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Title: Quantitative Trait Locus Mapping of Yield and Yield Components in Barley *(Hordeum vulgare. L)*.

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Patrick M. Hayes

Higher grain yield is a key objective in barley *(Hordeum vulgare. L)* breeding. Despite extensive research on the genetics of yield and its components, selection for yield *per se* is still the most extensively employed because of negative relationships among components, modest correlations between yield and any particular component, and the additional resources required for measuring the components. The development of quantitative trait locus (QTL) detection procedures allows for an alternative approach to this issue. The objective of this investigation was to determine the biological basis of observed grain yield QTLs, with particular reference to yield components and yield-related traits. Yield and yield component traits were assessed in a population of spring barley doubled haploids from a cross of 'Steptoe' x 'Morex'. The scope of inference of the experiment was broadened by using reference QTL data sets from the multiple environment assessment of the same population. Both positive

and negative relationships among yield, component, and related trait QTLs were observed. The QTL data indicate that indirect selection for yield via yield components would be ineffective. The yield QTL effects in this germplasm were largely attributable to lodging and basal internode length. Localization and interpretation of yield QTLs may be useful for studying orthologous gene expression in other germplasm and in developing multiple character selection strategies.

QUANTITATIVE TRAIT LOCUS MAPPING OF YIELD AND YIELD COMPONENTS IN BARLEY *(Hordeum vulgare L.)*

by

Abdoulaye Traore

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Redacted for Privacy

Associate Professor of Crop Science in charge of major

Redacted for Privacy

Head of the Department of Crop and Soil Science

Redacted for Privacy

Dean of the Graduate School

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QUANTITATIVE TRAIT LOCUS MAPPING OF YIELD AND YIELD COMPONENTS IN BARLEY *(Hordeum vulgare. L)*

INTRODUCTION

Higher grain yield is often the principal objective of small grains breeding programs. Grain yield is the final expression of the many complex events occurring in the crop growth cycle. Genetic analyses of this quantitative trait have typically employed statistical tools for estimating components of variance and covariance. Allard (1988) described the limited information that such techniques provide in terms of understanding genetic mechanisms and evolution. For example, estimates of grain yield heritability in barley range from 0 to 50% (Rutger et al., 1966; Rasmusson and Glass, 1967; Yap and Harvey, 1972).

One approach to circumventing the low heritability of yield has been to partition yield into its components: grain bearing inflorescences per unit area, kernels per spike, and kernel weight (Bendelkacem et al., 1984; Zahour et al., 1987; Dofing and Knight, 1992a and 1992b). In barley, heritabilities for yield components are generally higher than for yield itself and for some characters, positive phenotypic and genotypic correlations have been reported (Rasmusson and Cannell, 1970; McNeal et al., 1978). However, these correlations are often too small to justify indirect selection, yield component compensation can be problematic, and in some cases components of yield are negatively associated with yield (Rasmusson and Cannell, 1970; Gravois and Helms, 1992). An additional selection criterion proposed as an

alternative to yield per se is harvest index, the ratio of grain yield to total above ground biomass. However, as with the components of yield, a high harvest index is not necessarily a reliable predictor of yield (Boukerou and Rasmusson, 1990). Finally, measurement of some yield components and associated traits can be extremely tedious and time-consuming. Thus, in many cultivar development programs, the objective of higher yield is often addressed by (i) selecting for resistance to the biotic and abiotic stresses that can limit yield or (ii) basing selection decisions on long-term average yield performance.

Recently, there has been considerable interest in quantitative trait locus (QTL) analyses based on medium density linkage maps. The underlying principle is to reduce the complexity of quantitative trait expression to the relative simplicity of Mendelian-type analyses. In principle, markers positioned every 10 to 20 cM should allow for the identification of chromosome intervals associated with trait expression (Paterson et al., 1988). QTLs for a range of agronomic, quality and resistance traits have been reported in a number of crop species (reviewed by Paterson et al., 1991). In barley, the development of a medium density genome map by the North American Barley Genome Mapping Project (Kleinhofs et al., 1993) has allowed for identification of QTLs controlling a number of traits, including grain yield (Hayes et al., 1993). The objective of this research was to determine the biological basis of these observed yield QTLs with particular reference to the components of yield.

MATERIALS AND METHODS

The development of the genetic reference population and subsequent map construction were described by Kleinhofs et al. (1993). Briefly, two six-row spring habit cultivars - 'Steptoe' and 'Morex' - were crossed to generate source material for doubled haploid line production. Steptoe is a high yielding, broadly adapted six-row Coast-type feed barley selected from the cross of 'WA3564'/'Unitan' (Muir and Nilan, 1973). 'Morex', a midwestern six-row Manchurian-type, is the North American six-row malting quality standard. It was developed at the University of Minnesota from the cross of 'Cree'/'Bonanza' (Rasmusson and Wilcoxson, 1979). A population of 150 doubled haploid (DH) lines was developed from the F_1 of this cross using the *Hordeum bulbosum* technique, as described by Chen and Hayes (1989). A 295-point map provided an average density of 4 cM, with considerable overlap in certain regions (Kleinhofs et al. 1993). By selection of relatively evenly spaced markers, Hayes et al. (1993) generated a 123-point "skeleton" linkage map providing an average marker density of 9.6 cM. Hayes et al. (1993) identified QTLs for a range of agronomic and malting quality traits based on the performance of this population in five field tests conducted in 1991.

