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AB-QTL analysis for two populations of winter barley sharing the donor of *Hordeum vulgare* ssp. *spontaneum*

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To my *memorable years* in Bonn

难忘**Bonn**岁月

Abstrakt (in Deutsch)

Die Ziel des vorliegenden Projekts war, vorteilhafte exotische QTL-Allele für die Verbesserung der agronomischen Leistung, der Krankheitsresistenz und der unspezifischen Blattflecken in zwei BC_2DH-Populationnen zu ermitteln, die aus den Kreuzungen der beiden deutschen Wintergerstesorten Carola und Theresa (*Hordeum vulgare* ssp. *vulgare,* im folgenden mit *Hv* abgekürzt) mit der Wildgersten-Akzession ISR101-23 (*Hordeum vulgare* ssp. *spontaneum*, im folgenden mit *Hsp* abgekürzt) aus Israel abgeleitet wurden. Die zwei BC_2DH-Populationen (benannt C101 und T101) wurden mit 82 und 78 SSR-Markern genotypisiert. C101 und T101 bestanden aus 282 und 104 BC_2DH-Linien. Insgesamt 16 agronomische Merkmale, vier Krankheitsresistenzen sowie unspezifische Blattflecken wurden an bis zu sechs unterschiedlichen Umwelten und über zwei Jahre ausgewertet. Die QTL-Analyse wurde mit einer 3-faktoriellen ANOVA durchgeführt, mit dem Marker als fixen Effekt, der Linie geschachtelt in Markergenotyp, der Umwelt und den entsprechenden Interaktionen als zufällige Effekte. In C101 wurden 35 vorteilhafte exotische QTL-Effekte aus 183 putativen QTLs für 10 agronomische Merkmale, vier Krankheitsresistenzen und unspezifische Blattflecken ermittelt. Unter den vorteilhaften exotischen QTLs wurden 22 (19,1 %) vorteilhafte QTL-Effekte für agronomische Merkmale, und 13 (19,1 %) für Krankheitsresistenzen und unspezifische Blattflecken identifiziert. Ein crossover QTL-Effekt des *Hsp*-Alleles auf Ertrag, ermittelt auf Chromosom 6H in C101, war mit einer Ertragszunahme von 8,2 %, gemittelt über drei Umwelten, verbunden (Table 17). Allerdings war der *Hsp*-Effekt in den restlichen zwei Umwelten mit einer Ertragsabnahme von 4,6 % assoziert. Die Symptome für Zwergrost, Netzflecken, Mehltau, *Rynchosporium* und unspezifische Blattflecken wurden in C101 durch exotische Allele an den QTLs *QlrC101-3H, QnbC101-6Hd*, *QpmC101-2H*, *QrhC101-7Ha* und *QnpbC101-5Ha* um 26,2 %, 20,8 %, 17,8 %, 4,9 % beziehungsweise 14,9 % reduziert. In T101 wurden 85 putative QTLs für elf agronomische Merkmale, Krankheitsresistenzen und unspezifische Blattflecken entdeckt. Der exotische Genotyp verbesserte die Leistung bei 13 (18,6 %) von 70 QTLs, die für agronomische Merkmale ermittelt wurden (Table 19). Insgesamt 39 putative QTLs, die in C101 ermittelt wurden, wurden durch 40 QTLs in T101 bestätigt. Von 268 putativen QTLs und 48 vorteilhaften exotischen Effekten, die in beiden Populationen gefunden wurden, konnten 65 (24,3 %) QTLs beziehungsweise 21 (43,6 %) vorteilhafte exotische Effekte in anderen QTL-Analysen der Gerste wiedergefunden werden. Ungefähr 64 % der vorteilhaften exotischen QTL-Allele, die in dieser Studie identifiziert wurden, konnten nicht in anderen Studien der Gerste ermittelt werden. Diese vorteilhaften *Hsp*-Allele könnten daher neue Allele sein.

Abstract (in English)

The objective of the present study was to detect favourable exotic QTL alleles for the improvement of agronomic traits, pathogen resistance and non-parasitic browning in two BC_2DH populations derived from the crosses of two German winter barley varieties, Carola and Theresa (*Hordeum vulgare* ssp. *vulgare,* in the following abbreviated *Hv*), with the wild barley accession ISR101-23 (*Hordeum vulgare* ssp. *spontaneum,* in the following abbreviated *Hsp*) from Israel. The two BC_2DH populations (termed C101 and T101) were genotyped with 82 and 78 SSR markers, respectively. C101 and T101 consisted of 282 and 104 BC_2DH lines, respectively. Sixteen agronomic traits, four pathogen resistances and the non-parasitic browning were evaluated at up to six different locations and in two consecutive years. QTL analysis was carried out with a three-factorial ANOVA including the marker as fixed effect and the environment and lines nested in the marker genotype as well as the respective interactions as random effects. In addition, cold damage (COD) and neighbouring plots of the seriously cold-damaged plots (N) were used as co-variables for those traits which were significantly affected by COD and N. In C101, 35 favorable exotic QTL effects out of 183 putative QTLs were detected for ten agronomic traits, four pathogen resistances and non-parasitic browning. Among these putative QTLs, 22 (19.1 %) of 115 QTLs detected for agronomic traits exhibited favorable effects and 13 (19.1 %) of 68 QTLs identified for disease resistances and non-parasitic browning were associated with improvements. A crossover interaction QTL effect of the *Hsp* allele on yield, detected on chromosome 6H in C101, was associated with a yield increase of 8.2 % averaged across three environments. However, in the remaining two environments the *Hsp* effect was associated with a yield reduction of 4.6 %. In addition, favourable effects of exotic alleles were detected for all pathogen resistances and non-parasitic browning in this study. For instance, the symptoms of leaf rust, net blotch, powdery mildew, scald and non-parasitic browning symptoms at *QlrC101-3H, QnbC101-6Hd*, *QpmC101-2H*, *QrhC101-7Ha* and *QnpbC101-5Ha* were reduced by 26.2 %, 20.8 %, 17.8 %, 4.9 % and 14.9 % in C101, respectively (Table 17). In T101, 85 putative QTLs were discovered for eleven agronomic traits, four pathogen resistances and non-parasitic browning. The exotic genotype improved the performance at 13 (19.4 %) of 67 QTLs detected for agronomic traits and no favorable QTL effect was identified for disease resistances and non-parasitic browning in T101 (Table 19). Thirty-nine putative QTLs detected in C101 were confirmed by 40 QTLs detected in T101. Altogether, 65 (24.3 %) QTL effects among 268 putative QTLs localized in both populations and 21 (43.8 %) favorable QTL effects among 48 favorable QTL effects identified in both populations were verified in other barley QTL and linkage analyses. About 56 % favorable exotic QTL alleles identified in this study were so far not detected in other barley QTL studies. These favorable *Hsp* alleles may be new alleles.

INHALTSVERZEICHNIS

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1. Introduction

At the beginning of the 20th century, Mendel's laws (1865) were re-discovered by Correns, Tschermak and de Vries. Following Mendel's law, geneticist studied the inheritance of organisms by differentiating phenotypes of organisms (morphological or physiological characteristics) into different traits. However, a lot of traits exhibited continuous variation of phenotypes in a population and could not be distinctly classified (Kappert 1948). These traits are controlled by multiple genes, each segregating according to Mendel's laws. In addition, these traits can also be affected by the environment to varying degrees. Geldermann (1975) defined the multiple genes which control the continuous traits as 'quantitative trait loci' (QTL).

Most traits of agronomic importance, including yield, nutritional quality and stress tolerance, are quantitatively inherited. The ability to manipulate genes responsible for quantitative traits is a prerequisite for sustained improvement of crop plants (Allard 1960; Hallauer and Miranda 1988; Tanksley and Nelson 1996). Therefore, it is very important to study QTL for improving the traits of crop plants.

As we head into the next millennium, the world faces a greater demand on agricultural output than at any time in history. Despite efforts to curb birthrates, the Earth's human population is expected to rise to 8.9 billion by the year 2030, corresponding to a more than 50% increase from the current population of 5.7 billion (Brown 1994, Tanksley and McCouch 1997). In the past, we have met the demand for increased agricultural productivity by a combination of genetic improvements, greater farming inputs (fertilizers, pesticides, and water), and cultivation of more land. With dwindling freshwater reserves and petroleum resources (on which fertilizers and pesticides are based) and increased problems caused by agricultural pollution, we can hardly expect to increase or even maintain our current levels of agricultural inputs. Similarly, much existing farmland is falling victim to urban expansion, and it is unlikely that new farmland will become available in the near future. That leaves the genetic improvement of crops as the most viable approach by which food production can attempt to keep pace with the anticipated growth of the human population (Tanksley and McCouch 1997).

All crop species were originally domesticated from wild plants by humans – a process that inherently reduced genetic variation (Simmons 1976, Ladizinsky 1985). Although the exact series of steps by which plants were domesticated is unknown, it is likely that strong selection pressure exerted by humans on the genetic diversity found in the wild resulted in rapid and radical changes in plant species (Vavilov 1940). Certain traits would have been selected by early agriculturists, for instance, nonshattering of seeds, compact growth habit, or loss of germination inhibition, and so on (Harlan 1975). Selective propagation of lines containing these favourable mutations would have

resulted in a progressive narrowing of the genetic base of subsequent populations (Tanksley and McCouch 1997).

Following domestication, the genetic variation in crop plants has continued to be reduced by another force—modern plant breeding. Over the past century, the development and successful application of plant breeding methodologies has produced the high-yielding crop varieties on which modern agriculture is based. Yet, ironically, it is the plant-breeding process itself that threatens the genetic base on which breeding depends. Because new varieties are usually derived from crosses among genetically related modern varieties, genetically more variable but less productive primitive ancestors are excluded (Duvick 1977; Harlan 1987; Tanksley and McCouch 1997).

Intensive breeding of crop varieties by modern science has further narrowed the gene pool in many crops. This problem is especially acute in self-pollinated crops where the level of genetic variation in cultivated varieties is often a small fraction of that available in nature (Miller and Tanksley 1990; Tanksley and Nelson 1996). Soybeans and wheat are good examples of crops with very narrow genetic bases. Virtually all modern U.S. soybean varieties can be traced back to a dozen strains from a small area in north-eastern China, and the majority of hard red winter wheat varieties in the United States originated from just two lines imported from Poland and Russia (Duvick 1977; Harlan 1987).

The limited genetic diversity of crops renders them more vulnerable to disease and insect epidemics and jeopardizes the potential for sustained genetic improvement over the long term (Harlan 1975). The narrowed gene pool led to the outbreak of Southern corn leaf blight in 1970. This disease drastically reduced corn yields in the United States and was attributed to an extensive use of a single genetic male sterility factor that, unfortunately, was genetically linked to disease susceptibility (Tanksley and McCouch 1997). Reduced genetic variation is likely to have another subtle effect: a slower rate of crop improvement by plant breeders. The lower the genetic variation in breeding populations, the less likely breeders are to identify new and useful combinations of genes (Tanksley and Nelson 1996).

For the genetic approach to succeed, we must harness the wealth of genetic variation provided by nature and currently warehoused in our seed repositories. Until now we have been only modestly successful in utilizing these resources for plant improvement. New findings from genome research indicate that there is a tremendous genetic potential locked up in seed banks that can be released only by shifting the paradigm from searching for phenotypes to searching for superior genes with the aid of molecular linkage maps (Tanksley and McCouch 1997).

1.1 Taxonomy and origin of barley

Cultivated barley (*Hordeum vulgare* ssp *vulgare*, in the following termed *H. vulgare* or abbreviated *Hv*) belongs to the tribe *Triticeae* in the grass family, *Poaceae*. The *Triticeae* is a temperate plant group and is distributed over most areas of the world but with a main centre in Central and South-western Asia (Bothmer 1992). The *Poaceae* is the largest family of monocotyledonous plants. The taxon *Hordeum* comprises about 30 species. The genetic circumscription of *Hordeum* has been rather stable over the years and most scientists agree on the species content of the genus. However, there has been a suggestion to separate the cultivated barley, *H. vulgare* together with *H. bulbosum* into a genus of its own (*Hordeum* in a narrow sense), but this view has not been widely accepted because this view does not reflect the actual relationship (Bothmer 1992). The progenitor of barley is considered to be a subspecies of cultivated barley: *H. vulgare* ssp. *spontaneum* (C. Koch) Tell (in the following termed *H. spontaneum* or abbreviated *Hsp*). Both cultivated and wild barley have winter and summer annual forms. According to spike morphology, barley can be divided into two-rowed and six-rowed types; however, intermediate types do exist. In two-rowed barley the lateral spikelets are female sterile, while in six-rowed barley all spikelets are fertile (Briggs 1978).

About the origin of barley, there are two hypothesises. The most widely accepted hypothesis on the origin of cultivated barley defines the Fertile Crescent as its centre of origin (Harlan 1976). Remains of barley (*H. vulgare*) grains found at archaeological sites in the Fertile Crescent indicate that about 10,000 years ago the crop was domesticated there from its wild relative *H. spontaneum* (Badr et al. 2000). A hypothesis of multicentric origin of barley has also been proposed (Molina-Cano *et al*. 1999). The results from cDNA analysis suggests that barley has been taken into cultivation more than once, but that only very few domestication events have occurred (Zohary 1969, Neale *et al.* 1988). ALFP fingerprint analysis indicated that the Israel-Jordan area is the region in which barley was brought into culture, and the Himalayas can be considered a region of domesticated barley diversification (Badr et al. 2000).

