	*Rbcs*	4.6	0.79M	0.89M	0.95M	
Rbcs	*ABG2*	11.5	0.76M	0.88M	**0.99M**	**0.63M**
ABG2	*ABG459*	9.0		0.74M	0.93M	
ABG459	*Pox*	6.8			0.85M	
Pox	*Adh8*	5.5				
Adh8	*ABG19*	11.7				
ABG19	***ABC162***	6.6				
ABC162	*ABG14*	8.3				
ABG14	*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	*ABA5*	8.6				

Table 3.4. QTL genotype differences for group environments malt extract (%) on chromosome 2, where LOD≥2.5. The letter suffix indicates the parent contributing the larger value allele (M=Morex; S=Steptoe). The value in bold indicates the QTL peak. Adjacent values indicate the 90% confidence interval. Marker intervals in bold type indicate the centromere location.

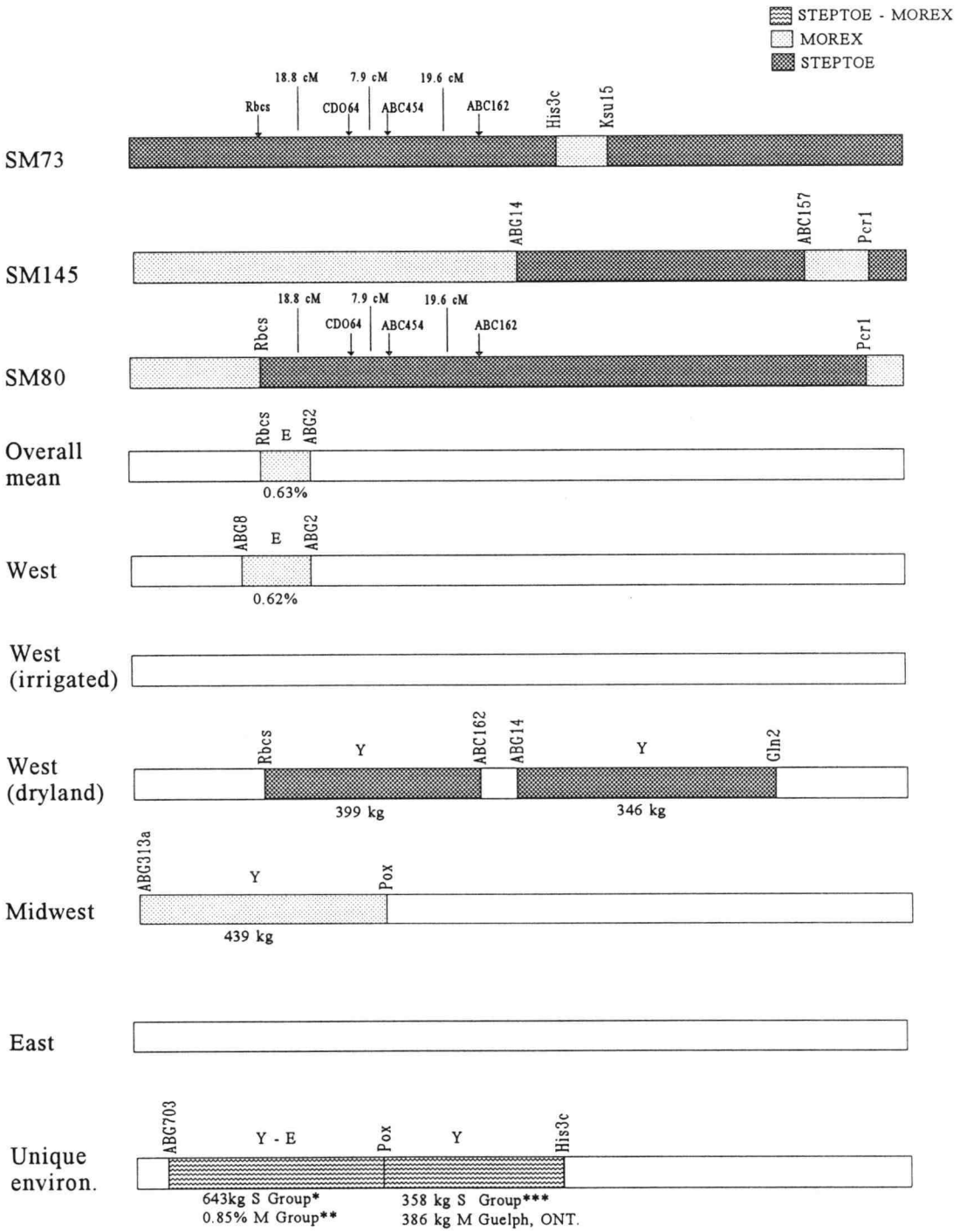
Chromosome marker interval		% Recomb.	Group†	Western
ABG313A	*ABG703*	7.9	0.66M	
ABG703	*Chs1B*	11.0	0.70M	
Chs1B	*ABG8*	7.2	0.77M	
ABG8	*Rbcs*	4.6	0.83M	0.61M
Rbcs	*ABG2*	11.5	**0.85M**	**0.62M**
ABG2	*ABG459*	9.0	0.77M	
ABG459	*Pox*	6.8	0.68M	
Pox	*Adh8*	5.5	0.63M	
Adh8	*ABG19*	11.7		
ABG19	***ABC162***	6.6		
ABC162	*ABG14*	8.3		
ABG14	*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	*ABA5*	8.6		

†Group=mean of environments Pullman WA. 1992, Bozeman (irrigated) MT. 1992, Aberdeen ID. 1991, Klamath Falls OR. 1991, and Pullman WA. 1991.

Figure 2
Genome structure of the parents of the IG (SM73 X SM145) and MD (SM80 X SM145) crosses and positions of QTL effects detected in various datasets on chromosome 2. QTL effects are shown with 90% confidence intervals. "E" indicates a malt extract QTL and "Y" a yield QTL. The parent contributing the favorable allele is indicated with the shading pattern described by the legend. Marker designations perpendicular to the chromosomes indicate breakpoints. Markers parallel to the chromosomes are those that will be used to genotype cross progeny. Distances between these markers are indicated in cM.

Figure 2, continued

Chromosome 2



*Group=mean of Tetonia, ID., Pullman, WA. 1991, Bozeman (dry) MT. 1991.
**Group=mean of Pullman, WA. 1992, Bozeman (irr), MT. 1992, Aberdeen, ID., K. Falls, OR., Pullman, WA. 1991.
***Group=mean of Ithaca, NY., Pullman, WA. 1992, Bozeman (dry) MT., Pullman, WA. 1991.

Table 4.1. QTL genotype differences for grain yield (kg/ha) on chromosome 3, where LOD≥2.5. The letter suffix indicates the parent contributing the larger value allele (M=Morex; S=Steptoe). The value in bold indicates the QTL peak. Adjacent values indicate the 90% confidence interval. Marker intervals in bold type indicate the centromere location.

Chromosome marker interval		% Recomb.	Crookston MN.1992	Ithaca NY.1992	Guelph ONT.1992	Brandon MAN.1992	Tetonia ID.1992	Bozeman (irrigated) MT.1992	Aberdeen ID.1991	Pullman WA.1991	Bozeman (irrigated) MT.1991	Bozeman (dryland) MT.1991	Overall mean
ABA303	*ABC171*	23.0											
ABC171	*ABG57*	13.5											
ABG57	*ABG471*	3.6							640S				244S
ABG471	***Dor4A***	19.8	541S	**556S**	362S	**459S**	**781S**	614S	1186S	628S	1429S	678S	469S
Dor4A	*ABG396*	6.4	**542S**	555S	392S	393S	780S	633S	**1193S**	632S	**1463S**	682S	472S
ABG396	*ABG703A*	9.4	514S	509S	**402S**	**414S**	773S	**702S**	1165S	**653S**	1437S	**686S**	**500S**
ABG703A	*PSR156*	9.3	436S	476S	338S	358S	740S	677S	959S	628S	1389S	632S	457S
PSR156	*ABG377*	7.6		411S			538S	590S	654S	528S	1158S	498S	320S
ABG377	*ABG453*	10.5						497S		464S	1011S		244S
ABG453	*ABC307B*	10.2						471S		434S	867S		243S
ABC307B	*CDO113B*	12.3						442S			788S		
CDO113B	*His4B*	16.9									741S		
His4B	*ABG4*	14.1											
ABG4	*mPub*	7.3											
mPub	*ABC174*	13.4											
ABC174	*ABC166*	11.6											
ABC166	*ABC172*	11.0											

Table 4.2. QTL genotype differences for group environments grain yield (kg/ha) on chromosome 3, where LOD≥2.5. The letter suffix indicates the parent contributing the larger value allele (M=Morex; S=Steptoe). The value in bold indicates the QTL peak. Adjacent values indicate the 90% confidence interval. Marker intervals in bold type indicate the centromere location.