In addition to the data generated directly for this research (described in a subsequent section) the grain yield, plant height, and lodging data presented by Hayes et al. (1993) were used as a reference for this research because any single environment is not likely to reveal all possible QTLs. For the same reason, the only

additional 1,000 kernel weight data available for this population - based on assessments at Guelph, Ontario; Brandon, Manitoba; Saskatoon, Saskatchewan; and Goodale, Saskatchewan in 1992 - were used as a reference. In the remainder of this report, these reference data sets will be identified with an "R" suffix, i.e. "Yield-R", "1,000 kernel weight-R", etc.

The QTL analysis procedures described by Hayes et al. (1993) were also employed in this work. Briefly, analyses were performed using QTL-STAT (B.H. Liu and S.J. Knapp, unpublished). The QTL parameters were estimated by using least squares interval mapping methods (Haley and Knott, 1992; Knapp et al., 1990). QTL genotype means were estimated and the hypothesis of "no QTL" was tested against the hypothesis of "one QTL" for every marker bracket. Hypotheses about QTL and QTL X E effects were tested using Wald statistics (Knapp, 1989; Knapp and Bridges, 1990). QTL effects were considered significant if they exceed a Wald statistic of 10.0, which is approximately equal to $p = .001$. Wald Support Intervals (WSIs) $\geq$ 90% were specified at Wald = 10, following the LOD Support Interval (LSI) concept described by van Ooijen (1992).

Grain yield and yield components were measured on a uni-replicate evaluation of the DH population grown near Corvallis, Oregon in 1992. The use of one replication was justified based on limited land availability and the consideration that the primary determinant of the power of tests of hypotheses about QTL genotype means is the number of replications of QTL genotypes (i.e. the number of individuals in the genetic reference population), not the number of times each individual line is

replicated (Knapp et al., 1990). Seeding rate, fertility, and other agronomic management procedures were in accordance with recommended practices for this location. Supplemental irrigation was supplied throughout the growing season. Each four row plot measured 1.8 m^2. In each plot, three rows were harvested with a self-propelled binder, or cut by hand, and threshed in a stationary thresher. Every effort was made to recover all grain from each plot. If necessary, shattered grain or broken inflorescences were collected from the ground. Badly lodged plots were cut by hand. From the fourth row, a 1 m section was cut by hand, bundled, and bagged. Harvest index (the ratio of grain weight to total above ground biomass) was determined from this sample, as was the weight of 1,000 kernels, and the number of fertile tillers per linear meter. Spike length (exclusive of awns), number of kernels per spike, and basal internode length were determined from a sample of 10 inflorescences collected from the remainder of the fourth row in each plot.

RESULTS AND DISCUSSION

Plant development was excellent, and no biotic or abiotic stresses were observed that would limit the expression of yield potential. Shattering and spike breakage at the basal internode were severe in certain plots. As described in the preceding section, every effort was made to recover grain from these plots. The frequency distributions for agronomic traits (Figure 1) underscore the quantitative nature of trait inheritance. 'Steptoe' was higher yielding and had a higher harvest index. 'Morex' was taller, with longer spikes and longer basal internodes. The presence of positive and negative phenotypic transgressive segregants suggests that there is substantial allelic variation between the parents for these characters. Phenotypic correlations among yield, yield components, plant height, and basal internode length were modest and did not exceed $\pm$ 0.30, except for the correlation of basal internode length and spike length, which was 0.42. Thus, components of yield and the associated characters would be of little utility for indirect phenotypic selection for grain yield, based on this assessment of the DH population.

QTLs associated with all traits were detected at multiple locations throughout the genome. The results of the QTL analyses are presented in Table 1. Values in each column represent QTL genotype differences, expressed in the units at the head of each column, for the entire support interval, and Wald peak values are shown in bold type. The letter suffix indicates the parent contributing the larger value allele: 'S' = Steptoe and 'M' = Morex. As described in the Materials and Methods, the

column headers with an "R" suffix represent reference data sets.

A cursory examination of Table 1 confirms that current levels of QTL resolution are far from desirable. The significance of QTL effects and the position of QTL peaks have been observed to shift in analyses of the same trait measured in the same population evaluated in different environments. This lack of resolution may be due to random errors associated with phenotyping or to a failure of the analysis procedures to distinguish between the effects of single and linked QTLs (Martinez and Curnow, 1992). By employing conservative criteria for QTL detection, we hope to produce an overall view of QTL effects in the barley genome, and identify trait relationships that merit further detailed analysis. Due to the complexity of these trait relationships, the results and discussion will be presented on a chromosome, rather than a trait basis.