Barley is a self-pollinating diploid with 2n = 2x = 14 chromosomes (Bothmer 1992). Consequently, its variation is structured in true breeding lines. In contrast to wild barley, all cultivars have non-brittle ears, and the spike stays intact after ripening and is harvested and threshed by humans. However, the wild barley forms always have brittle ears. Non-brittleness in cultivated barley is governed by a mutation in either one of two tightly linked 'brittle' genes (*Bt1, Bt2*). The brittle wild-type allele of each locus is dominant, whereas, the non-brittle alleles are recessive. Many cultivars are homozygous for both recessive mutations. Others carry only one mutation (Takahashi 1972). The Non-brittle mutation survived only under domestication.

The wild ancestor of the cultivated barley is well known. The crop shows close affinities to a group of wild and weedy barley forms which are traditionally grouped in *H. spontaneum* C. Koch, but which are, in fact, the wild race or subspecies of the cultivated crop. The correct name for this wild form is therefore *H. vulgare* L. ssp. s*pontaneum* (C. Koch); Tell (Zohary and Hopf 1993). These are annual, brittle, two- rowed, diploid (2n = 14), predominantly self-pollinated barley forms and the only wild *Hordeum* stock that is cross compatible and fully interceptive with the cultivated barley. *H. vulgare* x *H. spontaneum* hybrids show normal chromosome pairing and segregation during meiosis (Nevo 1992). Morphologically, the differences between wild *H. spontaneum* and cultivated two-rowed barley are rather minor. They differ mainly in their modes of seed dispersal. The cultivated forms have a tough rachis that does not break even on threshing, while the wild forms have a brittle rachis that disarticulates at maturity into individual units each containing one seed and two sterile lateral spikelets. These are highly specialized devices, which ensure the survival of the plant under wild conditions. Under cultivation this specialization broke down and non-brittle mutants were automatically selected for in the man-made system of sowing, reaping and threshing (Harlan and Zohary 1966; Zohary 1969).

The genetic affinity between the cultivated barley and wild *H. spontaneum* is also indicated by spontaneous hybridizations that occur sporadically when wild and cultivated forms grow side by side. Some of such hybridization products, combining brittle ears and fertile lateral spikelets, were in the past erroneously regarded as genuinely wild types and even given a specific rank (*i.e. H. agriocrithon* Åberg). Extensive isozyme, seed storage proteins, and DNA tests have already been carried out in barley (Nevo 1992). The results confirm the close relationships between the wild and cultivated entities grouped in the *H. vulgare* complex. They also clearly show that genetic diversity in *H.* s*pontaneum* is much wider than that present in the cultivated gene pool. *H.* s*pontaneum* is spread over the East-Mediterranean basin and West Asia, penetrating as far as Turkmenia, Afghanistan, Ladakh, and Tibet. Wild barley occupies primary habitats and man-made habitats. Its centre of origin lies in the 'fertile crescent', starting from Israel and Jordan in the Southwest, stretching North towards South Turkey and bending Southeast Iraq and Southwest Iran. In this area, wild *H. spontaneum* is continuously and massively distributed. It constitutes an important annual component of open herbaceous formations, and it is particularly common in the summer-dry deciduous oak park-forest, East, North, and West of the Syrian Desert and the Euphrates basin, and on the slopes facing the Jordan Rift Valley. From here, *H. spontaneum* spills over the drier steppes and semi-deserts. In the Near Eastern countries, wild barley also occupies a whole array of secondary habitats, *i.e.* opened-up Mediterranean marquis, abandoned fields, and roadsides. It also infests cereal cultivation and fruit tree plantations (Harlan and Zohary 1966;

Manninen 2000). Further west, in the Aegean region, the Mediterranean shore of Egypt and Cyrenaica and further East in Northeast Iran, Central Asia and Afghanistan, wild *H. spontaneum* is much more sporadic in its distribution; it rarely builds large stands and seems to be completely restricted to segetal habitats, ruins, or to sites which have been drastically churned by human activity. In general, wild barley does not tolerate extreme cold and it is only occasionally found above 1500 m. It is almost completely absent from the elevated continental plateaus of Turkey and Iran. On the other hand, it is somewhat more drought tolerant than the wild wheat and penetrates relatively deep into the warm steppes and deserts (Zohary and Hopf 1993).

1.2 The barley genome

Bennett and Smith (1976) estimated that barley contains around 5.5 picograms of DNA per haploid genome, equivalent to approximately 5.3×10^9 bp. In barley, as in other cereals, the genome consists of a complex mixture of unique and repeated nucleotide sequences (Flavell 1980). The interspersed *copia*-like retrotransposon *BARE*-1 comprises almost 7 % of the barley genome (Manninen and Schulman 1993). Rimpau et al. (1980) reported that approximately 10-20 % of the barley genome is of tandemly arranged repeated sequences while 50-60 % is of repeated sequences interspersed among one another or among unique nucleotide sequences. According to the estimates from Miklos and Rubin (1996), the gene number in higher plants varies between 25,000 and 43,000. Grass genomes seem to contain regions that are highly enriched with genes with very little or no repetitive DNA (Feuillet and Keller 1999, Barakat et al. 1997). In barley, a gene density of one gene per 123-212 kb can be expected if genes are distributed equidistantly (Panstruga et al. 1998). However, Panstruga et al. (1998) found three genes on a 60 kb stretch of DNA around the powdery mildew resistance locus, *mlo*. Feuillet and Keller (1999) found five genes on a 23 kb stretch of around the receptor-like kinase gene *Lrk10* in wheat.

1.3 Cultivation and use of the barley crop

Barley is one of the founder crops of the old world agriculture (Badr et al. 2000) and a crop of worldwide importance (Matus et al. 2003). Cultivated barley is a short season, early maturing cereal with a high yield potential, and may be found on the fringes of agriculture, in widely varying environments (Harlan 1976). All over the area, barley is a universal companion of wheat, but in comparison with the latter it is regarded as an inferior staple and the poor people's bread. But barley is adapted to drier conditions, poorer soils and extent of some salinity. Because of these qualities, it has been the principal cereal produced in numerous areas and an important element of the human diet. Barley is also the main cereal used for beer fermentation in the old world. The preparation of

this beverage seems to be a very old tradition. The crop was, and still is an important feed supplement for domestic animals (Samuel 1996; Mohammed 2004).

The barley grain is used to make malt, which in turn is used to make beer, whisky and some other products. In Western countries most barley grain is used to feed farm animals – cattle, sheep, goats, pigs, horses and poultry. In Eastern countries large quantities of barley are used in human food and drink (Briggs 1978).

After maize, rice and wheat, barley ranks as the fourth most important crop in the world. The annual world production of barley amounts to 141,503,090 million tons (FAO, 2003).

In Germany, the average barley yield progressed from 43 dt/ha to approx. 59 dt/ha in the last 20 years. In 2000, approx. 12 million tons of barley was harvested, with 9 million tons used as a feed. A tenth of the barley world production, mainly summer barley, is used as malt for beer and whisky. The smallest portion serves directly for human nutrition in the form of barley grains (Zacharias 2001).

Winter barley is mainly distributed in North American, Australia and Europe. Winter barley is one of the most important fodder crops in the world. Likewise, winter barley is an important material for the brewing industry. Hayes et al. (2002) reported that winter barley offers the U.S. malt industry a new source of supply and Pacific Northwest growers an alternative crop. Winter malting barley is an option to the weather- and disease-related risks of spring barley in the upper Midwest, weather-related risks and variable quality in western dry land spring barley, and to the cost of western irrigated spring barley (Hébrard 1998). In France, 40 % of the total production of malt belongs to winter barley (Hébrard 1998). According to Anonym (2001), two-row winter barley is fully accepted by the malting industry in England. The main reason for using winter barley is the 20-30% higher yield and the lack of significant differences in malting quality parameters in comparison to spring barley (Spunar et al. 2002).

1.4 Barley breeding

The strategy of the crop breeder is to build into the cultivar a superior genetic potential for yield, protection against production hazards, and improved quality. The specific characteristics desired will, of course, vary with the particular crop species, the climate in which it will be grown, the cultural practices to be used, the utility of the product, traditional preparation methods, and many other factors (Harlan 1975).

Breeding new barley varieties is based on creating new allele combinations and subsequent testing and selection of the desirable phenotypes during the selfing generations. Heritable variation

is created mainly by controlled crosses between adapted high yielding cultivars and breeding lines (Manninen 2000). Although variety breeding is based on elite germplasm, specific traits may be introgressed from wild barley and landraces in backcrossing programs (Nevo 1992). Spontaneous mutations, as well as mutations induced by radiation or chemical treatments, have also been used (Briggs 1978). Recently, transgenetics has been added to the tools for creating new variation in barley (Ritala et al. 1994, Wan and Lemaux 1994).

Following the goal of different breeding projects, the selection for desirable traits is made both in the field and in the laboratory. In the field, agronomical characters including earliness, plant height, lodging resistance and disease resistance are evaluated. After harvest, yield, thousand-grain weight, hectoliter weight and grading are measured as well as the protein content of the grain. Selection for specific traits is done during the selfing generations starting from the F_2 generation. In a breeding program several traits have to be considered simultaneously to reach the desired agronomical type (Manninen 2000).

Plant breeders need to predict the potential value of crosses in breeding programmes at the earliest opportunity to discard inferior combinations (Pickering and Devaux 1992). However, the early generations following the crosses are highly heterozygous, making reliable selection difficult until an acceptable level of homozygosity is reached. Doubled haploid lines could avoid those problems caused by heterozygosity in the early generations in barley. As few as 20 doubled haploids produced from early generation hybrids were required for this, after assessing yield in hill plots (Reinbergs et al. 1976). More doubled haploids could then be produced from superior hybrid combinations. However, Bjornstad and Aastveit (1990) pointed out that lager numbers of doubled haploids would be needed to obtain this result in cases where there are negative pleiotropic effects on the mean of a character. Doubled haploid lines can be produced either from immature pollen grains by anther or microspore culture, or through interspecific crosses between barley and *H. bulbosum* with subsequent chromosome elimination. Both methods are used in commercial barley breeding programs and several doubled haploid varieties have been released (Pickering and Devaux 1992).

1.5 DNA markers in barley breeding

In this chapter, DNA markers, linkage maps and QTL analysis are presented for barley.

1.5.1 DNA markers

The advantages of DNA markers include their ability to reveal the sites of variation in DNA segments, their abundance compared to phenotypic markers, and their immunity to genotype by environment interactions.

Markers differ from each other in many respects: the initial workload and costs for building up the marker system, running costs and ease of use, level of polymorphisms, dominance, number of loci analyzed per assay, reproducibility and distribution on the chromosomes. Detection of polymorphism at the DNA level is usually based either on restriction patterns or differential amplification of DNA. The choice of the best marker system depends on whether it will be used in evolutionary or population studies, genetic mapping or fingerprinting (Manninen 2000).

Table 1: Comparison of different DNA-marker systems. Modified from Rafalski and Tingey (1993), Kalendar et al. (1999), Ridout and Donini (1999) and Manninen (2000).

	RFLP	RAPD	SSR	AFLP	SNP
Principle	Restriction, southern blotting, hybridization	DNA amplification with random primers	PCR of simple sequence repeats	Restriction, ligation of adapters, selective PCR	Detection of single base substitution
Type of polymorphisms	Single base changes, insertions, deletions	Single base changes, insertions, deletions	Changes in number of repeats	Single base changes, insertions, deletions	Single base changes
Level of polymorphisms	High	Medium	Very high	Medium	Low
Inheritance	Codominant	Dominant	Codominant	Dominant	Codominant
Number of loci analyzed per assay	1-2	5-10	1	100-150	1-10,000
DNA required per assay	2-10 µg	20 ng	50 ng	0.5-1.0 µg	20 ng
Sequence information required	No	No	Yes	No	Yes
Development costs	High	Low	High	Medium	High
Running costs per assay	Medium	Low	Medium	Medium	Low
Repeatability	Very high	Low	Very high	High	Very high
Ease of use	Labour intensive	Easy	Easy	Difficult initially	Easy

The use of molecular markers to enhance plant breeding efforts is being widely studied. A major area of research is the use of molecular markers to identify and manipulate QTLs controlling quantitative traits (Dudley 1993). With the use of molecular techniques, it is possible to hasten the transfer of desirable genes among varieties and to introgress novel genes from related wild species.

Polygenic characters which were previously very difficult to analyse using traditional plant breeding methods, are now easily tagged using molecular markers (Mohan et al. 1997). Up to now, many DNA markers, such as random-amplified polymorphic DNAs (RAPDs), restriction fragment length polymorphisms (RFLPs), simple sequence repeats (SSRs)/microsatellites, sequence-tagged sites (STS), amplified fragment length polymorphic DNAs (AFLPs) and single nucleotide polymorphisms (SNP) using F_2 and back-cross populations, near-isogenic lines, doubled haploids and recombinant inbred lines, are used for marker-assisted selection (MAS) in plant breeding (Table 1).