Chromosome marker interval		% Recomb.	Group†	Western	Western (irrigated)	Western (dryland)	Eastern
ABA303	*ABC171*	23.0					
ABC171	*ABG57*	13.5		324S	439S		313S
ABG57	*ABG471*	3.6	400S	314S	428S		327S
ABG471	***Dor4A***	19.8	694S	624S	824S	464S	454S
Dor4A	*ABG396*	6.4	695S	628S	845S	466S	**454S**
ABG396	*ABG703A*	9.4	**703S**	**654S**	**860S**	**470S**	438S
ABG703A	*PSR156*	9.3	654S	603S	792S	435S	390S
PSR156	*ABG377*	7.6	496S	436S	544S	355S	299S
ABG377	*ABG453*	10.5	364S	339S		283S	
ABG453	*ABC307B*	10.2	323S	325S		258S	
ABC307B	*CDO113B*	12.3	304S	308S	449S		
CDO113B	*His4B*	16.9	291S		**451S**		
His4B	*ABG4*	14.1					
ABG4	*mPub*	7.3					
mPub	*ABC174*	13.4					
ABC174	*ABC166*	11.6					
ABC166	*ABC172*	11.0					

†Group=mean of environments Crookston MN. 1992, Ithaca, NY. 1992, Guelph ONT. 1992, Brandon MAN. 1992, Outlook SASK. 1992, Tetonia ID. 1992, Bozeman (irrigated) MT. 1992, Aberdeen ID. 1991, Pullman WA. 1991, Bozeman (irrigated) MT. 1991, and Bozeman (dryland) MT. 1991.

peak shifted in a proximal direction one interval in the Eastern dataset. Although a significant effect was detected in Crookston, Minnesota, no significant differences were detected in the Saskatchewan or Manitoba trials, and the effect was not significant in the overall analysis of Midwest environments. An additional peak was detected in the Western irrigated environments (Table 4.2), although significant effects were not detected in this region in any of the individual environment datasets.

No malt extract QTLs were detected on this chromosome, making the yield QTLs unambiguous targets for selection. As is apparent in Figure 3, alleles at both yield QTLs are positively fixed in the IG cross and both are segregating in the MD cross. Four markers, spanning a 50.9 cM region, will be used to genotype the progeny of the MD cross for the first QTL. Interval length ranges from 9.1 to 28.1 cM. Two markers, spanning a 23.8 cM distance, will be used to genotype the progeny of the MD cross for the second QTL effect.

Chromosome 4

A significant grain yield QTL was detected in only one of the sixteen environments (Bozeman, Montana dryland, 1992) (Table 5.1). This effect was not apparent in any of the grouped analyses or in the overall average. The favorable Steptoe allele is fixed in the MD cross. The peak for this QTL was located at the *ABG472 - ABG500b* interval. ABG472 defines the breakpoint in the SM73 parent. If the peak is indeed the correct position of the QTL, then the favorable allele is also fixed in the IG cross. If the true position of the QTL is distal to the peak, then segregation can be expected in the progeny of the IG cross.

Figure 3
Genome structure of the parents of the IG (SM73 X SM145) and MD (SM80 X SM145) crosses and positions of QTL effects detected in various datasets on chromosome 3. QTL effects are shown with 90% confidence intervals. "E" indicates a malt extract QTL and "Y" a yield QTL. The parent contributing the favorable allele is indicated with the shading pattern described by the legend. Marker designations perpendicular to the chromosomes indicate breakpoints. Markers parallel to the chromosomes are those that will be used to genotype cross progeny. Distances between these markers are indicated in cM.

Figure 3, continued

Chromosome 3

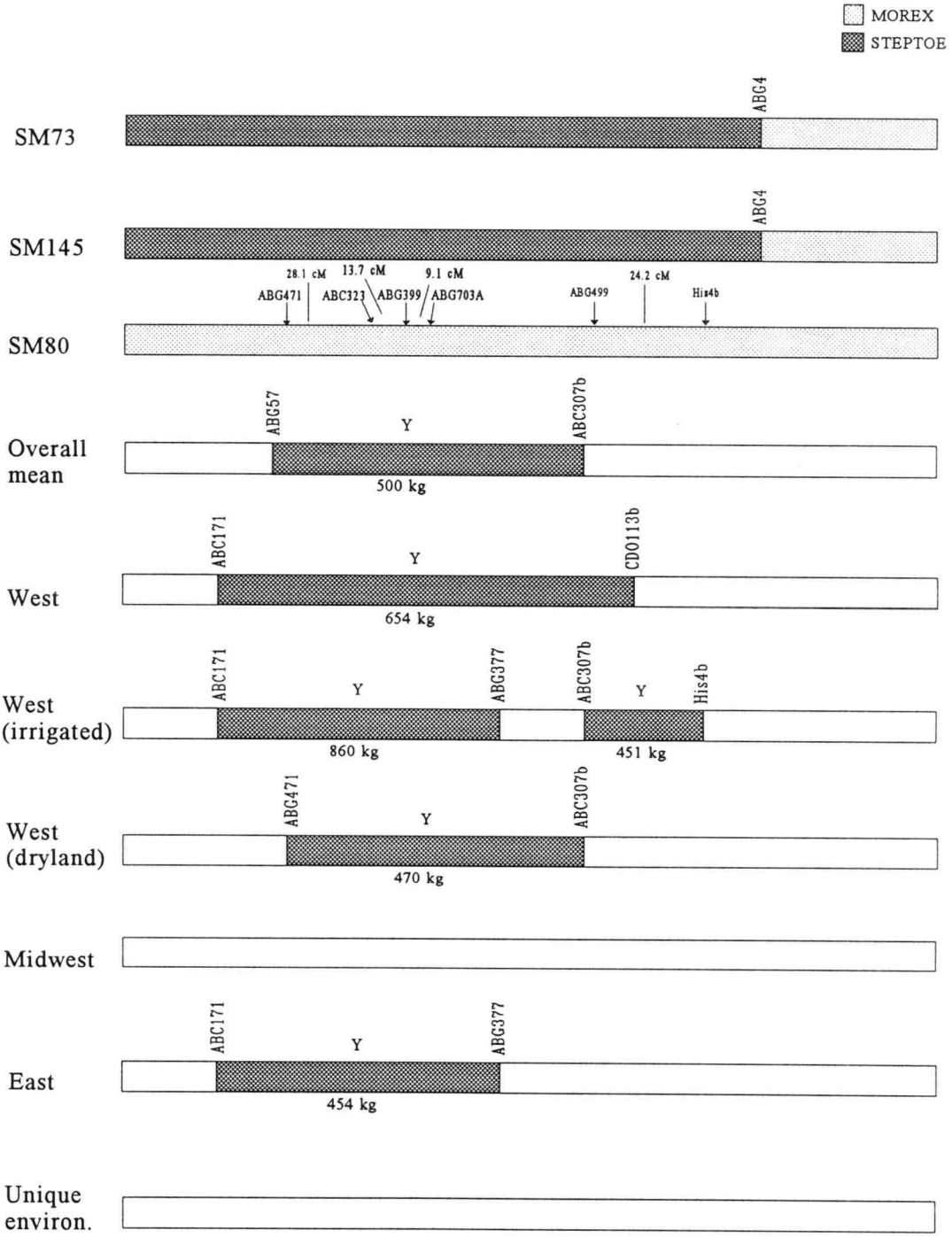


Table 5.1. QTL genotype differences for grain yield (kg/ha) on chromosome 4, where LOD≥2.5. The letter suffix indicates the parent contributing the larger value allele (M=Morex; S=Steptoe). The value in bold indicates the QTL peak. Adjacent values indicate the 90% confidence interval. Marker intervals in bold type indicate the centromere location.

Chromosome marker interval		% Recomb.	Bozeman,MT dryland, 1992
WG622	*ABG313B*	10.5	
ABG313B	*CDO669*	4.6	
CDO669	*BCD402B*	14.0	
BCD402B	*TubA1*	10.3	
TubA1	*ABG3*	4.8	
ABG3	***ABG484***	5.4	
ABG484	*WG464*	10.4	
WG464	*ABG472*	15.8	718S
ABG472	*ABG500B*	16.1	**718S**
ABG500B	*ABG397*	7.0	
ABG397	*Bmy1*	25.4	
Bmy1	*ksuH11*	3.3	

Malt extract QTLs were identified in seven of the nine environments and in the overall analysis (Table 5.2). In the latter dataset, as well as in three of the individual environments, there were two distinct peaks, with Morex contributing the favorable alleles in both cases. One QTL peak was located in the *CDO669 - BCD402B* interval and the other in the *ABG484 - WG464* interval. These peak intervals were also identified in the various grouped analyses (Table 5.3). As shown in Figure 4, alleles at the first of these QTLs (*CDO669 - BCD402B*) will segregate in the MD cross. However, alleles at this QTL are negatively fixed in the IG cross, and alleles for the second QTL are negatively fixed in both crosses.

Two markers, spanning a distance of 17.2 cM, will be used to genotype the progeny of the MD cross for the first of the extract QTLs. Two markers, spanning a distance of 34.5 cM, will be used to genotype the progeny of the IG cross for the distal position of the yield QTL confidence interval.

Chromosome 5

Grain yield QTLs were detected in two individual environments (1991 and 1992 at the Bozeman, Montana dryland sites) (Table 6.1). In both cases, the peak was defined by the *His3b* and *iPgd2* markers. The effect was not seen in the analysis of the overall mean, but it was confirmed in the average of the two Montana dryland datasets (Table 6.2) and the Western dryland subset. In the latter dataset, in addition to the *His3b - iPgd2* peak, there was an additional peak at *ABA2 - ABG373*. As shown in Figure 5, the configuration of the IG parents will allow for segregation at the first of the QTL peaks. The favorable Steptoe allele is fixed for the second QTL. The

Table 5.2. QTL genotype differences for malt extract (%) on chromosome 4, where LOD≥2.5. The letter suffix indicates the parent contributing the larger value allele (M=Morex; S=Steptoe). The value in bold indicates the QTL peak. Adjacent values indicate the 90% confidence interval. Marker intervals in bold type indicate the centromere location.