Chromosome 1

A yield QTL was detected on the short arm of the chromosome, with a peak at the *ABG380-ABC158* interval, that was adjacent to the Yield-R peak. In both cases, Steptoe contributed the favorable allele. The support interval for a tillers per meter QTL, where Morex contributed the larger value allele, overlapped with the yield QTL support intervals. Whether these overlapping QTL effects are the consequence of adjacent QTLs or pleiotropic effects of the same QTL cannot be determined at this point. However, this negative relationship between tillering and yield is intriguing, as late-developing tillers can actually be "parasitic", in terms of source and sink

relationships within the barley plant (Simmons et al., 1982). The phenotypic correlation of tillers per meter and grain yield was 0.21. If phenotypic selection for tiller number had been based on this positive, albeit modest, relationship, a negative correlated response might have been obtained. The positive yield effect attributable to Steptoe may be due to the production of excess tillers by Morex, but better resolution of these QTLs is required before definitive conclusions can be reached. A yield QTL was detected on the long arm of chromosome 1 that was not seen in the analysis of the Yield-R data. There were overlapping support intervals for plant height and lodging. In all cases Steptoe contributed the larger value allele. The plant height and lodging peaks were adjacent, but were some distance from the yield peak. If these are indeed effects of the same QTL or closely linked QTL, the detection of a yield effect may be a consequence of the extra precautions taken to recover all grain in this experiment. In more typical field environments, such as those from which the Yield-R data were derived, height and consequently lodging may have canceled the positive yield effects of this locus.

Chromosome 2

No yield QTLs were detected that corresponded to the Yield-R effects. On the short arm of the chromosome, an interesting pattern of yield component QTLs and the Yield-R effect was observed. At the *Rbcs-Abg2* interval, Steptoe contributed the favorable allele for yield. Coincident QTLs were detected for harvest index, kernels per spike, basal internode length, and plant height. The pattern was such that Steptoe

contributed favorable alleles for harvest index and kernel weight, while the larger value alleles for kernels per spike, basal internode length, and plant height were contributed by Morex. This is an example of the negative relationship between kernels per spike and kernel weight reported by Dofing and Knight (1992a and 1992b). Morex contributed larger value alleles for plant growth, including overall height, and basal internode length, but not spike length. Spikes with long, and presumably weaker, basal internodes could lead to greater spike breakage and thus yield loss. This would be reflected in a favorable yield effect for Steptoe under combine-harvested conditions, but not where all grain was recovered. Shorter, thicker basal internodes are also reported to be associated with higher kernel weight (R.T Ramage, personal communication). The shorter stature of genotypes with the Steptoe height QTL allele would account for the Steptoe favorable allele for harvest index. Interestingly, no lodging QTL was detected in the vicinity of the Morex height effect. Lodging can be due to excessive plant height or to poor straw strength (weak straw). In fact, somewhat downstream from the *Rbcs-ABG2* interval, with a peak at *ABG19-ABC162*, Steptoe contributed a lodging susceptibility allele that did not correspond to a plant height effect. This information could provide for the basis for further, more rigorous analyses to separate the effects of plant height and straw strength on lodging. The only QTL effects for yield and related traits on the long arm of chromosome 2 were seen in the "R" data sets, where a favorable yield QTL allele from Steptoe had an overlapping WSI with height and lodging effects where Morex gave the larger value allele.

Chromosome 3

The hypothesis that Morex may contribute negative alleles for overall growth, perhaps in terms of longer and weaker internodes, is strengthened by the detection of QTLs on chromosome 3. Around the centromere of this chromosome, in the *Dor4a-ABG396* interval, Hayes et al. (1993) found the largest yield QTL, which accounted for a 734 kg ha^{-1} difference in QTL genotype means. The peak of the QTL has been seen to shift several intervals in either direction in additional analyses of this population in other environments (data not shown), but it is a consistent effect that has been detected in every row plot environment where this population has been grown and combine-harvested. That no yield QTLs were detected in this region in the Corvallis '92 data may again be attributable to the extra precautions taken at harvest. In the same or adjacent intervals, there were QTL effects for plant height, lodging, 1,000 kernel weight, spike length, and basal internode length. As on chromosome 2, Morex contributed all the larger value alleles for the plant growth traits and Steptoe contributed the favorable allele for kernel weight. Unlike chromosome 2, however, a QTL effect was detected for spike length but not for kernels per spike. Thus, this significant yield effect may be directly attributable to the propensity of genotypes with Morex alleles at key QTLs to be taller, more lodging susceptible, and to have longer spikes with longer basal internodes. This combination of phenotypes would be expected to be very detrimental to yield. Phenotypic selection for long spikes would obviously have a negative correlated effect on yield. Marker assisted selection for this

character, however, could be effective, as a favorable allele for spike length was detected downstream, with a peak at the *mPub-ABC 174* interval. This may account for the well-resolved yield QTL with a peak at *CDO113b-His4b* interval.