1.5.1.1 Restriction fragment length polymorphism (RFLP)

Restriction fragment length polymorphism (RFLP) was first used for creating a linkage map in human by Botstein et al. (1980) and the first applications in plant breeding were proposed by Burr et al. (1983). RFLPs are visualized after Southern blotting (Southern 1975) by hybridization to labelled DNA probes and subsequent autoradiography. If two organisms differ in the distance between sites of cleavage of a particular restriction endonuclease, the length of the fragments after restriction will differ. Differences in the restriction patterns are caused by single nucleotide mutations at the restriction site or by longer deletions/insertions between restriction sites. A genomic or cDNA library is needed as a source of single or low copy probes. RFLP probes are useful as anchor markers for comparative studies within or between species and have been used for comparative mapping in the grass genera (Van Deynze et al. 1998). Cloned genes with a function related to the trait of interest, and thus representing candidate genes, may be used as probes in mapping (Faris et al. 1999). RFLP markers were intensively used for the construction of polymorphisms map (Heun et al. 1991; Graner et al. 1991; Kleinhofs et al. 1993; Graner et al. 1994) or QTL mapping in barley (Bezant et al. 1997; Chetelat and Meglic 2000; Vaz Patto et al. 2003).

1.5.1.2 Random Amplified Polymorphic DNA (RAPD)

Random amplified polymorphic DNA (RAPD) was used as a new DNA marker in polymorphism assays by Williams et al. (1990). To amplify template DNA, RAPD uses a single primer of 10 nucleotides length in a polymerase chain reaction (PCR, Mullis and Falcoona 1987). These polymorphisms, simply detected as DNA fragments which amplify from one parent but not the other, are inherited in a Mendelian fashion and can be used to construct genetic maps in a variety of species (Williams et al. 1990). Relative to RFLP, the large merit of RAPDs is that the radioactivity is avoided during the detection of polymorphism in the laboratory (Deragon and Landry 1992). RAPDs are useful genetic markers due to the fact that the polymorphisms among the

amplification products are detected frequently, and can be detected through examination of an ethidium bromide-stained agarose gel, in other words, they are cheap to produce (Gu et al. 1998). In addition, the overall genome screen may be easy and fast because each RAPD analysis simultaneously screens several loci (Williams et al. 1990). The disadvantage is that the reproducibility of RAPDs can be low. Also, RAPDs are dominant, whereas RFLPs are co-dominant. Therefore, RAPDs provide only half the information of codominant markers in genetic crosses. Even if RAPD markers have some disadvantages for genetic analysis, they still play a very important role in constructing genetic maps, single gene and QTL mapping and in studies of genetic diversity (Barua et al. 1993; Kleinhofs et al. 1993; Gu et al. 1998; Nevo et al. 1998; Scheurer et al. 2001).

1.5.1.3 Sequence Tagged Sites (STSs)

A sequence Tagged Site (STS) is a unique, single-copy segment of the genome whose DNA sequence is known and which can be amplified by specific PCR. When STS loci contain DNA length polymorphisms (*e.g.* simple sequence length polymorphisms, SSLPs), they become valuable genetic markers (Olson et al. 1989). The main advantage of STS loci lies in the speed with which they can be analyzed once PCR primer pairs have been identified. Like RFLP loci, STS loci can be analyzed as co-dominant genetic markers and can in theory, be studied in closely related species, provided that the DNA sequence is conserved at the PCR primer sites. Analysis with STS markers thus combines the speed of the RAPD markers with the informativeness of RFLP markers. STS markers have been developed in several crop plants (Williams et al. 1991 ; Tragoonrung et al. 1992; Konieczny and Ausubel 1993).

1.5.1.4 Simple Sequence Repeats (SSRs)

Simple Sequence Repeats (SSRs, Tautz et al. 1986) or microsatellites (Litt and Luty 1989) are tandem-repeated sequence motifs of 1 to 6 base pairs found in high abundance in the genomes of prokaryotes and eukaryotes. The presence of SSRs in the coding regions and in the regulatory regions of the genome influences gene expression and transcriptional activity. SSRs are reported to be ubiquitous, abundant and highly polymorphic markers. The main advantages of SSRs are their large amount of allelic variability and co-dominant inheritance. This gives the researchers the ability to perform parentage analysis and to directly measure gene flow using a few loci (Streiff et al. 1999). They have been well characterized in mammalian genomes, in plant genomes and in tree genomes (Akkaya et al. 1992; Zhao and Kochert 1993; Smith and Devey 1994; Röder et al. 1995). Their characteristics, including their ability to be rapidly typed using PCR techniques, makes SSRs

an attractive option for mapping and fingerprinting. Besides, they are usually multi-allelic, thereby having the potential for more information per marker.

In barley, SSRs are intensively used for the construction of genetic maps, QTL mapping and study of genetic diversity (Liu et al. 1996; Russell et al. 1997; Ramsay et al. 2000; Pillen et al. 2000, 2003, 2004; Thiel et al. 2003; Behn et al. 2004).

1.5.1.5 Amplified fragment length polymorphism (AFLP)

Amplified fragment length polymorphism (AFLP) is essentially a combination of RFLP and PCR techniques. AFLPs are DNA fragments (80-500 bp) obtained from endonuclease restriction, followed by ligation of oligonucleotide adapters to the fragments and selective amplification by PCR. The PCR-primers consist of a core sequence (part of the adapter), a restriction enzyme specific sequence and 1-3 selective nucleotides. The AFLP-technique simultaneously generates fragments from many genomic sites (usually 50-100 fragments per reaction) that are separated by gel-electrophoresis and generally scored as a dominant marker (Vos et al. 1995). If radiolabeled nucleotides are not used in the PCR step, fluorescence or silver staining techniques can be used to visualise the amplification products (Chalhoub et al. 1997). By using automatic gel scanners, heterozygotes may be distinguished from homozygotes based on band intensity differences. Because of the highly informative fingerprinting profiles generally obtained, AFLPs can be applied in studies involving genetic identity, parentage and identification of clones and cultivars. Due to their high genomic abundance and random distribution throughout the genome, AFLPs are also considered relevant markers in gene mapping studies (Vos et al., 1995). AFLP analysis is similar to RAPD assays in that no prior knowledge of the sequence is required, however, AFLP detects a greater number of loci than RAPD does (Russell et al. 1997). The disadvantages of AFLPs are (i) purified, high molecular weight DNA is required; (ii) band profiles can not be interpreted in terms of loci and alleles; (iii) dominance of alleles; (iv) similar sized fragments may not be homologous.

In the past years, the AFLP technique has been used for various studies, such as the characterisation of species (Russell et al. 1997), molecular evolution and biological diversity (Keim et al. 1997), chromosome landing (Cnops et al. 1996), and gene or QTL mapping (Otsen et al. 1996; Yin et al. 1999). In barley, AFLP markers were used to construct high density molecular maps, gene mapping or QTL mapping (Qi et al. 1998b; Yin et al. 1999; Raman et al. 2002).

1.5.1.6 Single nucleotide polymorphisms (SNP)

Single nucleotide polymorphisms or SNPs (pronounced "snips") are DNA sequence variations that occur when a single nucleotide (A, T, C, or G) in the genome sequence is altered (Anonym 2004b). It is considered that the least frequent SNP allele should have a frequency of 1% or greater to be considered as an SNP (Vignal et al. 2002). Two of every three SNPs involve the replacement of cytosine (C) with thymine (T) (Anonym 2004b). Although in principle, at each position of a sequence stretch, any of the four possible nucleotide bases can be present, SNPs are usually biallelic in practice. One of the reasons for this is the low frequency of single nucleotide substitutions at the origin of SNPs, estimated to be between 1×10^9 and 5×10^9 per nucleotide and per year at neutral positions in mammals (Li et al. 1981; Martinez-Arias et al. 2001). Therefore, the probability of two independent base changes occurring at a single position is very low. Another reason is due to a bias in mutations, leading to the prevalence of two SNP types (Vignal et al. 2002).

SNPs can occur in both coding (gene) and non-coding regions of the genome (Collins et al. 1997) and are the most common form of sequence variation (Nickerson et al. 1998). One advantage of SNP is that they are usually linked to the gene of interest, and association of the SNP with traits of economic importance can be analyzed using candidate gene approaches (Emara and Kim 2003). SNPs are the most common source of genetic variation in populations and are thus most likely to account for the majority of phenotypic and behavioral differences between individuals or strains. (Guryev et al. 2004). In the past few years, the SNP markers were intensively used for developing third generation genetic maps, studies of genetic diversity, gene mapping, and gene cloning (Collins et al. 1997; Nairz et al. 2002; Smulders et al. 2003; Bundock and Henry 2004; Gupta et al. 2003). SNPs are used in barley to construct high density maps (Kota et al. 2003)

1.5.2 Linkage maps

Genetic maps are very useful tools in various fields of genetic research, both fundamental and applied (Stam 1993). Construction of genetic linkage maps are based on observed recombinations between marker loci in the experimental crosses. Different segregating families, such as F_2 or BC_1 progenies, F_3 families or single seed descent lines are commonly used for construction of linkage maps. Due to the conceptual advantages of the system in barley, most major maps have been constructed in such progenies. Doubled haploid lines have undergone only one meiotic cycle and carry a completely homozygous chromosome set. This means that the genetic information per plant is constant irrespective of the marker system used (Graner 1996).

Based on recombination fractions between loci, genetic distances are determined. Computer programs, such as Mapmarker/Exp (Lander et al. 1987) and JoinMap (Stam 1993) were developed for full multipoint linkage analysis. For calculation of genetic distance, the Haldane or Kosambi

mapping functions are usually used to convert the recombination fractions to map units or centiMorgans (cM). The Haldane mapping function takes the occurrence of multiple crossovers into account but the Kosambi mapping function accounts also for interference, which is the phenomenon of one crossing-over inhibiting the formation of another in its neighborhood (Ott 1985).

Based on the early linkage maps of barley which were constructed by morphological markers, von Wettstein-Knowles (1992) integrated isozyme markers with morphological marker maps. Heun et al. (1991) and Graner et al. (1991) published the first DNA marker maps of the barley genome. These maps, as well as the Steptoe/Morex map (Kleinhofs et al. 1993), were predominantly based on RFLP markers. Later, several linkage maps of the barley genome were developed based on other kinds of markers, such as RAPD markers (Giese et al. 1994), AFLPs (Becker et al. 1995; Qi et al. 1998b), SSRs (Liu et al. 1996; Dávila et al. 1999; Ramsay et al. 2000) and STSs (Mano et al. 1999). Consensus maps are integrated barley maps, based on segregation information of several independent doubled haploid populations (Sherman et al. 1995; Qi et al. 1996; Thiel et al. 2003). Due to the large gaps present in the individual maps, the consensus maps are very useful for QTL mapping or/and when locations of genes are compared in crosses lacking common markers.

The total genetic length of the barley genome is very different in individual maps, for instance, 1096 cM (Heun et al. 1991) and 1873 cM (Becker and Heun 1995). However, in the most comprehensive consensus maps (Qi and Lindhout 1996; Thiel et al. 2003), the total genetic length of the barley genome was approximately 1060 cM and the lengths of the seven linkage groups range from 117 to 201 cM. One cM on the barley maps corresponds to approximately 1000-5000 kbp. However, the genetic distances can not be directly translated into the physical distances because recombination appears less frequent in the centromeric regions of the chromosome arms (Pedersen and Linde-Laursen 1995). It implies that a 1 cM distance in the distal part of the arm corresponds to a shorter physical distance than 1 cM in the proximal part of the arm. The marker order in the different barley maps is highly conserved and major differences in the genetic lengths of the homologous intervals are rare (Graner 1996). Comparative genetic studies have demonstrated that gene content and orders are highly conserved, both at the map and megabase level, between different species within the grass family (Devos and Gale 1997).

1.5.3 Mapping quantitative trait loci

1.5.3.1 Quantitative traits

A quantitative trait corresponds to a phenotype that can vary in a quantitative manner when measured among different individuals. The variation in expression can be due to combinations of genetic and environmental factors, as well as to chance. Quantitative traits are often controlled by

the cumulative action of alleles at multiple loci (Anonym 2004a). In crop plants, most traits of economic importance, including yield, earliness, height and many quality traits are quantitative. A polymorphic locus which contains alleles that differentially affect the expression of a continuously distributed phenotypic trait is commonly referred to as quantitative trait locus (QTL) (Anonym 2004a). Biometrical approaches have traditionally been used for studying quantitative traits, where the statistical quantitative genetic models assume that essentially infinitely genes with tiny effects work together to express a trait. However, the details of the genetic basis of quantitative traits remained unclear until the generation of detailed genetic maps based on DNA markers were available.

1.5.3.2 Methods of QTL mapping

Since the proposal of the multiple-factor hypothesis by both Nilson-Ehle and East in 1909, continuous variation has been thought to arise largely from the collective effects of numerous genes, each having a small effect. Because these effects have not generally been resolvable individually, quantitative geneticists have dealt largely with the characterization of these factors *en masse,* using biometrical procedures. Many issues in quantitative genetics and evolution are difficult to address without additional empirical information about the genes which underlie continuous variation. The identification and examination of individual quantitative genes should provide information about the organization of genomes and gives insight into the relative contributions of “major” and “minor” genes to continuous variation. The ability to identify specific quantitative genes would also lead to a more powerful means of investigating epistasis, pleiotropy and the genetic basis of heterosis. As these aspects of quantitative genetics are increasingly better understood, new methods might be developed to contribute to current approaches of plant improvement (Edwards et al. 1987).