Chromosome marker interval		% Recomb.	Pullman WA.1992	Tetonia ID.1992	Bozeman (irrigated) MT.1992	Bozeman (dryland MT.1992	Aberdeen ID.1991	Pullman WA..1991	Bozeman (irrigated) MT.1991	Overall mean
WG622	*ABG313B*	10.5	0.85M		1.02M	1.19M		0.92M	1.01M	0.84M
ABG313B	*CDO669*	4.6	0.93M		1.07M	1.37M		0.94M	1.10M	0.91M
CDO669	*BCD402B*	14.0	**1.00M**		**1.19M**	**1.66M**		**0.95M**	**1.36M**	**1.00M**
BCD402B	*TubA 1*	10.3	0.80M	0.72M	1.18M	1.42M		0.78M	1.32M	0.87M
TubA 1	*ABG3*	4.8		0.74M	1.17M	1.17M			1.30M	0.78M
ABG3	***ABG484***	5.4		**0.75M**	1.23M	1.13M	0.79M		**1.39M**	0.82M
ABG484	*WG464*	10.4		0.69M	**1.31M**	**1.20M**	**0.83M**		1.34M	**0.85M**
WG464	*ABG472*	15.8			1.21M	0.98M	0.80M		**1.52M**	0.77M
ABG472	*ABG500B*	16.1			0.89M		0.71M		1.36M	0.64M
ABG500B	*ABG397*	7.0								
ABG397	*Bmy1*	25.4								
Bmy1	*ksuH11*	3.3								

Table 5.3. QTL genotype differences for group environments malt extract (%) for chromosome 4, where LOD≥2.5. The letter suffix indicates the parent contributing the larger value allele (M=Morex; S=Steptoe). The value in bold indicates the QTL peak. Adjacent values indicate the 90% confidence interval. Marker intervals in bold type indicate the centromere location.

Chromosome marker interval		% Recomb.	Group†	Group††	Group‡	Western	Western (irrigated)	Western (dryland)
WG622	*ABG313B*	10.5	0.90M	0.84M	0.86M	0.81M	0.77M	0.93M
ABG313B	*CDO669*	4.6	0.96M	0.91M	0.93M	0.87M	0.83M	0.93M
CDO669	*BCD402B*	14.0	**1.09M**	**1.05M**	**1.06M**	**0.95M**	**0.97M**	**0.95M**
BCD402B	*TubA 1*	10.3	0.96M	0.94M	0.93M	0.79M	0.87M	0.78M
TubA 1	*ABG3*	4.8	0.83M	0.85M	0.83M	0.71M	0.75M	
ABG3	***ABG484***	5.4	0.90M	0.91M	0.89M	0.76M	**0.81M**	0.76M
ABG484	*WG464*	10.4	**0.95M**	**0.94M**	**0.94M**	**0.79M**	0.79M	**0.83M**
WG464	*ABG472*	15.8	0.90M	0.88M	0.88M	0.69M	0.63M	0.76M
ABG472	*ABG500B*	16.1	0.73M	0.71M	0.71M			
ABG500B	*ABG397*	7.0						
ABG397	*Bmy1*	25.4						
Bmy1	*ksuH11*	3.3						

†Group=mean of environments Pullman WA. 1992, Bozeman (irrigated) MT. 1992, Bozeman (dryland) MT. 1992, Aberdeen ID. 1991, Klamath Falls OR. 1991, Pullman WA. 1991, and Bozeman (irrigated) MT. 1991.
††Group=mean of environments Pullman WA. 1992, Tetonia ID. 1992, Bozeman (irrigated) MT. 1992, Bozeman (dryland) MT. 1992, Aberdeen ID. 1991, Klamath Falls OR. 1991, and Bozeman (irrigated) MT. 1991.
‡Group=mean of group† and group††

Figure 4
Genome structure of the parents of the IG (SM73 X SM145) and MD (SM80 X SM145) crosses and positions of QTL effects detected in various datasets on chromosome 4. QTL effects are shown with 90% confidence intervals. "E" indicates a malt extract QTL and "Y" a yield QTL. The parent contributing the favorable allele is indicated with the shading pattern described by the legend. Marker designations perpendicular to the chromosomes indicate breakpoints. Markers parallel to the chromosomes are those that will be used to genotype cross progeny. Distances between these markers are indicated in cM.

Figure 4, continued

Chromosome 4

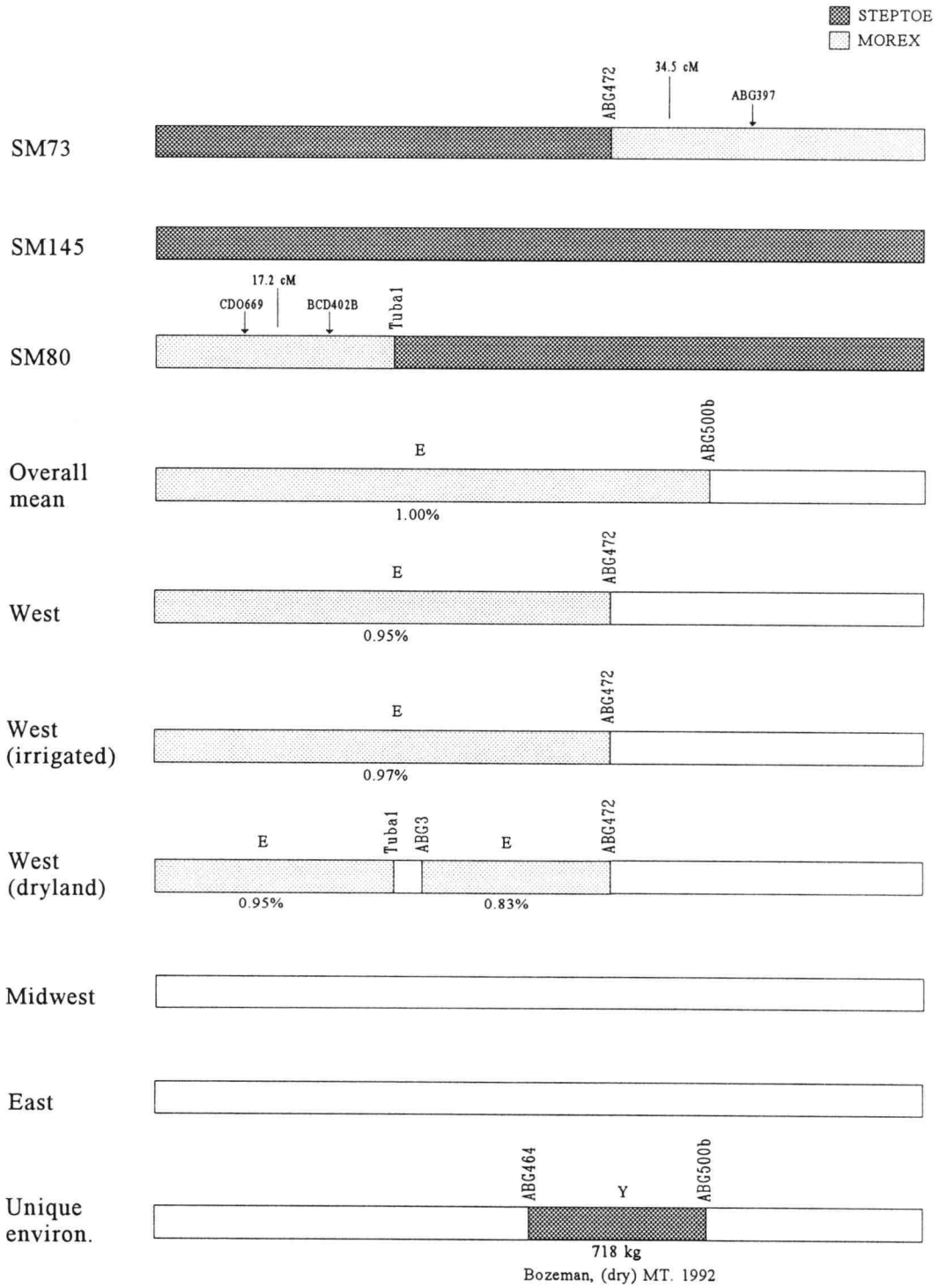


Table 6.1. QTL genotype differences for grain yield (kg/ha) on chromosome 5, where LOD≥2.5. The letter suffix indicates the parent contributing the larger value allele (M=Morex; S=Steptoe). The value in bold indicates the QTL peak. Adjacent values indicate the 90% confidence interval. Marker intervals in bold type indicate the centromere location.