Chromosomes 4 and 5

The only yield or yield component effects detected on these chromosomes was a 1,000 kernel weight effect in the "R" data set, with a peak at the *Tubal-ABG3* interval on chromosome 4 (data not shown). Morex contributed the favorable allele.

Chromosome 6

No QTLs were detected on this chromosome from the Corvallis data, but Hayes et al. (1993) detected a yield QTL, with Morex contributing the favorable allele, on this chromosome, and this effect could be explained by the coincident height and lodging effects, where Steptoe contributed the larger value allele.

Chromosome 7

On chromosome 7, a negative relationship between grain yield and 1,000 kernel weight QTLs was detected. In the yield data set, Steptoe contributed a favorable allele for grain yield in the *Rm2-Ltp1* interval, while Morex contributed a favorable allele for kernel weight at the same position. A harvest index QTL, unrelated to plant height, with Steptoe contributing the favorable allele, was detected in an adjacent interval. Plant height and basal internode length QTLs were detected

elsewhere on the chromosome, with Morex again contributing the larger value alleles, but these effects did not correspond to yield QTLs in any of the analyses.

CONCLUSIONS

Evidence for yield component compensation and both positive and negative relationships among yield and related traits were detected at several points in the genome. On the short arm of chromosome 1, there was a negative association of QTLs for grain yield and tillers per meter. On chromosome 2, there was a negative association of kernels per spike with kernel weight and grain yield, and on chromosome 7 there was a negative relationship of 1,000 kernel weight and grain yield. Harvest index was always positively associated with grain yield, but a number of yield QTLs were not associated with harvest index. Thus, harvest index alone would not be an appropriate selection criterion. The principal determinants of grain yield in this germplasm appear to be lodging and basal internode length. The results of these QTL analyses indicate that indirect selection for grain yield via yield components may not be a productive allocation of resources. There may be negative associations between components and yield in a particular chromosome region, or yield may be determined by a factor other than the yield components, such as lodging or poor grain retention. The results of these QTL analyses, like the conventional approaches that preceded them, are necessarily limited to this germplasm and set of environments. However, having bracketed yield QTLs and to some extent determined the underlying biological basis of yield QTL effects in this germplasm sets the stage for determining the level of orthologous expression in other cross combinations. Furthermore, locating grain yield QTLs is particularly relevant when considering

simultaneous marker assisted selection for multiple traits, such as grain yield and components of grain quality.

Figure 1. Population frequency distributions for plant height, grain yield and yield components (a - h) from a population of 150 doubled haploid lines derived from the cross of Steptoe x Morex and evaluated near Corvallis in 1992.