The earliest association of morphological markers with quantitative traits in plants was reported by Sax (1923). And the first steps towards mapping of QTLs or polygenes were taken based on the scarce markers available (Thoday 1961). Law (1967) used an intervarietal chromosome substitution line to study effects associated with four morphological marker loci on chromosome 7B in wheat. Currently, complete genetic maps exist for many crop species and algorithms have been developed for QTL mapping in a wide range of pedigrees and experimental designs including F2, backcross, recombinant inbred, doubled haploid and many other designs (Paterson 1995). QTL mapping shares the basic principle with qualitative gene mapping: testing association between marker genotypes and quantitative phenotypes.

QTL mapping programs can be roughly classified into different groups according to the number of markers or genetic models and analytical approaches applied (Liu 1998; Hoeschele et al. 1997). Based on the number of markers, single-QTL models and multiple-loci models can be classified (Liu 1998). According to the analytical technology, the methods can be grouped into one-way ANOVA (simple t-test), simple linear regression, multiple linear regressions, nonlinear regression, log-linear regression, likelihood functions, MCMC (Markoff Chain Monte Carlo), mixed linear models, and Bayesian approach (Weller 1986; Lander and Botstein 1989; Haley and Knott 1992; Jansen 1992; Zeng 1994; Wang et al. 1999). Recent advances in QTL mapping procedures include analysis of QTL x environment interaction (Tinker and Mather 1995a, 1995b; Jansen et al. 1995; Korol et al. 1998), a nonparametric approach to map QTLs (Kruglyak and Lander 1995; Lebreton et al. 1998), Bayesian mapping of QTLs (Satagopan et al. 1996; Sillanpää and Arjas 1998) and AB-QTL analysis (Tanksley and Nelson 1996).

1.5.3.2.1 Single-marker analysis

For QTL mapping, the most simple methods were based on single marker analysis, where the difference between the phenotypic means of the genotype classes of a marker are compared using F-statistics, T-tests, linear regression or nonparametric tests (Sax 1923, Edwards et al. 1987, Soller and Brody 1976). The chief advantage of analysis of variance at the marker loci is its simplicity. In addition, a genetic map for the markers is not required, and the method may be easily extended to account for multiple loci. A further advantage is the opptunity to include covariates, such as sex, treatment, or an environment effect. Many phenotypes show marked sex differences, and these must be accounted for in QTL mapping. In addition, one may apply a treatment to some individuals but not others, or raise some individuals in one environment and others in a different environment (Brown 2001). However, the approach does not define the likely position of the QTL. In particular, it cannot distinguish between tight linkage to a QTL with small effect and loose linkage to a QTL with large effect (Lander and Botstein 1989).

1.5.3.2.2 Simple interval mapping

In order to overcome the disadvantages of analysis of variance at marker loci, Lander and Botstein (1989) developed interval mapping, which uses two flanking markers for mapping QTLs between markers or at one marker site. In interval mapping based on maximum likelihood methods (Lander and Botstein 1989) or multiple regressions (Haley and Knott 1992), the test statistics for the presence of a putative QTL can be plotted along the chromosomes to present the evidence for QTLs at the various positions of the genome. The computer program MapmakerQTL (Lander and

Botstein 1989) has been used extensively for performing interval mapping in plant studies. Interval mapping, searching for a single target QTL throughout a mapped genome, is called simple interval mapping (SIM) now. Compared with the traditional method, the interval mapping method has a number of advantages, for instance, the speed and simplicity of the program. However, it still has several problems. One of the major problems is the influence of closely linked QTLs. Simulation results indicated that a "ghost QTL" might appear between two real linked QTLs in interval mapping because the two real QTLs are hidden by the "ghost QTL" (Moreno-Gonzalez 1992). When there are two or more QTLs located on a chromosome, the mapping of QTLs can be seriously biased, and QTLs can be mapped to wrong positions (Knott. and Haley 1992; Martinez and Curnow 1992). And when multiple QTLs segregate, the sampling error associated with detection of a QTL may be inflated by the effects of other QTLs and furthermore, linked QTLs can cause biased estimates of a QTL position (Tinker and Mather 1995a).

1.5.3.2.3 Composite interval mapping

To overcome the problems of low testing power and "ghost QTLs", composite interval mapping (CIM) approaches were proposed (Zeng 1993, 1994; Jansen 1993b). CIM performs the analysis in the same way as SIM, but the difference between CIM and SIM is that the variance from other QTLs is accounted for by including partial regression coefficients from markers ("cofactors") in other regions of the genome in the CIM model. The simulation results showed that composite interval mapping has a higher resolution and detection power than interval mapping (Zeng 1994). To date, there are some different algorithms for CIM, such as multiple linear regressions (Jansen 1993a), maximum likelihood function (Zeng 1993, 1994) and the Markov Chain Monte Carlo (MCMC). However, such methods have their own limitations. For example, CIM can only detect single-locus QTLs and estimate the genetic effects in single environment. Therefore digenic epistasis and genotype × environment (GE) interactions of QTLs can not be dissected, simultaneously. Recently, the mixed linear model approach was introduced to composite interval mapping (Wang et al. 1999; Piepho 2000). Due to the flexibility of the mixed linear model approach, the genetic model can be easily extended to more complex genetic situations where GE interaction and epistasis are included (Wang et al. 1999).

1.5.3.2.4 QTL × environment interaction

Genotype by environment interaction is a common phenomenon for quantitative traits, demonstrated by classical genetic studies, and has been of great concern for plant breeding programs (Lin et al.1986; Westcott 1986). QTL mapping integrates DNA marker and biometric

analysis into one process, which makes it feasible to trace genotype by environment interactions between individual QTLs and environments. There are numerous reports about inconsistency in detection of QTLs across different environments. However, according to Stuber et al. (1992) and Schön et al. (1994), QTL detection was relatively consistent across diverse environments. In most QTL mapping studies, the putative interactions between QTL and environment were analyzed by comparing the QTLs detected separately in each environment. It suggested that a QTL detected in one environment but not in another might indicate QTL x environment (Q × E) interaction. However, even in the absence of true interaction of QTL x environment, a QTL can be detected in one environment but not in another, because the chance of simultaneous detection in both environments is naturally small (Jansen et al. 1995). On the other hand, QTLs that were consistently detected at different environments may not conclusively indicate the absence of interaction of QTL x environment. Recently, some methods have been proposed for dealing with Q × E interactions (Jansen et al. 1995; Romagosa et al.1996; Wang et al. 1999; Piepho 2000) and several reports were published to detect Q × E interaction effects (Jansen et al. 1995; Romagosa et al. 1996; Yan et al. 1998, 1999; Xing et al. 2002; Pillen et al. 2000, 2003, 2004)

1.5.3.2.5 Significance thresholds

The significance thresholds for detecting QTLs are very important. Because QTL mapping involves many analyses of independent genetic markers throughout the genome, there are many opportunities for false-positive results if the significance thresholds are inexactly given. The appropriate threshold for controlling the type I error rate depends on the size of the genome and on the density of markers genotyped: a logarithm of odds (LOD) threshold of 2.4 was considered adequate in SIM for a genome with a 20 cM marker interval (Lander and Botstein 1989). This threshold was deduced from an assumed distribution for the test statistics, but the true distribution may deviate from the assumed distribution due to random distribution of the markers on the map (Tinker and Mather 1995b). Alternate methods are based on re-sampling. The permutation involves shuffling the phenotypes so that the effects of the parameters are lost and the distribution of test statistics under the null hypothesis can be derived from repeated permutations (Churchill and Doerge 1994).

1.5.3.2.6 QTL detecting power

The chance of detecting a QTL is called ‘power’. Suppose that under the null hypothesis of no segregating QTL, one obtains a maximum genomewide LOD score, of at least 3.0 in only 5% of the time, so that the threshold of 3.0 may be used to define significant evidence for the presence of a

QTL. In this case, the power to detect a QTL is the chance that one will obtain a LOD score above 3.0 in the region of the QTL. This power depends on the type of cross, the size of the effect of the QTL, the number of individuals examined, the density of markers genotyped in the region of the QTL, and the stringency of the chosen LOD threshold (*i.e.*, the significance level) (Brown 2001). The power of finding a QTL can be increased by decreasing the variation caused by the environment as well as by the background genome. Environmental variation can be decreased by repeated phenotype measurements or by using progeny testing for phenotype measures (Lander and Botstein 1989). Based on computer simulation studies, progeny sizes from a few hundreds to a thousand have been suggested to detect QTLs of minor effect. In practical barley studies, doubled haploid progenies of 100-200 lines have frequently been used for mapping purposes. The density of the marker map is not as important as the progeny size: a map with 50 cM marker spacings is adequate for detection of QTLs (Darvasi and Soller 1994). However, a denser map helps to locate the QTLs more precisely (Darvasi et al. 1993).

1.5.3.3 Conclusions from QTL mapping experiments

In the traditional models of quantitative genetics, simplifying assumptions were made about equality and strict additivity of gene effects (Falconer and Mackay 1996). According to the recent results of the QTL mapping experiments, it has become clear that such assumptions are incorrect. In many mapping experiments, a relatively small number of QTLs accounts for very large portions of the phenotypic variance, with increasing numbers of genes accounting for progressively smaller portions of variance, until the significance threshold is reached (Paterson 1995; Tanksley et al. 1996; Fulton *et al.*1997; Pillen et al. 2003, 2004). The number of QTLs detected for particular traits varies in different studies, for example, from one to twenty (Pillen et al. 2003). Up to seven QTLs affecting one trait (plant height) have been located on the same chromosome 7H in barley (Pillen et al. 2003). QTLs affecting several traits are very common (Hayes et al. 1993a; Tanksley et al. 1996; Pillen et al. 2003, 2004), and it may be due to pleiotropy or close linkage. Although QTLs are usually distributed over all chromosomes, clusters of QTLs in certain chromosomal regions have been observed as well (Yin et al. 1999; Fulton et al. 2000; Scheurer et al. 2001; Pillen et al. 2003, 2004). The proportion of phenotypic variation explained by each QTL and all QTLs together depends on the heritability of the trait as well as on the portion of revealed QTLs. Individual QTLs may explain from 1 to 82 % of the phenotypic variation in each trait in barley (Barua et al. 1993, Yin et al. 1999). Differences occur in QTL incidence when quantitative traits are scored in many environments or during many years. There might be only a few QTLs with general effects and more with specific effects (Backes et al. 1995). However, comparative studies between related species

have revealed conservation not only in marker order but also in locations of some QTLs (Lin et al. 1995).

1.5.4 QTLs for agronomic traits

Most traits of agronomic importance, such as grain yield and yield components are quantitative in nature and are controlled by multiple genes. The advent of DNA markers has made it feasible to localise individual genes for this type of traits (Yin et al. 1999). By means of QTL mapping, the variations of quantitative traits could be dissected into individual QTL effects, environmental effects and interaction of QTL x environment. Simultaneously, the QTLs could be located on specific chromosomes. Compared to conventional plant breeding, marker-assisted breeding of quantitative traits might be more efficient, effective and reliable. For this reason, the QTLs for agronomic traits have been intensively studied worldwide (Hayes et al. 1993a, 1993b; Hayes et al. 1996; Bezant et al. 1997; Fulton et al. 1997; Thomas et al. 1998; Marquez-Cedillo et al. 2001; Teulat et al. 2001; Pillen et al. 2003 and 2004). For instance, Bezant et al. (1997) located 31 QTLs for plot yield, plant grain weight, thousand-grain weight and ear grain number on all chromosomes except 5H. The largest QTL effect for plot yield was located on chromosome 2HL and increased plot yield by 19 %. Yin et al. (1999) reported 45 QTLs for six agronomic traits including yield which were located on all chromosomes.

1.5.5 QTLs for disease resistance

Genetic pathogen resistance is the most cost-effective and environmentally appropriate approach to disease management in crop plants. The durability of resistance is of great importance because quantitative resistance is often more durable than qualitative resistance (Toojinda et al. 2000). Qualitative disease resistance genes have been extensively studied in terms of genome location (Giese et al. 1993; Graner and Tekauz 1996) and specificity (Thomas et al. 1995). QTL mapping tools allow for the systematic dissection of quantitative resistance into estimates of locus number, location, effect, and interaction of resistance genes (Young 1996). Disease resistance QTLs have been described for a number of host pathogen systems (Williamson et al. 1994; Maisonneuve et al. 1994), including barley (Graner and Bauer 1993; Hayes et al. 1996). However, the structure and function of quantitative resistance genes is still a matter of conjecture.