Chromosome marker interval		% Recomb.	Bozeman (dryland) MT.1992	Bozeman (dryland) MT. 1991
Aga6	*Hor2*	2.5		
Hor2	*Hor1*	10.5		
Hor1	*ABA4*	6.6		
ABA4	*CDO99*	8.0		
CDO99	*Ica1*	11.2		
Ica1	*ABG500A*	7.9		
ABG500A	*ABG494*	9.9		
ABG494	***Glb1***	7.6		
Glb1	*ABC160*	8.8		
ABC160	*ABG464*	14.7		
ABG464	*His3B*	9.6	441S	
His3B	*iPgd2*	16.6	**464S**	**344S**
iPgd2	*ABG702*	12.6	439S	330S
ABG702	*ABA2*	6.4		
ABA2	*ABG373*	8.3		
ABG373	*ABG387A*	5.3		

Table 6.2. QTL genotype differences for group environments grain yield (kg/ha) on chromosome 5, where LOD≥2.5. The letter suffix indicates the parent contributing the larger value allele (M=Morex; S=Steptoe). The value in bold indicates the QTL peak. Adjacent values indicate the 90% confidence interval. Marker intervals in bold type indicate the centromere location.

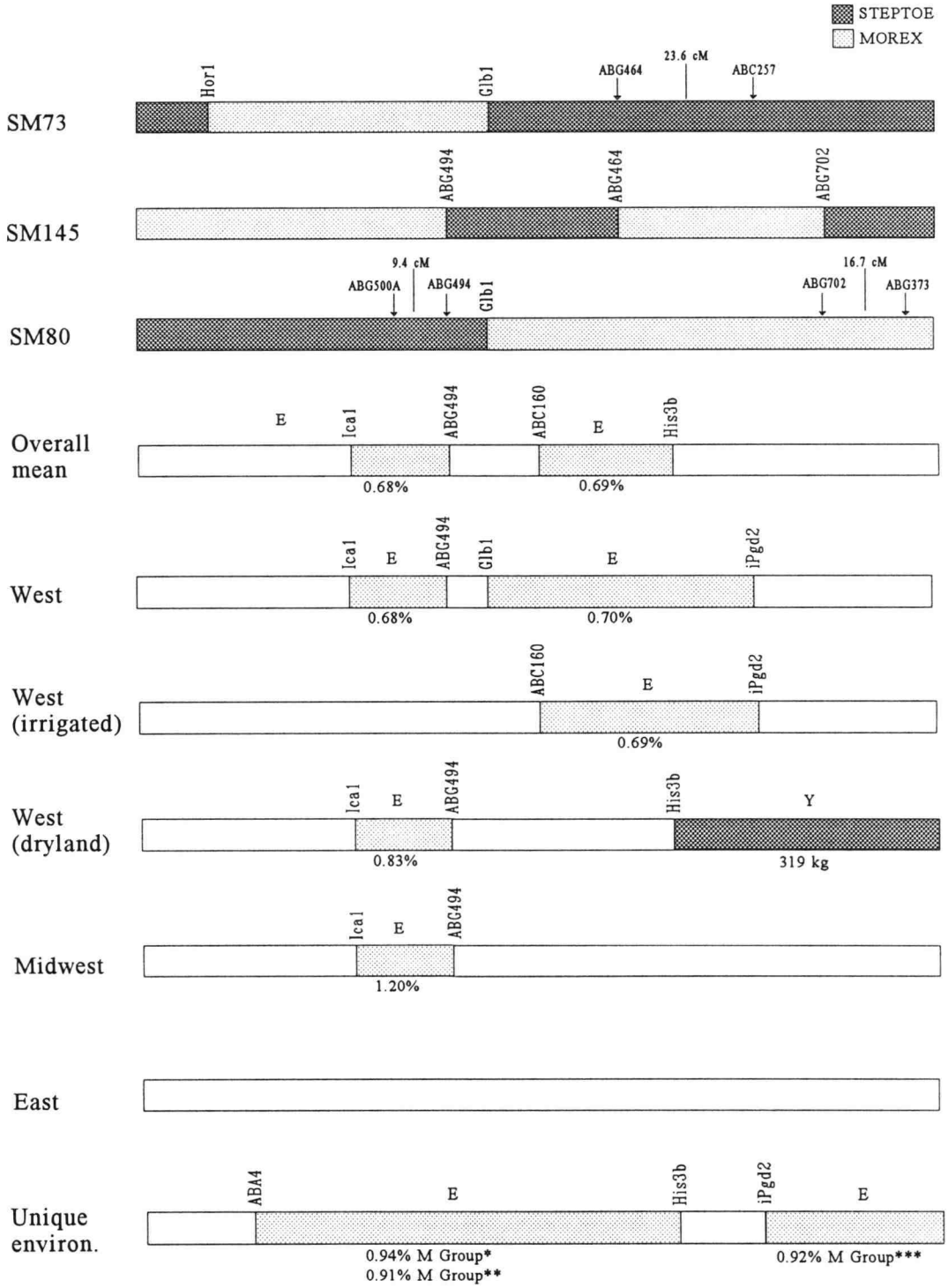
Chromosome marker interval		% Recomb.	Group†	Western (dryland)
Aga6	*Hor2*	2.5		
Hor2	*Hor1*	10.5		
Hor1	*ABA4*	6.6		
ABA4	*CDO99*	8.0		
CDO99	*Ica1*	11.2		
Ica1	*ABG500A*	7.9		
ABG500A	*ABG494*	9.9		
ABG494	***Glb1***	7.6		
Glb1	*ABC160*	8.8		
ABC160	*ABG464*	14.7	310S	
ABG464	*His3B*	9.6	364S	
His3B	*iPgd2*	16.6	**415S**	**319S**
iPgd2	*ABG702*	12.6	374S	284S
ABG702	*ABA2*	6.4	305S	278S
ABA2	*ABG373*	8.3		**297S**
ABG373	*ABG387A*	5.3		290S

†group=mean of environments Bozeman (dryland) MT. 1991 and Bozeman (dryland) MT. 1992.

Figure 5
Genome structure of the parents of the IG (SM73 X SM145) and MD (SM80 X SM145) crosses and positions of QTL effects detected in various datasets on chromosome 5. QTL effects are shown with 90% confidence intervals. "E" indicates a malt extract QTL and "Y" a yield QTL. The parent contributing the favorable allele is indicated with the shading pattern described by the legend. Marker designations perpendicular to the chromosomes indicate breakpoints. Markers parallel to the chromosomes are those that will be used to genotype cross progeny. Distances between these markers are indicated in cM.

Figure 5, continued

Chromosome 5



*Group=mean of Crookston, MN., Tetonia, ID., Bozeman (irr.), MT. 1992, and K. Falls, OR.
**Group=mean of Tetonia, ID., Bozeman (irr.) MT. 1992., Bozeman (dry) MT. 1992, and K. Falls, OR.
***Group=mean of Tetonia, ID. and K. Falls, OR.

parents of the MD cross are negatively fixed for the *His3b - iPgd2* QTL, but there will be segregation for the QTL with peak at the *ABA2 - ABG373* interval.

Malt extract QTLs were detected in three of the nine environments and in the overall analysis (Table 6.3). Peaks shifted in the datasets, but there appear to be at least three principal regions of QTL expression. In all cases, Morex contributes the favorable allele (Table 6.4). The boundary of one region is defined by *ABG500A*, the second lies somewhere between *Glb1* and *iPgd2*, while the third peaked at *ABG702 - ABA2*. This lack of resolution hampers MMAS and validation efforts. As is apparent in Figure 5, in the IG cross the positive Morex allele is fixed up to the interval defined by *ABG494*. The progeny of the MD cross will segregate for the QTL. Segregation for the second, poorly resolved QTL effect is possible in the progeny of the IG cross in a region defined by *ABG464* and *ABG702*. The MD cross has the positive Morex allele fixed for this region. The IG cross is at fixation for Steptoe alleles for the chromosome distal to *ABG702*, while Morex contributes the favorable allele for malt extract in this same interval. The MD cross will segregate for the region distal to *ABG702*, so that genotypes with either the favorable allele for extract or the favorable allele for yield may be recovered.

Two markers will be used in the MD cross for the first of the extract QTLs. These markers define a 9.4 cM interval. Two markers, spanning a 23.6 cM interval, will be used to genotype the IG cross for the second extract QTL. Two markers, defining a 16.7 cM interval, will be used to genotype the MD cross for the distal

Table 6.3. QTL genotype differences for malt extract (%) on chromosome 5, where LOD≥2.5. The letter suffix indicates the parent contributing the larger value allele (M=Morex; S=Steptoe). The value in bold indicates the QTL peak. Adjacent values indicate the 90% confidence interval. Marker intervals in bold type indicate the centromere location.

Chromosome marker interval		% Recomb.	Crookston MN.1992	Tetonia ID.1992	K. Falls OR.1991	Overall mean
Aga6	*Hor2*	2.5				
Hor2	*Hor1*	10.5				
Hor1	*ABA4*	6.6			0.79M	
ABA4	*CDO99*	8.0			0.96M	
CDO99	*Ica1*	11.2			**1.14M**	
Ica1	*ABG500A*	7.9	1.09M	0.69M	1.08M	**0.68M**
ABG500A	*ABG494*	9.9	**1.20M**	**0.79M**	0.92M	0.66M
ABG494	***Glb1***	7.6		0.73M		
Glb1	*ABC160*	8.8		0.85M		
ABC160	*ABG464*	14.7		0.95M		**0.69M**
ABG464	*His3B*	9.6		**1.01M**		0.63M
His3B	*iPgd2*	16.6		0.96M	0.81M	
iPgd2	*ABG702*	12.6		0.84M	0.85M	
ABG702	*ABA2*	6.4		**0.94M**	**0.94M**	
ABA2	*ABG373*	8.3		0.83M	0.91M	
ABG373	*ABG387A*	5.3				

Table 6.4. QTL genotype differences for group environments malt extract (%) on chromosome 5, where LOD≥2.5. The letter suffix indicates the parent contributing the larger value allele (M=Morex; S=Steptoe). The value in bold indicates the QTL peak. Adjacent values indicate the 90% confidence interval. Marker intervals in bold type indicate the centromere location.