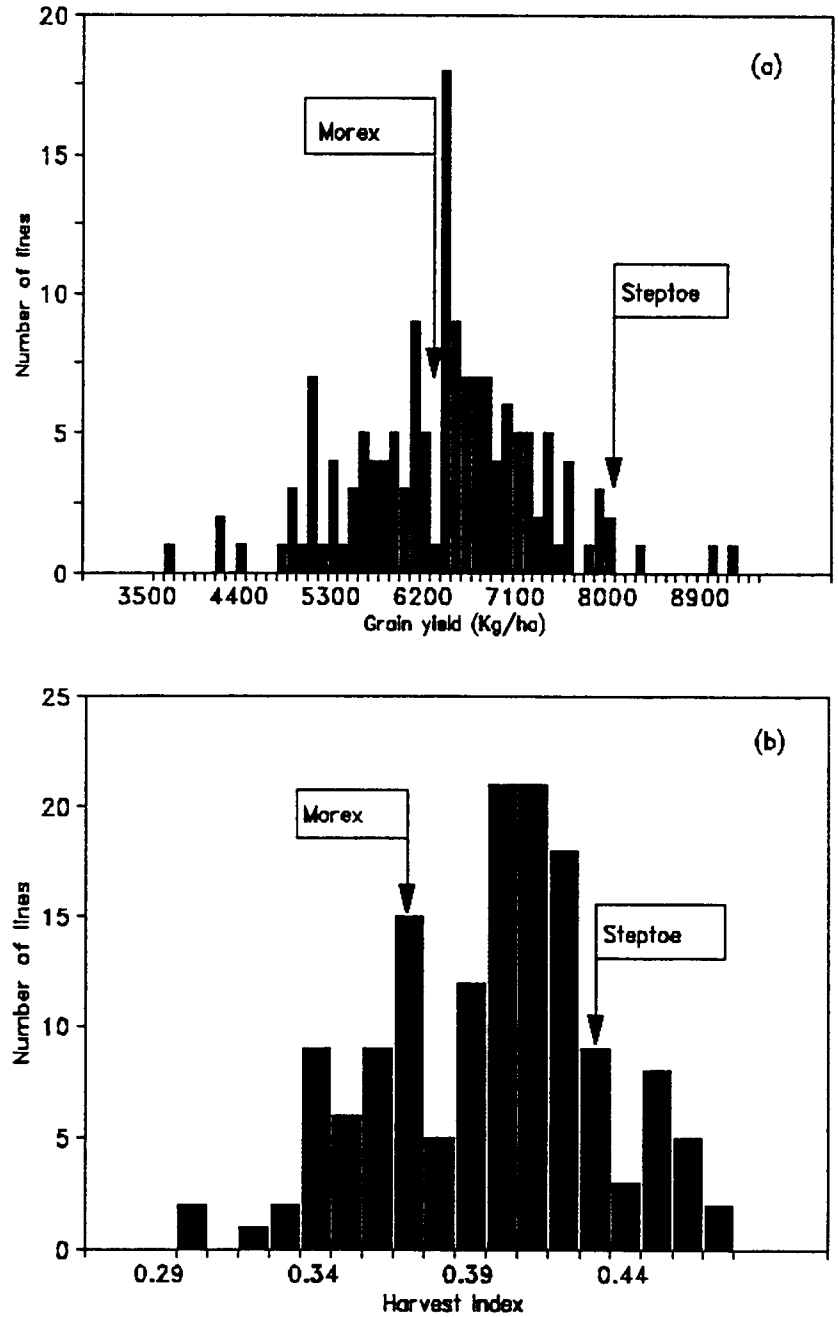

Figure 1, continued.

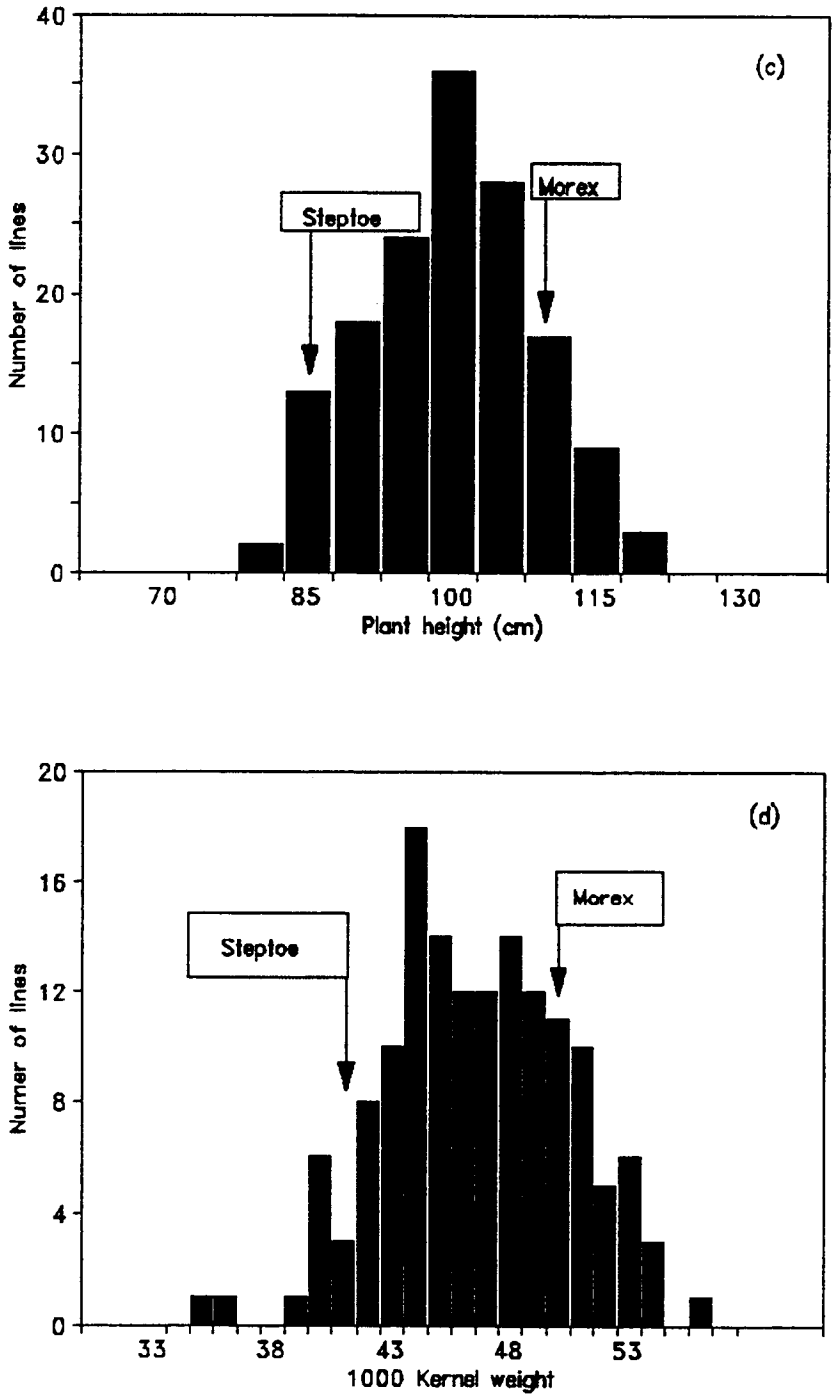

Figure 1, continued.