Intensive research in mapping important disease resistance genes in barley has been carried out worldwide and some of them were identified or are being successfully used for screening in practical breeding programs (Thomas et al. 1998; Richter et al. 1998; Qi et al. 1999; Manninen et al. 2000; Collins et al. 2001; Backes et al. 2003; Sayed et al. 2004). For powdery mildew, the

resistance gene *Ror1* was located to the centromeric region of chromosome 1H by Collins et al. (2001). Thomas et al. (1998) confirmed that the m*lo* powdery mildew resistance gene on chromosome 4H is associated with a reduction in yield. Net blotch is another serious disease in barley. Several QTL mappings for net blotch resistance have been reported. Twelve QTLs for net blotch resistance were located on all chromosomes except 5H by Richter et al. (1998). Manninen et al. (2000) located a net blotch resistant gene in the vicinity of locus HVM14 on chromosome 6H. For leaf scald, Patil et al. (2003) mapped two leaf scald resistant alleles *Rrs1* and *Rrs4* from the wild accession 'CI 11549' on chromosome 3H. Sayed et al. (2004) mapped 4 QTLs resistance to leaf scald on chromosomes 2H and 3H.

1.5.6 Marker assisted selection

The marker assisted selection (MAS) concept originated from Soller and Beckmann (1988). It is an indirect selection method relying on markers instead of the target gene. The idea behind marker assisted selection is that there may be genes with significant effects that may be targeted specifically in selection. Some traits are controlled by single genes (e.g. hair colour) but most traits of economic importance are quantitative traits that most likely are controlled by a fairly large number of genes. However, some of these genes might have a larger effect. Such genes can be called major genes located at a QTL. Although the term QTL strictly applies to genes of any effect, in practice it refers only to major genes, as only these will be large enough to be detected and mapped on the genome. Following the pattern of inheritance at such QTL might assist in selection (van der Werf 2001).

Marker assisted selection is not based on the phenotype but based on a genotype of a marker that is linked to the gene affecting the phenotype. In theory, MAS is more effective than phenotypic selection when correlation between the marker genotype scores and the phenotypic values is greater than the square root of the heritability of the trait, assuming that the heritability of the marker is 1 (Dudley 1993). MAS allows early selection before phenotypic evaluation is possible and simplifies selection of traits that are difficult to score. Several requirements must be fulfilled before markers can be used in selection. There is a close linkage between the marker and the target gene, segregation for both the marker and the target gene, linkage disequilibrium in the plant population to be selected and a known linkage phase between the marker and the target gene (Weber and Wricke 1994). The efficiency of MAS can be increased by using markers flanking the target gene instead of a single linked marker (Tanksley 1983).

Deterministic analysis, assuming very large sample sizes, indicates that molecular marker loci can be used to substantially increase the rate of improvement in quantitative characters by artificial

selection. The potential efficiency of marker assisted selection on a single trait utilizing a combination of molecular and phenotypic information, relative to standard methods of phenotypic selection, depends on the heritability of the character, the proportion of the additive genetic variance associated with the marker loci, and the selection scheme. Under individual selection, the relative efficiency of MAS is greatest for characters with low heritability, if a moderate or large fraction of the additive genetic variance is significantly associated with the marker loci**.** Further increases in the relative efficiency of MAS are possible when individuals that do not express the phenotypic traits of interest can be selected on the basis of their molecular markers. If very large samples are available, MAS on multiple traits is more efficient in a multivariate context than in a univariate analysis of total economic value alone. This is because the molecular marker loci provide different amounts of information on different characters, which affects their weightings in a multivariate selection index (Lande and Thompson 1990).

There is a question: What is the moderate distance between a marker and the interesting trait for an efficient MAS? Paran et al. (1991) reported that the moderate distance between marker and trait should be within 10 cM. Hospital et al. (1992) thought that the distance between marker and trait could reach 20 cM in early generations but should be within 5 cM in later generations. Mohan et al. (1997) suggested that marker(s) should co-segregate with the desired trait or be closely linked (1 cM or less).

The efficiency of MAS is enhanced and may be more efficient than traditional selection under the following circumstances: defined by Lee et al. (1995): 1) the trait under selection has a low heritability; 2) presence of tight linkage between QTL and marker (<5cM); 3) in earlier generations of selection prior to fixation of alleles at or near marker loci and recombinational erosion of marker-QTL associations; 4) when large sample sizes for mapping and selecting QTL are used to improve estimates of QTL alleles. Markers very closely linked to the target genes or even located within the gene can greatly enhance the use of MAS in advanced generations, where the linkage disequilibrium becomes smaller.

In crop improvement, two general strategies have been proposed to use marker-QTL associations for marker-assisted selection (MAS). One involves introgression of a limited number of QTLs via marker-assisted backcrossing (Dudley 1993). Through this process, molecular markers can minimize linkage drag and expedite the transfer of target genome blocks from exotic germplasm into a desired background (Young and Tanksley 1989; Tanksley and Nelson 1996). In barley, this approach has been used to introgress QTLs conferring adult plant resistance to stripe rust (*Puccinia striiformis f.* sp. *hordei*) into a genetic background unrelated to the mapping population (Toojinda et al. 1998). Another strategy, suitable for a larger number of QTLs and for

multiple-trait selection, is to use QTL information to design matings that will maximize the probability of pyramiding most, if not all, favorable QTL alleles in a single genotype (Dudley 1993; Hayes et al. 1996).

In variety development, good characteristics from all parents should be combined in a single line (Weber and Wricke 1994). In breeding autogamous species, lines are developed from crossing schemes including two or more parents. However, a few traits would be transferred from a donor to a recipient in a backcross program. If the backcrossing approach is combined with the information on mapped QTLs, the efficiency of pyramiding QTLs could be much more enhanced. For traits with significant interactions between QTLs, emphasis should be placed on identification of the best multi-locus allelic combinations instead of simply collecting many alleles with positive effects (Zhu et al. 1999). The relative efficacies of MAS and traditional selection for improving quantitative traits have been considered in several simulation studies. The accurate chromosomal locations of QTLs, as well as the magnitude of QTL effects, should be verified prior to their use in an applied breeding program. In barley, the effect of four yield QTLs was verified using a set of DH lines different from the lines used for mapping (Romagosa et al. 1999). In that study, selections based on marker genotypes, or combined information from markers and phenotype, were at least as efficient as phenotypic selection alone, but qualitative QTL x E interactions decreased the efficiency of MAS for some of the QTLs. In the same barley lines, effects of only one of the two major QTL regions for several malting quality traits were verified, the effects of the other region were lost probably due to inaccurate location of the QTL (Han et al. 1997).

Simultaneous selection for multiple traits complicates the use of MAS in breeding. Information on several markers needs to be combined when selection is made. One method is to determine the marker genotype of each line being tested and sum the significant additive effects of each marker locus to an index value (Dudley 1997). A large number of plants have to be scored in order to find the desired marker combination in the progeny, which may render the selection procedure costly (Graner 1996).

1.5.7 Introgression

Introgression means infiltration of the genes of one species into the gene pool of another through repeated backcrossing of an interspecific hybrid with one of its parents. By means of introgression, the target loci could be introgressed from unadapted germplasm into the elite loci of cultivars. Introgression of desirable alleles using markers may have several advantages over introgression restricted to phenotypic information. For the allele to be introgressed, marked chromosome segments ensure that the correct donor segment is incorporated into the recipient line.

For non-additive acting alleles, using markers may be the only way to ensure a successful introgression program. For the background genotype, using markers gives a direct estimate of the proportion of the donor genome that is still present in each backcross generation. This may be preferred over phenotypic selection, in particular for traits with low heritabilities that are difficult to measure (Visscher et al. 1996).

The backcrossing procedure is appropriate for traits controlled by a small number of loci. As the number of loci segregating for the trait increases, the number of backcross individuals which must be grown to have a high probability of recovering all favourable alleles also increases (Dudley 1993). Molecular markers can be used effectively to speed up and improve the precision of backcrossing. Firstly, molecular markers are used to monitor the incorporation of the desirable alleles from the donor source (Dudley 1993). Without markers it may be difficult to recognize individuals with the favourable allele among the backcross progeny because of low heritability, poor penetrance or because the allele is recessive. Single-copy markers with defined map locations, such as RFLPs or SSRs, are ideal for the ‘foreground selection’ step (Toojinda et al. 1998). Secondly, selection for the molecular marker alleles of the recurrent parent can be used to speed up the recovery of the recurrent parent genotype (Young and Tanksley 1989). Molecular markers with a higher information content per reaction, such as AFLPs, are ideal for this ‘background selection’ step (Toojinda et al. 1998). Thirdly, linkage drag could be reduced by selecting for recurrent alleles at loci linked to the target gene during backcrossing. Paterson et al. (1988) suggested that the use of the marker information could reduce the number of backcrosses required by half. However, Young and Tanksley (1989) estimated that by MAS for recurrent parent genotype, an introgressed segment could be reduced in two generations to a size that would require 100 generations without MAS.

Marker assisted backcrossing is useful to rapidly transfer resistance genes into advanced breeding lines from wild progenitors. Pyramiding of several resistance genes into a single genome could be greatly enhanced with molecular markers (Melchinger 1990). A new application of MAS is the backcrossing of transgenes from model varieties amenable to transformation to the most advanced germplasm as quickly as possible (Lee 1995). However, it is possible that positive factors for traits unrelated to the main objective will be eliminated.

Manipulation of QTLs in backcross breeding programs differs slightly from that of qualitative traits. The segregation of a single QTL can be observed only through linked markers, not directly from the phenotype (Manninen 2000). Since QTL locations are usually estimated imprecisely, using a marker spacing of 10-20 cM gave an advantage of one to two backcross generations of selection relative to a random or phenotypic selection (Visscher et al. 1996). According to simulation studies, it is possible to manipulate up to four unlinked QTLs simultaneously with population sizes of a few

hundred individuals, assuming optimally positioned markers (Hospital and Charcosset 1997). Toojinda et al. (1998) reported that two stripe rust resistance QTLs have been successfully introgressed into a genetic background unrelated to the mapping population with one cycle of marker-assisted backcrossing. But manipulation of QTLs can be problematic due to the loss of target loci though recombination, incorrect information regarding the location of the QTLs, and/or negatively altered expression of the QTLs in new genetic backgrounds (Hayes et al. 1996).

1.5.8 Near-isogenic lines (NILs) and crop improvement

Near-isogenic lines (NILs) are a group of lines that are genetically identical except of one or a few linked loci. NILs are developed by systematic backcrossing and using DNA markers to select the introgressions of exotic segments in the background of elite varieties. Recently, NILs were intensively used for verification and fine mapping of QTLs (Eshed and Zamir 1995; Kretschmer et al. 1997; Bernacchi et al. 1998b; Lin et al. 2000; Tacconi et al. 2001). A NIL has the following advantages in QTL studies and crop breeding: (1) NILs are homozygous lines, which allow infinite replication of measurements and experiments in different seasons and environments. (2) These lines have a high percentage of the recurrent parent and a low percentage of the wild parent, which reduces the probability of linkage drag and negative epistasis. (3) A practical advantage of NILs for commercial breeding purposes is that due to the low percentage of wild alleles the introduction of an interesting trait into the commercial cultivar will be relatively straightforward and rapid (Jeuken and Lindhout, 2004). NILs are a powerful tool for verification and fine mapping of QTLs. However, although NILs are a useful resource for developing a new variety, it is still a long way to go from a NILs to a commercial variety.

1.5.9 Map-based cloning

Map-based or positional cloning has been used successfully in a number of instances to isolate genes from plants (Arondel et al. 1993; Yoshimura et al. 1996; Patocchi et al. 1999). The original concept behind map-based cloning was to find a DNA marker linked to a gene of interest, and then walk to the gene via overlapping clones (cosmids or yeast artificial chromosomes, YACs; Wicking and Williamson 1991). This method was called ’chromosome walking’. However, chromosome walking in large and complex plant genomes, for example, the wheat genome, is hampered both by the large amount of DNA being traversed and by the prevalence of repetitive DNA (Tanksley et al. 1995).

In order to overcome the problems during chromosome walking, Tanksley et al. (1995) suggested that one first isolates one or more DNA marker(s) at a physical distance from the targeted

gene that is less than the average insert size of the genomic library being used for clone isolation; the DNA marker is then used to screen the library and isolate (or 'land' on) the clone containing the gene, without any need for chromosome walking and its associated problems. This approach, termed chromosome landing (Tanksley et al. 1995), includes mapping of the target gene on a restricted area of a chromosome, confirming the gene location for example with marker assisted introgression, fine mapping the area using for example bulked segregate analysis (BSA) and NILs, and selecting YAC and bacterial artificial chromosome (BAC) clones with markers closely linked to the target locus. Chromosome landing has been used for isolating and sequencing the powdery mildew resistance genes *mlo* (Büschges et al. 1997) and *Mla* (Wei et al. 1999) in barley. The synteny between rice and barley has been used to saturate the region containing the stem rust resistance genes, with molecular markers (Kilian et al. 1997). Chromosome landing has also been used for identifying YAC clones encompassing the barley *Rar1* gene, which is involved in the powdery mildew defence response (Lahaye et al. 1998).