Chromosome marker interval		% Recomb.	Group†	Group††	Group‡	Group‡‡	Western	Western (irrigated)	Western (dryland)	Midwest
Aga6	*Hor2*	2.5								
Hor2	*Hor1*	10.5								
Hor1	*ABA4*	6.6								
ABA4	*CDO99*	8.0	0.66M			0.63M				
CDO99	*Ica1*	11.2	0.79M			0.75M				
Ica1	*ABG500A*	7.9	0.92M			0.85M	**0.68M**		**0.83M**	1.09M
ABG500A	*ABG494*	9.9	**0.94M**			**0.86M**	0.67M		0.81M	**1.20M**
ABG494	***Glb1***	7.6	0.78M	0.66M		0.74M				
Glb1	*ABC160*	8.8	**0.84M**	0.76M		0.80M	0.60M			
ABC160	*ABG464*	14.7		**0.91M**		**0.90M**	**0.70M**	**0.67M**		
ABG464	*His3B*	9.6		0.86M		0.83M	0.64M	0.65M		
His3B	*iPgd2*	16.6					**0.67M**	**0.69M**		
iPgd2	*ABG702*	12.6			0.84M					
ABG702	*ABA2*	6.4			**0.92M**					
ABA2	*ABG373*	8.3			0.86M					
ABG373	*ABG387A*	5.3			0.67M					

†Group=mean of environments Crookston NY. 1992, Tetonia ID. 1992, Bozeman (irrigated) MT. 1992, and Klamath Falls OR. 1991.
††Group=mean of environments Tetonia ID. 1992, Bozeman (irrigated) MT. 1992, Bozeman (dryland) MT. 1992, and Klamath Falls OR. 1991.
‡Group=mean of environments Tetonia ID. 1992 and Klamath Falls OR. 1991.
‡‡Group=mean of group†, group†† and group‡.

position of the long arm of the chromosome. Alternative genotypes may be recovered that have the either favorable QTL allele for malt extract or yield.

Chromosome 6

Chromosome 6 was remarkable for a paucity of consistent yield and extract QTLs. Yield QTLs were identified in only two of the sixteen environments (Table 7.1) Both environments were within the subset of Western irrigated environments (Table 7.2). In the Western irrigated mean dataset the peak was resolved to the *Rm1* - *ABG474* interval and Morex contributed the favorable allele. As shown in Figure 6, alleles at this locus will segregate in both the IG and MD crosses.

Malt extract QTL effects were detected in only one of the nine environments (Table 7.3) and Steptoe contributed the favorable allele. As shown in Figure 6, in the IG cross, the allele for this QTL is positively fixed while there will be segregation in the MD cross.

Two markers which define a 12.6 cM interval will be used to genotype the progeny of the IG cross for the yield QTL. Two markers defining a 5.9 cM interval will be used to genotype the progeny of the MD cross for the malt extract QTL.

Chromosome 7

Grain yield QTLs were detected in two of the sixteen environments (Table 8.1) and the same peak (*Ale* - *ABC302*) was identified in the average of these two data sets (Table 8.2). Morex contributed the favorable allele. The effect was not apparent in any of the agrogeographic pooled datasets subset analyses. It is apparent from

Table 7.1. QTL genotype differences for grain yield (kg/ha) on chromosome 6, where LOD≥2.5. The letter suffix indicates the parent contributing the larger value allele (M=Morex; S=Steptoe). The value in bold indicates the QTL peak. Adjacent values indicate the 90% confidence interval. Marker intervals in bold type indicate centromer location.

Chromosome marker interval		% Recomb.	Aberdeen ID.1991	K. Falls OR.1991
PSR167	*Nar1*	6.3		
Nar1	*ABG378*	5.2		
ABG378	*Cxp3*	9.0		
Cxp3	*PSR106*	16.7		
PSR106	*ABG387B*	4.5		723M
ABG387B	*ABG458*	14.5		**849M**
ABG458	*Rrn1*	6.3	851M	686M
Rrn1	*ABG474*	7.1	**926M**	**690M**
ABG474	***ksuD17***	4.1	908M	688M
ksuD17	*ksuA3D*	7.3	838M	
ksuA3D	*Nar7*	8.7		
Nar7	*Nir*	5.5		
Nir	*Psr154*	12.3		

Table 7.2. QTL genotype differences for group environments grain yield (kg/ha) on chromosome 6, where LOD≥2.5. The letter suffix indicates the parent contributing the larger value allele (M=Morex; S=Steptoe). The value in bold indicates the QTL peak. Adjacent values indicate the 90% confidence interval. Marker intervals in bold type indicate the centromere location.

Chromosome marker interval		% Recomb.	Group[†]	Western (irrigated)
PSR167	*Nar1*	6.3		
Nar1	*ABG378*	5.2		
ABG378	*Cxp3*	9.0		
Cxp3	*PSR106*	16.7		
PSR106	*ABG387B*	4.5	545M	
ABG387B	*ABG458*	14.5	713M	
ABG458	*Rrn1*	6.3	737M	412M
Rrn1	*ABG474*	7.1	**804M**	**433M**
ABG474	***ksuD17***	4.1	803M	426M
ksuD17	*ksuA3D*	7.3	628M	
ksuA3D	*Nar7*	8.7		
Nar7	*Nir*	5.5		
Nir	*Psr154*	12.3		

[†]Group=mean of environments Aberdeen ID. 1991 and Klamath Falls OR. 1991.

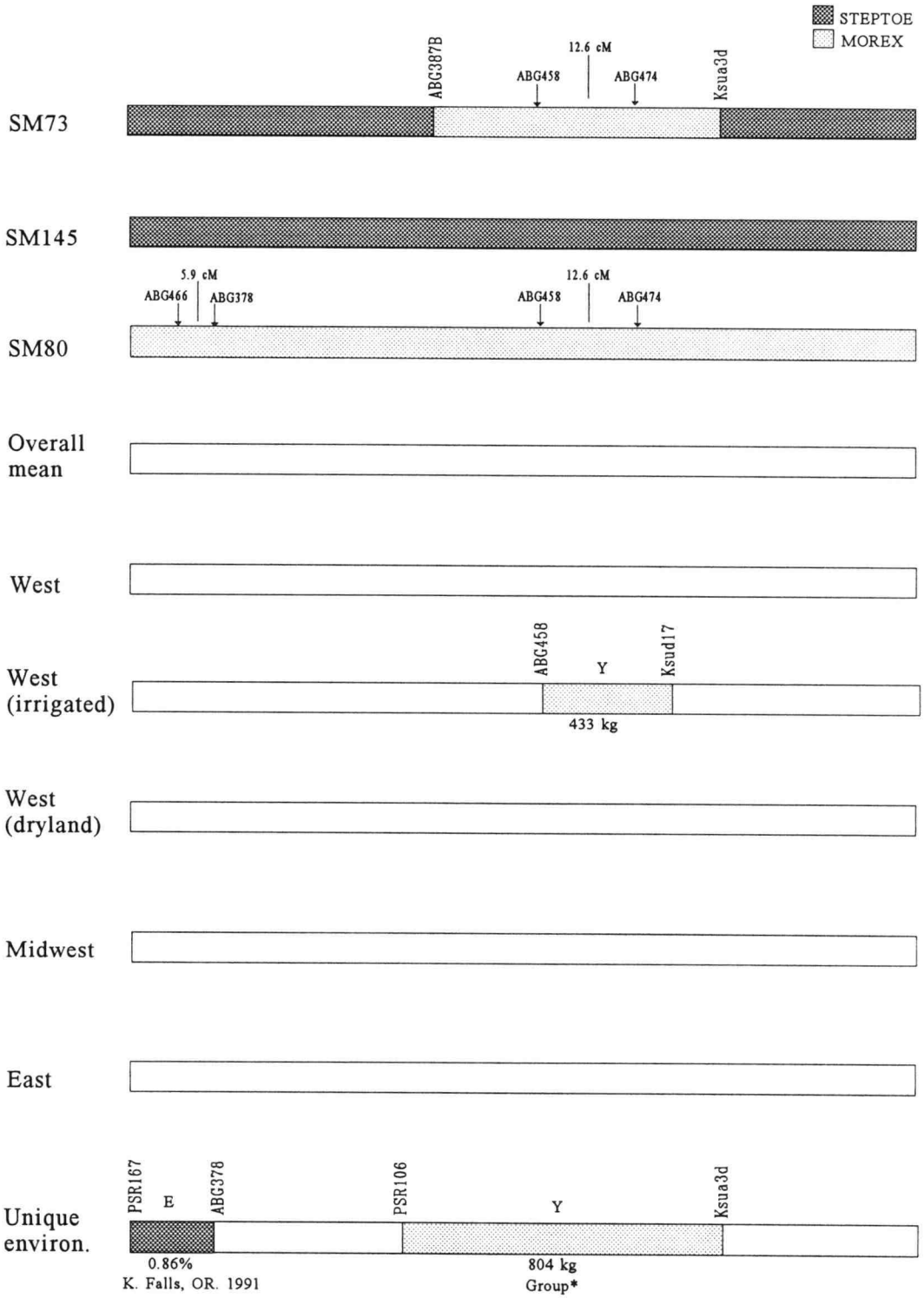
Table 7.3. QTL genotype differences for malt extract (%) on chromosome 6, where LOD≥2.5. The letter suffix indicates the parent contributing the larger value allele (M=Morex; S=Steptoe). The value in bold indicates the QTL peak. Adjacent values indicate the 90% confidence interval. Marker intervals in bold type indicate the centromere location.