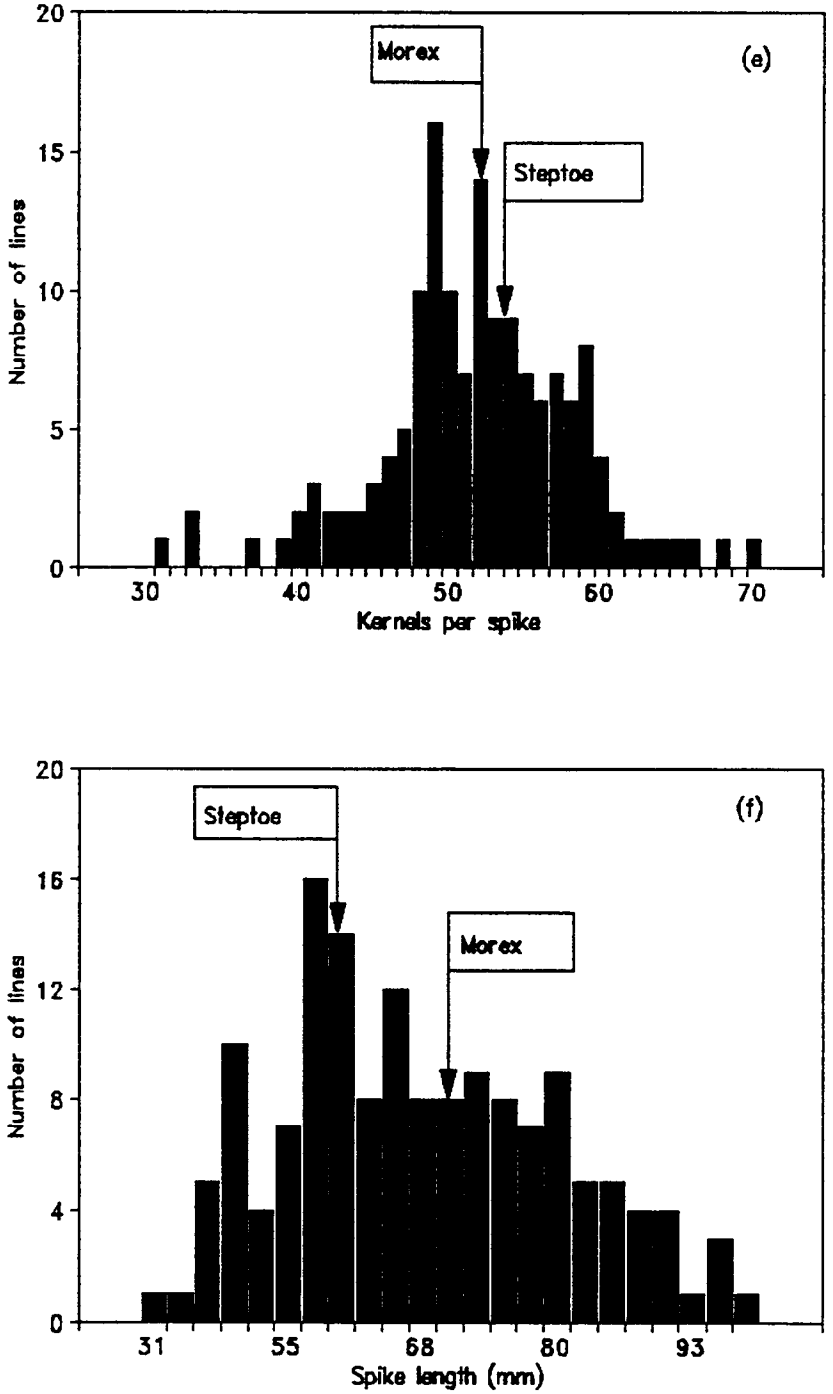

Figure 1, continued.