1.6 Doubled haploid population

Doubled haploids are commonly used in many plant species, which are amenable to anther or microspore culture followed by chromosome doubling or F_1 × *H. bulbosum*. Because the plant has two identical homologue chromosomes, the amount of recombination information is exactly equivalent to a backcross. However, DH individuals are completely homozygous, and can be self-pollinated to produce large numbers of progenies, which are all genetically identical. This permit replicated testing of phenotypes, and also facilitates distribution of identical DH populations to many researchers. Thus, a DH population can also be called a permanent population (Zhao et al. 2002). For genetic studies, the advantages of a doubled haploid population, compared with, e.g., an F_2, are twofold: the individual DH genotypes can be maintained indefinitely through selfing, as they are fully homozygous; and because all heterozygous genotypes are missing the segregation patterns are less complicated. In the case of quantitative characters, there is an additional advantage: the absence of intermediate heterozygous genotypes makes it easier to discriminate between the different genotypic classes (Voorrips et al. 2003). A major drawback of DH populations is that the rates of pollen or microspores successfully turned into DH plants vary between genotypes, which may cause segregation distortion and false linkage between some marker loci (Zhao 2002).

1.7 AB-QTL analysis

The advanced backcross quantitative trait locus (AB-QTL) strategy was proposed as a method of combing QTL analysis with variety development by Tanksley and Nelson (1996). The authors

integrated the mapping of favourable QTL alleles and the introgression of these alleles into one process. In order to achieve this goal, they utilized exotic germplasm (wild accession and/or landrace) as the genetic donor for the improvement of quantitative traits like yield parameters or quality components and conducted the marker and phenotype analysis in advanced backcross generations like BC2 or BC3. The AB-QTL strategy has the following advantages: (i) negative exotic alleles, linkage drag from donor and the epistatic interactions between exotic QTL alleles and other wild alleles are reduced compared to QTL studies in early generations like F_2; (ii) phenotypic selection in any generation except for F_1 is possible. Thus, exotic favorable QTL alleles will be quickly transferred into QTL-NILs; (iii) the level of genetic diversity in modern crop breeding can be enhanced through the introgression of new exotic favorable QTL alleles.

To date, there are some reports on the successful application of the AB-QTL strategy to improve important agronomic traits by means of favourable exotic QTLs in tomato, rice, maize, wheat and barley. In all cases, favorable exotic QTL alleles for important agronomic traits have been identified. For instance, fruit yield could be improved in tomato through the introgression of wild species alleles from *Lycopersicon pimpinellifolium* and *L. peruvianum* by 17 % and 34 %, respectively (Tanksley *et al*. 1996; Fulton *et al.*1997). A further AB-QTL study, which used *L. hirsutum* as the donor species, revealed 25 favourable wild-species QTL alleles out of 121 detected QTLs (Bernacchi *et al.* 1998a). In rice the results of AB-QTL studies are in accordance with tomato. Two favorable wild species alleles which increased yield by 17 % and 18 % were identified on chromosome 1 and 11, respectively (Xiao et al. 1996, 1998). Subsequently, the yield QTL effect on chromosome 1 was validated in a second cross using the same *Oryza rufipogon* donor accession (Moncada *et al.* 2001). Recently, reports appeared on the first AB-QTL analyses in maize (Ho *et al*. 2002), wheat (Huang *et al*. 2003) and barley (Pillen *et al*. 2003; 2004). In most instances, favorable QTLs of significant improvements in yield and yield components could be detected from the exotic donor. For instance, exotic QTL effects on yield in maize, wheat and barley reached levels of 11 %, 15 % and 7 %, respectively.

Before favorable wild-species QTL alleles are useful as a breeding resource, they have to be fixed in nearly isogenic lines (QTL-NILs) and the superior performance of a QTL-NIL must be confirmed in comparison to the recurrent elite line. Bernacchi *et al*. (1998b) have already validated the effects of exotic tomato QTLs in QTL-NILs. In field evaluations at five locations worldwide, 22 QTL-NILs out of 25 tested (88 %) exhibited phenotypic improvements compared to the recurrent parent, as had been predicted in the previous AB-QTL analysis. For instance, a QTL-NIL possessing an exotic QTL allele for a 15 % yield increase did, indeed, outperform the control line

by 12 %. These reports clearly illustrate that the AB-QTL strategy is a powerful tool for the improvement of quantitative agronomic traits in elite varieties.

Pillen et al. (2003) analyzed 13 agronomic traits by means of the AB-QTL strategy and identified 29 exotic favorable QTL alleles. The favorable wild allele at locus GMS89 on chromosome 4H was associated with a yield increase of 7.7 % averaged across the six environments tested.

1.8 Aims of the study

The major objective of this research work was to apply the AB-QTL strategy to the simultaneous detection and introgression of favorable barley wild species genes for agronomic traits and disease resistance by means of DNA markers.

The specific aims were:

1) Identification of introgressions in two BC_2DH winter barley populations with SSR markers.
2) Identification of QTLs regulating agronomic traits and pathogen resistance in two BC_2DH winter barley populations.
3) Localization of favorable *Hsp* QTL alleles regulating agronomic traits and pathogen resistances.

2. Material and methods

The present study applies the AB-QTL strategy to detect favorable exotic QTL alleles for agronomic traits and disease resistances in two BC_2DH populations derived from crosses between two German winter barley varieties with an exotic barley accession from Israel. This study was divided into two phases.

During the first phase (Sept. 1999 through Aug. 2002), two winter barley populations, the Carola (*Hordeum vulgare* ssp *vulgare,* in the following abbreviated *Hv*) population with 282 BC_2DH lines and the Theresa (*Hordeum vulgare* ssp *vulgare,* in the following abbreviated *Hv*) population with 104 BC_2DH lines were generated and genotyped with SSRs markers. The DH lines were produced at the lab of the Saaten-Union Resistenzlabor, Leopoldshöhe, Germany. The genotyping of both BC_2DH populations were carried out at the S1 Labor, Department of Crop Science and Plant Breeding, Faculty of Agriculture, Rheinische Friedrich-Wilhelms-University Bonn.

During the second phase (Sept. 2002 through Aug. 2004), the two DH populations were evaluated in field trials for agronomic performance, pathogen resistance and non-parasitic browning.

2.1 Plant material

Two BC_2DH populations, C101 [from the cross Carola × IRS101-23 (*Hordeum vulgare* ssp. *Spontaneum,* in the following abbreviated *Hsp*)] and T101 (from the cross Theresa × IRS101-23), were developed according to the advanced backcross strategy of Tanksley and Nelson (1996). The German winter barley varieties Carola and Theresa were used as female recipients, and the wild accession ISR101-23 from Eastern Lower Galilee, Israel, (kindly provided by Prof. G. Fischbeck, Weihenstephan, Germany) was used as the male donor, to generate the F_1. Subsequently, a single F_1 plant was backcrossed with Carola and Theresa, respectively, as pollinators in each cross. Eight BC_1 plants from Carola and seven BC_1 plants from Theresa were backcrossed again with Carola and Theresa as pollinator, respectively. The anthers from 54 (Carola) and 59 (Theresa) BC_2F_1 plants were used to develop two doubled haploid populations at the lab of the Saaten-Union Resistenzlabor, Leopoldshöhe, Germany. In total, 785 and 280 BC_2DH plants were produced in C101 and T101, respectively. The Carola BC_2DH population consisted of 581 6-row-ear and 204 2-row-ear lines, and the Theresa BC_2DH population consisted of 194 6-row-ear and 86 2-row-ear lines. After harvest, the BC_2DH populations were restricted to fertile, spontaneously doubled 6-row type lines with more than 50 g of available seeds. Ultimately, the advanced backcross doubled haploid populations, C101 and T101 consisted of 282 and 104 lines, respectively (Figure 1).

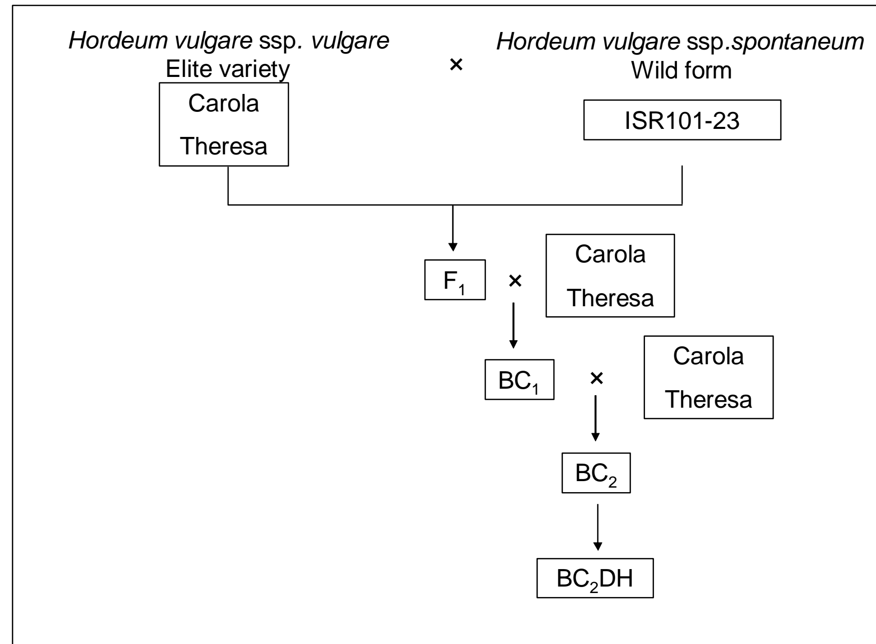


Figure 1: Development of two BC_2DH populations

Table 2: The growing conditions at test locations

	Season	Dikopshof	Gudow	Leutewitz	Irlbach	Estrées
Soil type		Para-brown, fine sandy loam	Sandy loam	Para-brown, fine sandy loam	Sandy loam	n.a.
N fertilizer (kg N/ha)	2002/03	140	n.a.	n.a.	159	n.a.
	2003/04	80	60	90	92	n.a.
Fungicide	02/03+03/04	Cerone + Opus	n.a.	Amistar	Amistar	n.a.
Herbicide	02/03+03/04	Fenikan	n.a.	Compasan	n.a.	n.a.
Insecticide	02/03+03/04	Karate	n.a.	n.a.	Karate	n.a.
Growth regulator	02/03+03/04	Cerone + Opus	n.a.	CCC	n.a.	n.a.
Rain fall (lm^2)	2002/03	624	660	570	764	n.a.
	2003/04	566	n.a.	n.a.	320	876
Temp. Mean (°C/year)	Many years	9.6	8.3	8.4	8.9	n.a.
Temp. (°C) (Max)	2002/03	38.5	n.a.	n.a.	37.1	n.a.
	2003/04	35.0	n.a.	n.a.	26.1	35.0
Temp. (°C) (Min)	2002/03	-12.8	n.a.	n.a.	-17.6	n.a.
	2003/04	-9.1	n.a.	n.a.	-14.6	-6.7

n.a.: data not available.

2.1.1 Test locations

The experiments for agronomic performance were carried out at the following four test locations during the period of 2002-2004: Dikopshof (University of Bonn, West Germany), Gudow

(Nordsaat Saatzucht, North Germany), Leutewitz (DSV, East Germany) and Irlbach (Dr. J. Ackermann Saatzucht, South Germany). The experiments for pathogen resistance and non-parasitic browning were carried out at the following four test locations: Dikopshof (University of Bonn, West Germany), Gudow (Nordsaat Saatzucht, North Germany), Leutewitz (DSV, East Germany) and Estrées (Saaten-Union Recherche, North France). The growing conditions and pest control at the five test locations were showed in Table 2.

2.1.2 Evaluation of agronomic traits, pathogen resistances and non-parasitic browning

For field testing of agronomic performance, the 282 BC_2DH lines from C101 and the 104 BC_2DH lines from T101 were grown at four locations during the seasons 2002/03 and 2003/04 in separate blocks. At each location, a randomized complete block design was applied, without replications. As a control, the recurrent parent was tested with 20 replications per block. Information about plot size (6–8 m^2) and seeding rate (280-320 kernels/m^2) are given in Table 3. The field management included N, P, and K fertilization and pest control according to the local practice at the respective field station. At each plot, the traits, heading date (HEA), plant height (HEI), bending of spike (BSP), lodging at harvest (LOH), stem breaking (SB), plot yield (YLD) and cold damage (COD) were scored (Table 4).

Table 3: Area of plots and seeding rate at five test locations for agronomic traits, pathogen resistance and non-parasitic browning

		Dikopshof	Gudow	Leutewitz	Irlbach	Estrées
AGR[1)]	**Area of plot (m^2)**	6.0	8.0	6.0	6.0	-
	Seeding rate (kernels/m^2)	300	280	320	300	-
DAN[2)]	**Plot**	2 m^2	6 rows	1 m^2	-	1 m^2
	Seeding rate (kernels/m^2)	400	400	400	-	400

[1)] AGR: experiment for agronomic traits. [2)] DAN: experiment for diseases and non-parasitic browning.

For the test of pathogen resistance and non-parasitic browning, all BC_2DH lines from two populations were grown in the same block. The plot size was 1 – 2.25 m^2 or 6 rows, and the seeding rate 400 kernels / m^2 (Table 3). At each location, a randomized complete block design was applied, without replications. For each plot, the powdery mildew (PM, *Erysiphe graminis*), net blotch (NB, *Drechslera teres*), leaf scald (RH, *Rhynchosporium secalis*), leaf rust (LR, *Puccinia hordei*) and non-parasitic browning (NPB) were scored from 1 to 9 according to the visual rating of the severity of symptoms (Table 4).