Chromosome marker interval		% Recomb.	K. Falls OR.1991
PSR167	*Nar1*	6.3	0.85S
Nar1	*ABG378*	5.2	**0.86S**
ABG378	*Cxp3*	9.0	
Cxp3	*PSR106*	16.7	
PSR106	*ABG387B*	4.5	
ABG387B	*ABG458*	14.5	
ABG458	*Rm1*	6.3	
Rm1	*ABG474*	7.1	
ABG474	***ksuD17***	4.1	
ksuD17	*ksuA3D*	7.3	
ksuA3D	*Nar7*	8.7	
Nar7	*Nir*	5.5	
Nir	*Psr154*	12.3	

Figure 6
Genome structure of the parents of the IG (SM73 X SM145) and MD (SM80 X SM145) crosses and positions of QTL effects detected in various datasets on chromosome 6. QTL effects are shown with 90% confidence intervals. "E" indicates a malt extract QTL and "Y" a yield QTL. The parent contributing the favorable allele is indicated with the shading pattern described by the legend. Marker designations perpendicular to the chromosomes indicate breakpoints. Markers parallel to the chromosomes are those that will be used to genotype cross progeny. Distances between these markers are indicated in cM.

Figure 6, continued

Chromosome 6



*Group=mean of Aberdeen, ID. and K. Falls, OR.

Table 8.1. QTL genotype differences for grain yield (kg/ha) on chromosome 7, where LOD≥2.5. The letter suffix indicates the parent contributing the larger value allele (M=Morex; S=Steptoe). The value in bold indicates the QTL peak. Adjacent values indicate the 90% confidence interval. Marker intervals in bold type indicate the centromere location.

Chromosome marker interval		% Recomb.	Brandon MAN.1992	Bozeman MT. irrigated,1991
ABC483	*ABG705*	27.6		
ABG705	*ABg395*	7.9		
ABG395	*Rm2*	3.6		
Rm2	***Ltp1***	4.5	413M	
Ltp1	*ABC706*	5.8	496M	725M
ABC706	*Ale*	5.4	594M	933M
Ale	*ABC302*	10.1	**603M**	**965M**
ABC302	*CDO57B*	13.0	565M	768M
CDO57B	*mSrh*	5.4	441M	
mSrh	*CDO504*	6.5	360M	
CDO504	*WG908*	7.7		
WG908	*ABG495A*	8.8		
ABG495A	*ABG496*	6.2		
ABG496	*ABC482*	7.4		
ABC482	*ABG707*	7.2		
ABG707	*ABG463*	9.1		
ABG463	*ABA304*	8.6		

Table 8.2. QTL genotype differences for group environment grain yield (kg/ha) on chromosome 7, where LOD≥2.5. The letter suffix indicates the parent contributing the larger value allele (M=Morex; S=Steptoe). The value in bold indicates the QTL peak. Adjacent values indicate the 90% confidence interval. Marker intervals in bold type indicate the centromere location.

Chromosome marker interval		% Recomb.	Group†
ABC483	*ABG705*	27.6	
ABG705	*ABg395*	7.9	
ABG395	*Rrn2*	3.6	449M
Rrn2	***Ltp1***	4.5	464M
Ltp1	*ABC706*	5.8	611M
ABC706	*Ale*	5.4	766M
Ale	*ABC302*	10.1	**785M**
ABC302	*CDO57B*	13.0	666M
CDO57B	*mSrh*	5.4	440M
mSrh	*CDO504*	6.5	
CDO504	*WG908*	7.7	
WG908	*ABG495A*	8.8	
ABG495A	*ABG496*	6.2	
ABG496	*ABC482*	7.4	
ABC482	*ABG707*	7.2	
ABG707	*ABG463*	9.1	
ABG463	*ABA304*	8.6	

†Group=mean of environments Brandon MAN.1992 and Bozeman (irrigated) MT. 1991.

Figure 7 that segregation can be expected in the IG cross but both parents carry the Morex alleles in the interval from *Ale* to *CDO504* in the MD cross.

A malt extract QTL was detected in only one of the nine environments (Table 8.3) and the effect was not significant in any of the pooled datasets. As shown in Figure 7, all progeny of the IG cross will carry the positive Morex allele. Segregation will occur in the progeny of the MD cross.

Two markers defining a 11.5 cM segment will be used to genotype the progeny of the IG cross for the yield QTL and two markers spanning a 5.3 cM interval will be used to genotype the progeny of the MD cross for malt extract.

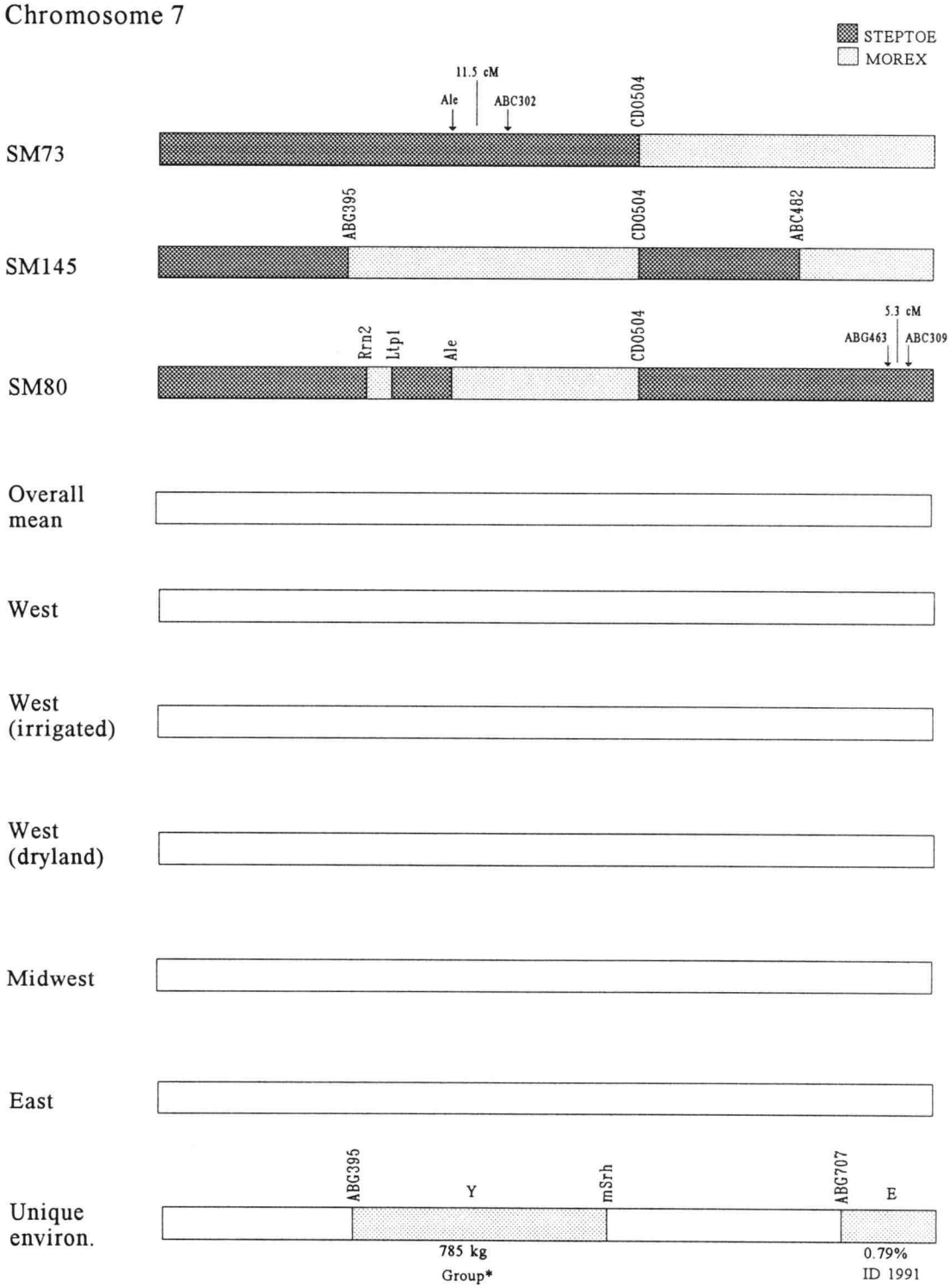
Table 8.3. QTL genotype differences for malt extract (%) on chromosome 7, where LOD≥2.5. The letter suffix indicates the parent contributing the larger value allele (M=Morex; S=Steptoe). The value in bold indicates the QTL peak. Adjacent values indicate the 90% confidence interval. Marker intervals in bold type indicate the centromere location.