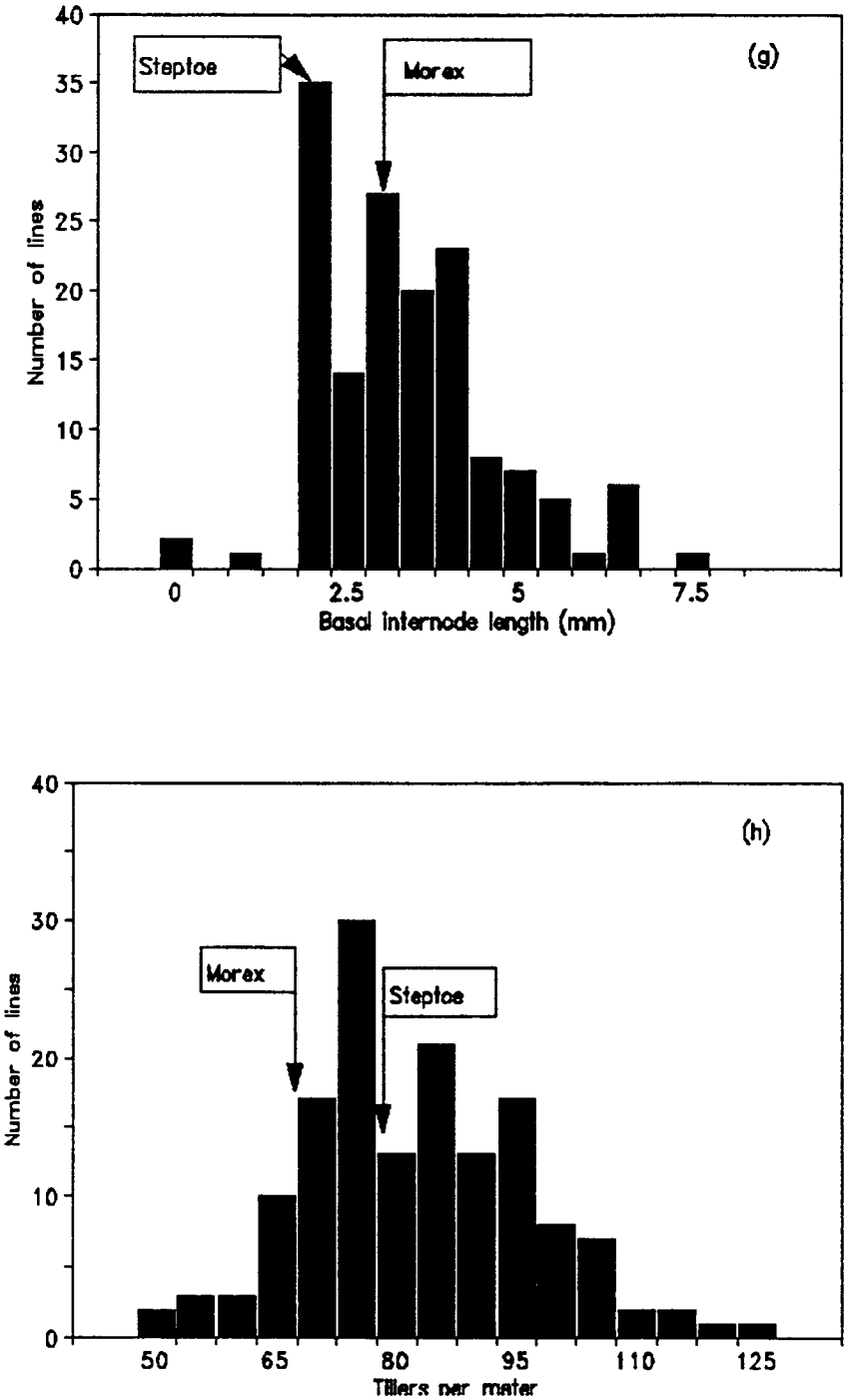

Table 1. QTL genotype differences for yield and yield components in a spring barley doubled haploid population evaluated in 1991 and 1992 where Wald $\geq$ 10. Environments are defined in the text. Values in bold type indicate Wald peaks. Adjacent values indicate the support interval. The letter suffix indicates the parent contributing the larger value allele; S = Steptoe; M = Morex. Marker intervals in bold type indicate centromere location.

Chromosome 1

Marker interval		% recom.	Yield	Yield R	Height	Height R	Lodging R	Harvest index	1,000 Kernel weight	1,000 Kernel weightR	Kernels per spike	Spike length	Tillers per meter	Basal internode length
			kg/ha	kg/ha	cm	cm	%		g	g		mm		mm
ABA301	-Plc	3.4				3S							3M	
Plc	-BCD129	7.5				3S							3M	
BCD129	-Glx	8.3				**3S**							7M	
Glx	-WG789a	5.5				3S							**8M**	
WG789a	-ABG380	4.9	273S	**354S**									5M	
ABG380	-ABC158	7.7	**470S**	301S									3M	
ABC158	-Ksua1a	6.1	409S	251S										
Ksua1a	-ABC154a	3.4	343S											
ABC154a	-Brz	7.3	321S											
Brz	-ABC156d	5.8	302S											
ABC156d	-ABG22a	12.8	265S		3S									
ABG22a	-ABG701	3.9			5S									
ABG701	-ABG11	4.4			5S									
ABG11	-ABC455	5.6			4S									
ABC455	**-Amy2**	6.9			4S		11S							
Amy2	-Ubi1	16.1	325S		**5S**		12S							
Ubi1	-ABC310b	4.0	348S		5S		**12S**							
ABC310b	-ABC305	6.7	317S		5S		10S							
ABC305	-PSR129	4.9	455S		5S		11S							
PSR129	-ABG461	13.0	513S		5S									
ABG461	-Cat3	19.7	**546S**		4S									

Table 1, continued.