Table 4: List of 16 quantitative traits measured in up to senven environments

Abbre-viation	Trait	Methode of measurement[1)]	Value[2)]	Model[3)]	Environment[4)] tested
BS	Breaking of stem	Visual rating (1–9) of the severity of breaking of spikes at harvest	-	(5)	D03, D04, G03, I03, I04
BSP	Bending of spike	Visual rating (1–9) of the severity of bending of spikes at harvest	-	(5)	D03, D04, G03, I03, I04
COD	Cold damage	Visual rating (1–9) of the severity of cold damage after winter	-	(5)	D03l, D03k, G03l, G03k, L03l, I03l, E03k*
EAR	Number of spikes	number of ears per square metre taken from a row of 50 cm	+	(5)	D03 (C101), D03, D04 (T101)
HEA	Days until heading	Number of days from begin of vegetation after winter to complete emergence of the spike	-	(5)	D03, D04, G03, L04, I03, I04
HEI	Plant Height	Plant height up to the tip of the ear (excluding awns) at maturity	-	(7) (C101), (5) (T101)	D03, D04, G03, L04, I03, I04
HI	Harvest index	the ratio between grain yield and biomass taken from a row of 50 cm	+	(5)	D03 (C101), D03, D04 (T101)
LOH	Lodging at harvest	Visual rating (1–9) of the severity of lodging at harvest	-	(5)	D03, D04, G03, L04, I03, I04
LR	Leaf rust (*Puccinia hordei*)	Visual rating (1–9) of the severity of disease symptoms	-	(6)	E03, E04
MAS	Biomass	the gross dry weight taken from a row of 50 cm (in g)	+	(5)	D03 (C101), D03, D04 (T101)
NB	Net blotch (*Drechslera teres*)	Visual rating (1–9) of the severity of disease symptoms	-	(5)	D03, D04, G03, G04a**, G04b, L04, E03
NPB	Non-parasitic browning	Visual rating (1–9) of the severity of symptoms	-	(5)	D03, G03, G04a, G04b, L04, E03
PM	Powdery mildew (*Erysiphe graminis*)	Visual rating (1–9) of the severity of disease symptoms	-	(5)	D04, G03, G04a, G04b, L04,
RH	Leaf scald (*Rhyncho-sporium secalis*)	Visual rating (1–9) of the severity of disease symptoms	-	(7) (C101), (5) (T101)	D03, D04, G03, G04a, G04b, L04,
TGW	Thousand-grain weight	Mass of 1,000 kernels harvested from the plot (in g)	+	(5)	D03, G03, L04, I03, I04
YLD	Yield	Plot yield, measured after harvesting with a combine and drying 3 days at 30 °C (in g / m^2)	+	(5, C101), (7, T101)	D03, D04 (T101), G03, L04, I03, I04

[1)] The visual rating (1-9) of the severity: 1 is best value and 9 is the worst value according to the breeding goal. [2)] The value of the trait should be increased (+) or reduced (–) with respect to the breeding goal. [3)] Model of GLM (General linear model) for QTL analysis. Numbers see chapter 2.3.2.3. [4)] Combination of the location [Dikopshof (D), Gudow (G); Leutewitz (L); Irlbach (I) Estrées (E)] and the season (2002/03, 2003/04). * 03l and 03k: evaluated in agronomic trait plots and disease resistance plots in 2002/03, respectively. ** G04a and G04b: only evaluated in C101.

2.2 Molecular markers analysis

Here, the DNA extraction, molecular marker and linkage map resource, PCR reaction and genotyping will be presented in this study.

2.2.1 DNA extraction

Leaf material was collected from four week old plants. Genomic DNA was extracted with CTAB from frozen leaves according to the procedure described by Saghai Maroof et al. (1984).

Sorbitol buffer, pH 7.5

Sorbitol	350 mM
Tris	100 mM
EDTA	5 mM
H_2O (high purity)	ad 2 L

Adjust to pH 7.5 with HCl and store at 4°C

Lauryl sarcosine 5%

Lauryl sarcosine	170.42 mM
H_2O (high purity)	ad 500 ml

Keep at room temperature

Nucleic lysis solution

Tris	200 mM
EDTA	50 mM
$NaCl_2$	2 M
CTAB	2 %
H_2O (high purity)	ad 5 L

Keep at room temperature

Tris-borate-EDTA-buffer (5x TBE), pH 8.3

Tris	450 mM
Boric acid	450 mM
EDTA	10 mM
H_2O (high purity)	ad 5 L

Adjust to pH 8.3 with NaOH at room temperature

Chloroform/isoamyl alcohol 24:1

24 volumes chloroform and 1 volume isoamyl alcohol were mixed.

Briefly, young expanded leaves were collected from each line and kept in -80 °C freezer. The leaf tissue from each line of the BC_2DH populations was used for DNA extraction. 15 ml sorbitol buffer was used 0.075 g sodium disulphite and was added to the leave samples and homogenized with an Ultra turrax. The filtrate was taken into a new tube. The filtrate was centrifuged at 5,000 rpm and 4 °C for 15 minutes. The pellet was resuspended in 2.5 ml sorbitol plus 0.0125 g sodium disulphite. Then 2.5 ml lysis buffer and 1 ml lauryl sarcosine was added. The suspension was incubated in a water bath under continuous gentle shaking at 60 °C for 30-60 minutes (150 rpm). Then, 6 ml chloroform/isoamyl alcohol was added and gently but thoroughly mixed for 10 minutes. The suspension was centrifuged at 5,000 rpm and 4 °C for 30 minutes. Then, 4.5 ml of the aqueous phase were transferred with a pipette into a new sterile tube. Then, 4.5ml of cold isopropyl alcohol were added and gently mixed to precipitate the nucleic acids. The solution was incubated at 4 °C for 60 minutes or over night. Thereupon, the solution was centrifuged at 5,000 rpm and 4°C for 30 minutes. The supernatant was discarded. Then, 2 ml ethanol (70 %) were added and centrifuged briefly at 5,000 rpm for 4 minutes at 4 °C. The supernatant was discarded again and the pellet was air-dried for 10 minutes at 60 °C. The DNA pellet was finally dissolved in 50 - 1000 µl ddH_2O (depending on DNA quantity) at 4 °C over night. Then, the DNA solution was centrifuged at 2,000 rpm for 5 minutes and the DNA was transferred in deep well plates and stored at -20 °C.

To exam the DNA quality and to estimate the DNA concentration, 10 µl DNA sample, mixed with 1 µl loading buffer were pipetted into the sample wells of a 1% agarose gel containing ethidium bromide (concentration 0.5 µg/ml) in 1x TBE-solution. The lid and power leads were placed on the apparatus and a current was applied for 30 – 60 minutes. DNA fragments were visualized by staining with ethidium bromide**.** To visualize the DNA, the gel was placed on an ultraviolet transilluminator after electrophoresis. The concentration of DNA could be estimated by comparing the bands of samples with a length-standard.

2.2.2 SSR marker analysis

In this chapter, the molecular and linkage map resources, PCR reaction and the molecular marker analysis by means of the Li-Cor system will be presented.

2.2.2.1 Marker and linkage map resources

More than 220 SSR markers were screened for polymorphism between the parents. The primer sequence information was taken from the following published sources: Becker and Heun (1995), Liu et al. (1996), Russell et al. (1997), Struss and Plieske (1998), Pillen et al. (2000), Ramsay et al. (2000), Thiel et al. (2003) and Li et al. (2003). Eighty-five polymorphic SSR markers

were selected for genotyping (82 SSR markers for C101 and 78 SSR markers for T101). Linkage distances between SSR markers were taken from von Korff et al. (2004) and Ramsay et al. (2000) or calculated with MAPMARKER software (Lander et al. 1987) in the F_2 population with 86 indivaduals derived from the cross Thuringia × ISR24-8.

2.2.2.2 Polymerase chain reaction (PCR)

PCR amplification was performed in 20 µl reactions containing 5 µl of template DNA (ca. 50 ng), 0.05 µl of *Taq* polymerase (5U/µl, Promega, Mannheim), 1.5 µl of 10 × PCR buffer (500 mM KCl, 100 mM Tris-HCl; pH 9.0, 1% Triton X-100), 1.5 µl of 25 mM $MgCl_2$, 0.75µl of dNTP (2 mM), 0.075 µl of the forward and reverse oligonucleotide primers (10 µM) and 0.5 µl of the M13 universal forward primer (1 µM). Each forward oligonucleotide primer was tailed by adding the M13 universal forward primer sequence at the 5' end. The M13 primer was labelled with either IRD700 or IRD800 at the 5'end for visualization. The amplification profile is given in Table 5. The samples of PCR amplification were stored at -20 °C before loading. To judge the polymorphisms of markers, the electrophoresis of the samples was performed on LI-COR DNA Sequencer 4200 (LI-COR, Bad Homburg) after adding 1x TBE buffer and heating for denaturing.

Table 5: Procedure of *touch down* PCR for SSR markers

Temperature (in °C)	Time (in min.)	No. of cycles
94	3	1
94 64 – 55 72	1 0.5 1	10
94 55 72	1 1 1	30
72	5	1
94	8	1
4	endless	1

2.2.2.3 Li-Cor system

The LI-COR DNA Sequencer 4200 was used as an automated DNA detection device. The Li-Cor system employs infrared fluorescence to detect DNA. During the PCR reaction, the DNA polymerase incorporates an infrared dye (IRD)-labelled primer into the PCR fragments. The IRD-labelled fragments separate according to size on an acrylamide gel. A solid-state diode excites the infrared dye on DNA fragments as they pass the detector window. A focusing fluorescence microscope containing a solid-state silicon avalanche photodiode scans back and forth across the

width of the gel collecting data in real time. The raw image data are series of bands displayed autoradiogram-like on the computer screen.

IRD800 is a heptamethine cyanine dye absorbing and fluorescing in the near infrared region of the spectrum. The absorption maximum at 795 nm is well-matched to the 785 nm laser of the DNA sequencer. The extremely high absorptivity and good quantum efficiency of the dye provide excellent sensitivity.

IRD700 is a pentamethine carbocyanine dye fluorescing in the near infrared region of the spectrum. The absorption maximum (685 nm) is just outside the visible region and matches the 685 nm laser of DNA sequencer. While the absorptivity of IRD700 is slightly less than that of IRD800, the higher fluorescence efficiency compensates for the absorption difference.

2.2.2.4 Genotype scoring

At each informative SSR locus, homozygous *Hv* (1) and homozygous *Hsp* (3) could be distinguished in the BC_2DH populations. The genotype data were stored in Excel sheets and later imported to SAS (SAS Institute 1999).

2.3 Data Analysis

In this chapter, the statistical methods will be introduced for (i) calculating the proportion of exotic alleles, the relative performance of the homozygous *Hsp* genotype and the explained genetic variation, (ii) analyzing the effects of lines, cold damage and neighbour plots, (iii) analyzing the genetic correlation and (iv) detecting QTLs in this study.

2.3.1 Proportion of exotic alleles

The proportion of exotic alleles (P [exotic]) was calculated as the percentage of exotic alleles present in a single BC_2DH line according to the formula:

$$P[exotic] = \frac{[aa]}{[aa] + [AA]}$$

In the above formula [*AA*] and [*aa*] correspond to the number of the homozygous elite (*Hv*) and homozygous exotic (*Hsp*) genotypes, respectively. All marker loci were subjected to a chi-square goodness-of-fit test for segregation analysis.

2.3.2 Statistical analysis of data

The statistical analysis of the data was conducted in two ways: ANOVA to detect line effects and ANOVA for QTL detection.

2.3.2.1 Variance analysis to detect line effects

For ANOVA, the data were calculated using the SAS software Version 8 (SAS Institute *1999*). Under normal conditions, the BC_2DH lines had no problem for surviving the winter, for example, in the 2000/01, 2001/02 and 2003/04 seasons. But in the 2002/03 season the lines caught the extreme low temperatures across all Europe during winter, for instance, the minimum temperature reached -13.0 °C and -17.6 °C at Dikopshof and Irlbach, respectively. However, the minimum temperature was about -9.1 °C and -14.6 °C at Dikopshof and Irlbach in the 2003/04 season, respectively. Under this condition, the lines reacted very different in regard to cold tolerance. According to the observation of cold damage (COD), lines with a COD score of 7 exhibited more than 15 % dead plants per plot and lines with a maximum COD score of 9 exhibited almost 50 % dead plants per plot. For analysis of cold damage affecting other agronomic traits in the 2002/03 season, the ANOVA was used to analyze the variation based on the different levels of COD across all environments. Comparisons were performed to compare the mean values of different traits in different groups (Duncan test). To reveal the relationship between seriously cold damaged plots and their neighbour plots, the plots at different test locations were distinguished into three groups: normal plots with COD < 7 (N = 0), seriously cold-damaged plots with COD ≥ 7 (N = 1) and neighbouring plots of the seriously cold-damaged plots (N = 2). Then, the ANOVA was performed to analyze the variation based on the three groups across all environments [Model (4)], and the Duncan test was performed to compare the LSMeans values of different traits, which were significant in ANOVA for N in the season 2002/03. Simultaneously, correlation analysis was used to detect the effect of COD on other traits in the season 2002/03.