Chromosome marker interval		% Recomb.	Aberdeen ID.1991
ABC483	*ABG705*	27.6	
ABG705	*ABg395*	7.9	
ABG395	*Rrn2*	3.6	
Rrn2	***Ltp1***	4.5	
Ltp1	*ABC706*	5.8	
ABC706	*Ale*	5.4	
Ale	*ABC302*	10.1	
ABC302	*CDO57B*	13.0	
CDO57B	*mSrh*	5.4	
mSrh	*CDO504*	6.5	
CDO504	*WG908*	7.7	
WG908	*ABG495A*	8.8	
ABG495A	*ABG496*	6.2	
ABG496	*ABC482*	7.4	
ABC482	*ABG707*	7.2	
ABG707	*ABG463*	9.1	0.73M
ABG463	*ABA304*	8.6	**0.79M**

Figure 7
Genome structure of the parents of the IG (SM73 X SM145) and MD (SM80 X SM145) crosses and positions of QTL effects detected in various datasets on chromosome 7. QTL effects are shown with 90% confidence intervals. "E" indicates a malt extract QTL and "Y" a yield QTL. The parent contributing the favorable allele is indicated with the shading pattern described by the legend. Marker designations perpendicular to the chromosomes indicate breakpoints. Markers parallel to the chromosomes are those that will be used to genotype cross progeny. Distances between these markers are indicated in cM.

Figure 7, continued

Chromosome 7



*Group=means of Brandon, MAN. 1992 and Bozeman (irrigated) MT. 1991.

DISCUSSION

The numbers of QTLs associated with each trait listed in Table 9 were determined based on a subjective integration of peak positions and confidence interval sizes in all available datasets. As such, these numbers can only be considered approximate. A precise determination of the number of QTLs may well have to be based on the results of the validation experiments. For the purposes of discussion, however, ten QTLs were identified for each trait. For yield, QTLs were detected on all chromosomes. Malt extract QTLs were detected on each chromosome except chromosome 3. For both traits, most QTLs were significant in three or fever environments. The most consistently expressed QTL for yield was on chromosome 3. For malt extract, consistent effects were detected on chromosomes 1 and 4. In general, these were the effects that were also detected in the analysis of the overall mean dataset. However, there were exceptions. For example, yield QTLs were detected on chromosome 2 in 11 out of the 16 environments. However, changes in favorable alleles led to cancellation of effects and consequently no significant effects were detected in the overall analysis. In the case of malt extract on chromosome 5, significant effects were detected in only three of the nine environments, yet a significant QTL effect was detected in the overall analysis.

The alternative favorable alleles for grain yield on chromosome 2 underscore the need to determine the nature and extent of QTL X E interaction in order to properly define target environments for MMAS. The coincident QTL for heading date in the *Rbcs - Abg2*, interval may be the biological determinant of grain yield. In

Table 9. Distribution of QTL effects for grain yield and malt extract in the Ideal Genotype (IG) and Maximum Difference (MD) crosses. F^+ indicates the favorable allele is fixed and F^- that the unfavorable allele is fixed. S indicates the population will segregate. A "c" indicates QTL conflicts, in terms of alternative favorable alleles for different target yield environments, or due to concident QTLs for different traits with alternative favorable alleles.

Chromosome	Interval		Favorable allele	Yield IG	Yield MD	Extract IG	Extract MD
1	*Plc*	*-ABG380*	S	F^+	F^+		
	ABC305	*-Cat3*	S	F^+	F^+		
	ABC154A	*-ABG22a*	M			F^+	S
	ABG701	*-Ubi1*	M			F^+	S
2	*ABG313A*	*-ABC162*	S/M	S^c	S^c		
	ABG14	*- Gln2*	S	F^+	F^+		
	ABG8	*-ABG2*	M			S^c	S^c
3	*ABC171*	*-ABG377*	S	F^+	S		
	ABC307B	*-His4b*	S	F^+	S		
4	*BCD402B*	*-ABG500B*	S	F^{+c}	F^{+c}		
	WG622	*-Tuba1*	M			F^-	S
	ABG3	*-ABG472*	M			F^-	F^{-c}
5	*His3B*	*-ABG387A*	S	F^{+c}	S^c		
	ABA4	*-ABG494*	M			F^+	S
	Glb1	*-His3b*	M			S	F^+
	iPgd2	*-ABG387A*	M			F^{-c}	S^c
6	*Psr106*	*-ksuA3D*	M	S	S		
	PSR167	*-ABG378*	S			F^+	S
7	*ABG395*	*-mSrh*	M	S	F^+		
	ABG707	*-ABA304*	M			F^+	S

Western environments, particularly under dryland conditions, maturity can be a principal determinant of yield as it affects grain filling and shattering loss.

Agrogeographic grouping of environments revealed one QTL effect on chromosome 3 that was not significant in any individual environment dataset. More data were available for the Western US environments, and a degree of specificity to irrigated and dryland environments was observed for both grain yield and extract. For example, yield QTLs on chromosome 2 were limited to the dryland environments (Figure 2), an additional yield QTL was detected on the long arm of chromosome 3 in the irrigated environments (Figure 3), and the yield effect on chromosome 6 (Figure 6) was limited to the irrigated environments. The two subsets of environments also revealed distinct malt extract QTLs on chromosome 5 (Figure 5). Nonetheless, it is difficult to directly ascribe these QTL effects as being specific to a particular set of environmental conditions. For example, the QTL peak for malt extract at *Ica1 - ABG494* on chromosome 5 detected in the Western dryland environments coincided directly with the peak observed for the Midwest environments.

It is of interest that despite the variable numbers of QTLs detected in the individual environments, the proportion of total phenotypic variance was similar between the various groupings. The r^2 values for individual environments varied considerably (Table 10). For example, across the 16 environments, grain yield r^2 values ranged from 0.14 (Crookston, Minnesota) to 0.58 (Bozeman, Montana dryland, 1991). Across the nine environments for which extract data were obtained, r^2 values ranged from 0.17 (Crookston, Minnesota) to 0.41 (Bozeman, Montana irrigated,

1992). As shown in Table 10, the r^2 values for the various groupings were occasionally higher than in any of the individual environment datasets. The r^2 for grain yield in the overall analysis was 0.40, despite the fact that only one QTL effect was significant. The maximum r^2 (0.55) was detected in the Western dryland data set. The minimum r^2 (0.28) was detected for the Eastern group, the mean of only two environments. Malt extract r^2 values ranged from 0.17 to 0.50 in the various agrogeographic groups, with the smallest value coming from the Midwest US. However, this value was based on a single environment (Crookston, MN).

Certain large-effect QTLs were readily detected, while others proved more elusive. Detection of these more elusive QTL effects may well be a function of the number of test environments, rather than the specific attributes of the test environment. In much of North America, economic and marketing conditions preclude the release of barley varieties with specific adaptation to a limited number of environments. As a consequence, superior performance in a specific range of environments is sacrificed in the interest of broad adaptation. Furthermore, particularly under non-irrigated conditions, precipitation and climatic conditions vary widely from year to year, and consistent performance in the face of variable growing conditions may be held in higher esteem than exceptional performance under a particular set of environmental conditions. It remains to be seen if environment-specific QTLs are indeed important determinants of stability.

A critical issue is the resolution of QTL effects and the numbers of QTLs that can be effectively manipulated in a MMAS breeding effort. Grouping of environments

Table 10. Proportion of phenotypic variance (r^2) for grain yield and malt extract accounted for by QTLs ≥ LOD 2.5 in various datasets derived from the assesment of the Steptoe X Morex population in multiple environments. See text for definition of the pooled datasets.

	Multilocus r^2	
Environments	Yield	Extract
Overall mean	0.40	0.49
Western US	0.46	0.50
Western US. (irrigated)	0.45	0.41
Western US. (dryland)	0.55	0.44
Midwest US/Canadian prairies	0.30	0.17[†]
Eastern US/Canada	0.28	-[††]

[†]Based on one environment only Crookston, MN. 1992.
[††] No malting analyses were conducted in these environments

by agrogeographic criteria or by common expression was effective in positioning QTL peaks, but whether these peaks indeed represent the correct chromosome locations of the gene or genes underlying trait expression can only be determined empirically. Greater marker density does little to resolve QTL effects (Hayes et al., 1993), and phenotyping of even larger populations is not feasible. Within the QTL validation populations we hope to recover recombinant genotypes that will allow for more exact positioning of QTL effects. That is, if lines sharing common flanking markers that would lead one to predict that they share a common QTL prove to have different phenotype values for the trait in question, they can subsequently be genotyped for additional markers in the interstitial region that will allow for the definition of breakpoints and consequently greater resolution of the QTL effect. A strategy relying on MMAS for fairly large chromosome segments, of course, requires that there be a minimum of adjacent QTLs with alternative favorable alleles.