Chromosome 2

Marker interval		% recom.	Yield	Yield R	Height	Height R	Lodging R	Harvest index	1,000 Kernel weight	1,000 Kernel weightR	Kernels per spike	Spike length	Tillers per meter	Basal internode length
			kg/ha	kg/ha	cm	cm	%		g	g		mm		mm
ABG313A	-ABG703	7.9									3.2M			0.5M
abg703	-Chs1B	11.0						0.02S			3.3M			0.6M
Chs1B	-ABG8	7.2						0.02S		0.8S	4.1M			0.6M
ABG8	-Rbcs	4.6		102S				0.02S		1.34S	4.4M			0.6M
Rbcs	-ABG2	11.5		263S	6M	8M		0.02S		1.13S	5.5M			0.8M
ABG2	-ABG459	9.0		222S	7M		5S	0.01S		0.90S	3.5M			0.7M
ABG459	-Pox	6.8		129S	6M		6S	0.02S						0.6M
Pox	-Adh8	5.5			5M		6S	0.02S						0.8M
Adh8	-ABG19	11.7					9S							0.8M
ABG19	-ABC162	6.6					11S							0.7M
ABC162	-ABG14	8.3					6S							0.7M
ABG14	-His3c	10.3		220S										0.7M
His3c	-Ksu15	11.9		107S										0.7M
Ksu15	-Crg3a	22.1		266S										0.7M
Crg3a	-Gln2	16.4		149S			9M							0.5M
Gln2	-ABC157	7.4		187S		4M	9M							
ABC157	-ABC165	7.4		199S		5M	11M							
ABC165	-Pcr1	7.5		198S		4M	12M							
Pcr1	-ABA5	8.6		160S			12M							

Table 1, continued.

Chromosome 3

Marker interval		% recom.	Yield	Yield R	Height	Height R	Lodging R	Harvest index	1,000 Kernel weight	1,000 Kernel weightR	Kernels per spike	Spike length	Tillers per meter	Basal internode length
			kg/ha	kg/ha	cm	cm	%		g	g		mm		mm
ABA303	-ABC171	23.0							2.3S					
ABC171	-ABG57	13.5							2.0S					
ABG57	-ABG471	3.6							1.8S					
ABG471	**-Dor4a**	**19.8**		**443S**	**9.81M**				**2.7S**					**1.74M**
Dor4a	-ABG396	6.4		**734S**	9.06M	**8M**	**30M**		1.7S			**16.4M**		1.60M
ABG396	-ABG703a	9.4		737S					1.7S					
ABG703a	-PSR156	9.3		723S					2.1S					
PSR156	-ABG377	7.6							1.0S					
ABG377	-ABG453	10.5												
ABG453	-ABC307b	10.2												
ABC307b	-CDO113b	12.3												
CDO113b	-His4b	16.9		**519S**										
His4b	-ABG4	14.1										3.2S		
ABG4	-mPub	7.3										5.2S		
mPub	-ABC174	13.4										**7.0S**		
ABC174	-ABC166	11.6										2.5S		
ABC166	-ABC172	11.0												

Table 1, Continued.

Chromosome 6

Marker interval		% recom.	Yield	Yield R	Height	Height R	Lodging R	Harvest index	1,000 Kernel weight	1,000 Kernel weightR	Kernels per spike	Spike length	Tillers per meter	Basal internode length
			kg/ha	kg/ha	cm	cm	%		g	g		mm		mm
PSR167	-Nar1	6.3												
Nar1	-ABG378	5.2												
ABG378	-Cxp3	9.0												
Cxp3	-PSR106	16.7												
PSR106	-ABG387B	4.5												
ABG387B	-ABG458	14.5		299M										
ABG458	-Rm1	6.3		311M										
Rm1	-ABG474	7.1		368M		1S								
ABG474	**-KsuD17**	4.1		371M		1S								
KsuD17	-Ksua3d	7.3		**386M**		2S	**13S**							
Ksua3d	-Nar7	8.7		321M		**2S**	12S							
Nar7	-Nir	5.5				2S								
Nir	-Psr154	12.3												

Table 1, continued.

Chromosome 7

Marker interval		% recom.	Yield	Yield R	Height	Height R	Lodging R	Harvest index	1,000 kernel weight	1,000 Kernel weightR	Kernels per spike	Spike length	Tillers per meter	Basal internode length
			kg/ha	kg/ha	cm	cm			g	g		mm		mm
ABC483	-ABG705	27.6	278S					0.02S						
ABG705	-ABG395	7.9	469S					0.02S		1.03M				
ABG395	-Rrn2	3.6	553S					0.02S		1.20M				
Rrn2	**-Ltp1**	4.5	**607S**					0.02S		**1.40M**				
Ltp1	-ABC706	5.8	574S					**0.02S**		1.01M				
ABC706	-Ale	5.4	376S		2.52M			0.02S		**1.40M**				
Ale	-ABC302	10.1			3.37M			0.02S		1.37M				
ABC302	-CDO57b	13.0			**5.39M**			0.01S		1.14M				
CDO57b	-mSrh	5.4			4.88M	**4M**								
msrh	ABG473	6.5			3.65M									
CDO504	-WG908	7.7												**0.9M**
WG908	-ABG495a	8.8												0.8M
ABG495a	-ABG496	6.2												0.8M
ABG496	-ABC482	7.4												0.7M
ABC482	-ABG707	7.2												
ABG707	-ABG463	9.1												
ABG463	-ABA304	8.6												

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