The chromosome 2 QTLs for grain yield, with alternative favorable alleles in different subsets of environments, were the only examples of alternative favorable alleles for the same character at adjacent or coincident QTLs in this dataset. However, an objective of an offensive MMAS strategy may well be to maximize the probability of recovering favorable alleles for two or more characters from both parents. In the case of this population, Steptoe contributed the majority of the favorable alleles for grain yield and Morex the majority of the favorable alleles for malt extract, although both parents did contribute favorable alleles for both characters.

The objective of selection is to accumulate all possible favorable alleles in a single genotype. This objective cannot be realized in this germplasm with the current level of QTL resolution. Chromosome 2 provides an example of coincident QTLs for contrasting characters and alternative favorable alleles. Grain yield and malt extract effects both map to the same region (Figure 2). MMAS for the Morex alleles in the *Rbcs - ABC162* region should lead to simultaneous improvement in the Midwestern environments, as Morex contributes the favorable alleles for both traits. In the Western environments, however, Steptoe contributes the favorable allele for yield and Morex the favorable allele for malt extract. Likewise, on chromosome 4, Steptoe contributed the favorable allele for grain yield in a region coinciding with a favorable allele for malt extract from Morex that was significant in the overall analysis, the Western environments, and both subsets of Western environments. Finally, Steptoe again contributed the favorable yield allele on chromosome 5 in the Western dryland environments, while extract QTL effects, with Morex contributing the favorable allele, were detected in adjacent or coincident regions (Figure 5).

In the cases of such trade-offs in favorable alleles for two traits, QTLs will have to be prioritized. Perhaps consistency of expression and overall value (measured as the percent of phenotypic variation accounted for or the effect of allele substitution) can serve as weights for the development of a selection index. In the case of chromosome 4, for example, the consistent 1% difference in malt extract may well be of more value than 718 kg of environment-specific yield. In general, however, the picture in this population is one of dispersed QTL effects that should allow for

recovery of most favorable QTLs for both characters. For example, as shown in Table 10, in the IG population, five of the yield and extract QTLs are positively fixed and only one extract QTL is negatively fixed. Two yield QTLs and one extract QTL are unambiguous targets for selection. For both traits, four QTLs are problematic, either due to coincident QTLs for the two characters with alternative favorable alleles, or due to the need target alternative favorable alleles for distinct environments. The latter issue can be dealt with by selecting alternative genotypes for subsets of target environments. However, the former requires an assessment of the relative values of the two QTL effects. In the MD cross, four yield QTLs and one extract QTL are favorably fixed. Three yield QTLs and six extract QTLs are unambiguous targets for selection. The number of problematic QTLs and the position of the problematic QTLs are the same as in the ID cross. The numbers of segregating and fixed QTLs, in the two crosses are not necessarily indicative of QTL weight importance. For example, of the six segregating yield QTLs in the IG cross, only the two on chromosome 2 were significant in more than two environments. In the MD cross, on the other hand, the five segregating QTLs include those on chromosome 2 as well as the large, consistent effect on chromosome 3.

Although the QTLs for grain yield and malt extract detected in this population provide less than ideal resolution and do not account for all of the variation in trait expression, these data provide an opportunity to empirically assess the value of QTL effects and to begin systematically assembling favorable alleles in single genotypes. With eight QTLs segregating in the IG cross, there is little likelihood of recovering an

individual genotype with all favorable QTL alleles. Additional matings to generate new DH populations, followed by genotyping and phenotyping may be required to realize this objective. The time required to complete such a selection scheme, however, may transform the process from one of offensive selection to academic exercise. The twelve QTLs segregating in the MD cross should allow for the recovery of genotypes with contrasting QTLs and a rigorous comparison of predicted vs. realized selection responses. The utility of QTL analysis as a predictive tool and MMAS as an offensive breeding strategy are attractive from a theoretical standpoint. Field performance will be the ultimate measure of effectiveness.

BIBLIOGRAPHY

Burger, W. C. and D. E. LaBerge. 1985. Malting and brewing quality. p. 367-401. *In* D. C. Rasmusson (ed.) Barley. Agronomy Monograph No. 26. Am. Soc. of Agron., Madison, Wisconsin.

Chen, F. and P. M. Hayes. 1989. A comparison of *Hordeum bulbosum* - mediated haploid production efficiency in barley using in vitro floret and tiller culture. Theor. Appl. Genet. 77:701-704.

Chen, F. Q., D. Prehn, P. M. Hayes, D. Mulrooney, A. Corey, and H. Vivar. 1994. Mapping genes for resistance to barley stripe rust (*Puccinia striiformis* f. sp. *hordei*). Theor. Appl. Genet. (in press).

Graner, A., A. Jahoor, J. Schondelmaier, H. Siedler, K. Pillen, G. Fischbeck, G. Wensel, and R. G. Herrmann. 1991. Construction of an RFLP map of barley. Theor. Appl. Genet. 83:250-256.

Hayes, P. M., T. K. Blake, T. H. H. Chen, S. Tragoonrung, F. Chen, A. Pan, and B. Liu. 1993a. Quantitative trait loci on barley (*Hordeum vulgare*) chromosome 7 associated with components of winterhardiness. Genome 36:66-71.

Hayes, P. M., B. H. Liu, S. J. Knapp, F. Chen, B. Jones, T. Blake, J. Franckowiak, D. Rasmusson, M. Sorrells, S. E. Ullrich, D. Wesenberg, and A. Kleinhofs. 1993b. Quantitative trait locus effects and environmental interaction in a sample of North American barley germplasm. Theor. Appl. Genet. 87:392-401.

Hayes, P. M., D. Matthews, and the NABGMP. 1994. Online dataset for the Steptoe X Morex barley mapping population. Files available via Internet Gopher, host greengenes.cit.cornell.edu.

Heun, M., A. E. Kennedy, J. A. Anderson, N. L. V. Lapitan, M. E. Sorrells, S. D. Tanksley. 1991. Construction of a restriction fragment length polymorphism map for barley (*Hordeum vulgare*). Genome 34:437-447.

Heun, M. 1992. Mapping quantitative powdery mildew resistance of barley using a restriction fragment length polymorphism map. Genome 35:1019-1025.

Khursheed, B. and J. C. Rogers. 1988. Barley α-amylase genes: quantitative comparison of steady-state mRNA levels from individual members of two different families expressed in aleurone cells. J. Bio. Chem. 263:18953-18960.

Kleinhofs, A., A. Kilian, M. A. Saghai Maroof, R. M. Bitashev, P. Hayes, F. Q. Chen, N. Lapitan, A. Fenwick, T. K. Blake, V. Kanazin, E. Ananiev, L. Dahleen, D. Kudrna, J. Bollinger, S. J. Knapp, B. Liu, M. Sorrells, M. Heun, J. D. Franckowiak, D. Hoffman, R. Skadsen, and B. J. Steffenson. 1993. A molecular, isozyme and morphological map of the barley (*Hordeum vulgare*) genome. Theor. Appl. Genet. 86:705-712.

Knapp, S. J. 1991. Using molecular markers to map multiple quantitative trait loci: models for backcross, recombinant inbred, and double haploid progeny. Theor. Appl. Genet. 81:333-338.

Lander, E., P. Green, J. Abrahamson, A. Barlow, M. Daley, S. Lincoln, and L. Newburg. 1987. MAPMAKER: An interactive computer package for constructing primary genetic linkage maps of experimental and natural populations. Genomics 1:174-181.

Lincoln, S., M. Daly, and E. Lander. 1992. Mapping genes controlling quantitative traits with MAPMAKER/QTL 1.1. Whitehead Institute Technical Report. 2nd edition.

Liu, B. H. and P. M. Hayes. 1992. Efficiency of genome map assisted plant breeding (GMAPB). Plant Genome I, The International Conference on the Plant Genome, San Diego, CA. pp:37.

Martinez, O. and R. N. Curnow. 1992. Estimating the locations and the sizes of the effects of quantitative trait loci using flanking markers. Theor. Appl. Genet. 85:480-488.

Muir, C. E. and R. A. Nilan. 1973. Registration of Steptoe barley. Crop Sci. 13:770.

Nilan, R. A. 1964. The cytology and genetics of barley. Monographic supplement. No 332:1 Washington State Univ. Press, Pullman, USA.

Paterson, A. H., S. Damon, J. D. Hewitt, D. Zamir, H. D. Rabinowitch, S. E. Lincoln, E. S. Lander, and S. D. Tanksley. 1991. Mendelian factors underlying quantitative traits in tomato: comparison across species, generations, and environments. Genetics 127:181-197.

Paterson, A. H., E. S. Lander, J. D. Hewitt, S. Peterson, S. E. Lincoln, and S. D. Tanksley. 1988. Resolution of quantitative traits into Mendelian factors using a complete RFLP linkage map. Nature 335:721-726.

Rasmusson, D. C. and R. Q. Channell. 1970. Selection for grain yield and compenents of yield in barley. Crop Sci. 10:51-54

Rasmusson, D. C. and R. W. Wilcoxon. 1979. Registration of Morex barley. Crop Sci. 19:293.

Tapsell, C. R. and W. T. B. Thomas. 1981. Estimating the genetical components for cross-prediction of yield and its components in barley. p. 79-83. *In* M. J. C. Asher et al. (eds.) Barley Genet. IV. Proc. 4th Int. Barley Genet. Symp. Edinburgh. 22-29 July 1981. Edinburgh University Press, Edinburgh.