In order to reveal the effect of cold damage and neighbour plots on other traits across all environments in the seasons 2002/03 and 2003/04, the models (1), (2) and (3) were used for ANOVA:

$$\mathbf{Y}_{ijk} = \mu + \mathbf{L}_i + \mathbf{E}_j + \mathbf{C} + \mathbf{N} + \mathbf{L}\times\mathbf{E}_{ij} + \mathbf{R}_{ijk} \quad (1)$$

$$\mathbf{Y}_{ij} = \mu + \mathbf{L}_i + \mathbf{C} + \mathbf{N} + \mathbf{R}_{ij} \quad (2)$$

$$\mathbf{Y}_{ijk} = \mu + \mathbf{L}_i + \mathbf{E}_j + \mathbf{L}\times\mathbf{E}_{ij} + \mathbf{R}_{ijk} \quad (3)$$

$$\mathbf{Y}_{ij} = \mu + \mathbf{N}_i + \mathbf{R}_{ij} \quad (4)$$

Y is a vector of the phenotypic values; **L** is the effect of *i* lines; **E** is the effect of *j* environments; **C** is the effect of the co-variable COD; **N** is the effect of the co-variable neighbouring plot from seriously cold-damaged plots in model (1) and model (2). **N** was used as a fixed effect in model (4); **L×E** is the interaction between *i* lines and *j* environments; **R** is the residual variable. Under the assumption of a mixed model, **L**, **E** and **L×E** as random effects, N and **C** as co-variables without classes.

Model (1) was used to analyze the variations of all traits except for EAR and MAS (in C101) and COD (in both populations); for EAR and MAS in C101, one-way ANOVA [model (2)] was employed to analyze the variation in both populations because these traits were evaluated only at Dikopshof in the season 2002/03; for COD, the model (3) was used for ANOVA in both populations; the model (4) was used to analyze the effects of neighbouring plots.

2.3.2.2 Analysis of genetic correlation

The genetic correlation coefficients were calculated by means of the SAS procedure CORR after the trait performances of each BC_2DH line was averaged by the least square means option across all environments.

2.3.2.3 Detection of putative QTLs

The QTL detection from BC_2DH genetic data and field data from multiple environments was conducted using the procedure GLM (General Linear Model) from the SAS software (SAS Institute 1999). Model (5) was used as the basic model for detection of putative QTLs. If the effect of COD was significant in models (1) or (2), then COD was used as a co-variable for QTL detection in these traits [model (6)]. Likewise, if the effect of N was significant in models (1) or (2), then N was used as a co-variable for QTL detection in these traits [model (7)]. Therefore, the models used to detect QTLs for different agronomic traits, pathogen resistances and non-parasitic browning could be expressed in the following three *split plot mixed models*:

$$\mathbf{Y}_{ijkl} = \mu + \mathbf{M}_i + \mathbf{L}(M)_j + \mathbf{E}_k + \mathbf{M}\times\mathbf{E}_{ik} + \mathbf{R}_{ijkl} \quad (5)$$

$$\mathbf{Y}_{ijkl} = \mu + \mathbf{M}_i + \mathbf{L}(M)_j + \mathbf{E}_k + \mathbf{C} + \mathbf{M}\times\mathbf{E}_{ik} + \mathbf{R}_{ijkl} \quad (6)$$

$$\mathbf{Y}_{ijkl} = \mu + \mathbf{M}_i + \mathbf{L}(M)_j + \mathbf{E}_k + \mathbf{N} + \mathbf{M}\times\mathbf{E}_{ik} + \mathbf{R}_{ijkl} \quad (7).$$

Y is a vector of phenotypic value; **M** is the effect of *i* marker genotypes; **L**(M) is effect of *j* lines, nested in *i* marker genotypes; **E** is the effect of *k* environments; **C** is the effect of the co-variable COD; **N** is the effect of the co-variable neighbouring plot from seriously cold-damaged plots; **M×E** is the interaction between *i* marker genotypes and *j* environments; **R** is the residual variable. Under the assumption of a mixed model, **M** was chosen as fixed effect, **L**(M), **E** and **M**×**E** as random effects and **N** and **C** as co-variables without classes.

Model (5) was used to detect QTLs for all traits except for LR (in both populations), RH (in C101) and YLD (in T101); model (6) was used to detect QTLs for LR in both populations; model (7) was used to detect QTLs for YLD (in T101) and RH in C101 (see Table 4).

Following Stuber et al. (1992), the presence of a stable QTL in the vicinity of a marker locus was accepted, if the marker main effect was significant with $P < 0.01$. Adjacent markers (≤ 20 cM)

which showed the same effect were considered as a single QTL. In addition, the presence of an environment-dependent QTL was accepted, if the M×E interaction was significant with $P < 0.01$. Adjacent markers (≤ 20 cM) which showed the same effect were also considered as a single QTL.

The explained genetic variation as a measure of the strength of a marker main effect (R^2_G) and an M×E interaction (R^2_{GI}), were calculated as follows:

$$R^2_G = SS_M/SS_{Line}$$

$$R^2_{GI} = SS_{M\times E}/SS_{Line}$$

Where SS_M and $SS_{M\times E}$ are the sum of squares of the factors marker and M×E interaction, which were obtained from models (5) – (7); SS_{Line} is the sum of squares of the factor line, which was obtained from models (1) – (3) in the ANOVA across both seasons, 2002/03 and 2003/04.

The relative performance of the homozygous *Hsp* genotype (RP[*Hsp*]) as a measure of the improvement of a trait by replacing both *Hv* elite alleles with the exotic *Hsp* alleles was calculated as follows:

$$RP[Hsp] = \frac{[aa]-[AA]}{[AA]} * 100$$

Where, for each trait, [*AA*] and [*aa*] are the least square means of the homozygous *Hv* and the homozygous *Hsp* genotypes, respectively, calculated across all environments.

2.3.2.4 Definition of favorable exotic QTL allele:

A favorable exotic allele was accepted if LSMEAN [aa] > LSMEAN [AA] for traits where the value of the trait should be increased with respect to the breeding goal (for example YLD) or LSMEAN [aa] < [AA] for traits where the value of the trait should be decreased with respect to the breeding goal (for example PM). The breeding goals of the traits are defined in Table 4.

3. Results

In this study, the goal was to detect favourable effects of QTL alleles, which could improve the agronomic performance, disease resistance and non-parasitic browning of BC_2DH lines, from the wild accession by means of AB-QTL strategy in two BC_2DH winter barley populations C101 and T101. First the genetic correlations between 16 investiagted traits (15 Traits in C101) in two BC_2DH populations are presented. Secondly, ANOVA with factors lines, COD and N (neighbour plot) for both populations are described. Subsequently, the genotyping and genetic constitution of the populations as revealed by SSR marker analysis are presented. Finally, the QTL detection is conducted for 15 (C101) or 16 (T101) traits in both populations by combining the phenotypic data of 15 or 16 investigated traits with the genetic data.

3.1 Analysis of genetic correlation for all traits in both BC_2DH populations

The results of genetic correlation for all evaluated traits in both populations are shown in Table 6. In the following, the genetic correlations are described in each population.

3.1.1 Analysis of genetic correlation for all traits in C101

The results of genetic correlation in C101 are shown in Table 6. Here, following Mohammed (2004), the correlation coefficients are classified into three levels: $r < 0.20$: weak, $0.20 \leq r < 0.50$: moderate and $r \geq 0.50$: strong. In the following, only significant correlations, which are at least moderate, are mentioned. The trait **BS** displayed moderate positive correlations with COD, LOH and P[*Hsp*] and moderate negative correlations with PM, TGW and YLD. For **BSP**, only moderate negative correlation was observed with HEA. Negative and strong correlation was observed for **COD** with YLD (r = - 0.64). Positive and moderate correlation was obtained for COD with BS and P[*Hsp*] and moderate negative correlation with HEA. Strong positive correlation was revealed for **EAR** with MAS (r = 0.78). **HEA** displayed moderate positive correlations with HEI and YLD and moderate negative correlations with BSP, COD, LR and NPB. Positive and moderate correlation was observed for **HEI** with HEA and moderate negative with NPB. **LOH** displayed moderate positive correlation with BS and P[*Hsp*] and moderate negative correlations with TGW and YLD. Only moderate negative correlation was revealed for **LR** with HEA. Strong positive correlation was observed for **MAS** and EAR (r = 0.78). Positive and moderate correlation was revealed for **NB** with NPB and TGW. The correlation appeared to be negative and moderate for **NPB** with HEA and HEA and moderate positive for NPB with NB. **PM** was revealed negative and moderate correlation with BS and moderate positive correlation with LR. **RH** displayed moderate positive correlation with COD and moderate and negative correlation with YLD. The correlation appeared to be

moderate and negative for **TGW** with BS, LOH and P[*Hsp*], but moderate and positive with NB and YLD. For **YLD** and COD, a strong negative correlation was observed, while YLD displayed moderate and negative correlations with BS, LOH, RH and P[*Hsp*] and a moderate and positive correlation with HEA and TGW. The correlation appeared to be positive and moderate for **P[*Hsp*]** with BS, COD and LOH, while negative and moderate correlation was revealed for P[*Hsp*] with EAR, TGW and YLD.

3.1.2 Analysis of genetic correlation for all traits in T101

Table 6 shows the results of genetic correlation in T101. The correlation appeared to be negative and moderate for **BS** with HEA, HEI and NB, while positive and moderate correlation was revealed for BS with BSP, HI and LR. For **BSP**, negative and moderate correlation was observed with HEA, HEI and LOH and positive and moderate correlation with BSP and YLD. **COD** displayed moderate positive correlation with HI, LOH, LR and RH and moderate negative correlation with TGW and YLD. Strong positive correlation was observed for **EAR** with MAS. EAR displayed moderate positive correlations with HI and LR and moderate negative correlations with RH and TGW. **HEA** displayed a moderate negative correlation with BS and BSP and a moderate positive correlation with HEI. **HEI** displayed moderate negative correlations with BS, BSP, HI, LR and RH and a moderate positive correlation with HEI. The correlations appeared to be moderate positive for **HI** with BS, COD, EAR, RH, and YLD and moderate negative correlations with HEI. Positive and moderate correlations were revealed for **LOH** with COD and EAR, while the correlations for LOH with TGW and YLD appeared to be negative and moderate. **LR** displayed moderate positive correlations with BS and COD and moderate negative correlations with HEI and TGW. A strong correlation was obtained for **MAS** with EAR, while moderate negative correlation was revealed between MAS and RH. **NB** showed negative and moderate correlations with BS and PM. **NPB** displayed only moderate negative correlation with YLD. Negative and moderate correlations were observed for **PM** with NB and RH. The correlations appeared to be negative and moderate for **RH** with EAR, HEI, MAS and PM, whereas positive and moderate correlations were revealed for RH with COD and HI. Negative and moderate correlations were observed for **TGW** with COD, EAR, LOH and LR, while a moderate positive correlation was revealed between TGWand YLD. YLD displayed moderate negative correlations with COD and LOH and moderate positive correlation with TGW. **P[*Hsp*]** revealed no significant correlation with other traits.

Table 6: Genetic correlation coefficients (r) between 16 quantitative traits[1)] acoss up to six environments and P[*Hsp*] in C101 and T101

Trait	BS	BSP	COD	EAR	HEA	HEI	HI	LOH	LR	MAS	NB	NPB	PM	RH	TGW	YLD	P[*HSP*]
BS		0,17 **	0,27 ***	0,09	-0,14 *	0,03		0,36 ***	-0,11	0,04	0,13 *	0,01	-0,26 ***	0,13 *	-0,27 ***	-0,32 ***	0,35 ***
BSP	0.34 ***		-0,17 **	-0,07	-0,21 ***	-0,05		0,05	-0,08	-0,13 *	0,12 *	0,05	-0,15 **	-0,10	-0,06	0,15 *	0,03
COD	0.19 *	-0.07		-0,05	-0,21 ***	-0,08		0,15 *	-0,07	0,05	-0,01	0,08	0,07	0,40 ***	-0,19 **	-0,64 ***	0,28 ***
EAR	0.05	0.11	-0.12		0,15 *	-0,13 *		0,06	0,05	0,78 ***	-0,03	-0,04	0,03	-0,06	-0,12 *	0,05	-0,20 ***
HEA	-0.22 *	-0.27 **	0.06	0.07		0,35 ***		-0,17 **	-0,20 ***	0,05	-0,16 **	-0,29 ***	-0,13 *	-0,06	-0,06	0,37 ***	-0,15 **
HEI	-0.32 **	-0.22 *	-0.10	-0.05	0.41 ***			0,13 *	-0,14 *	0,05	-0,10	-0,23 ***	-0,17 **	-0,16 **	0,16 **	0,18 **	-0,04
HI	0.24 *	0.09	0.30 **	0.23 *	-0.13	-0.43 ***											
LOH	-0.14	-0.24 *	0.28 **	0.21 *	0.19	0.12	-0.01		0,07	0,06	-0,19 **	-0,11	-0,02	0,04	-0,36 ***	-0,40 ***	0,07
LR	0.23 *	0.07	0.25 **	0.01	-0.16	-0.32 ***	0.16	-0.03		0,02	-0,19 **	-0,04	0,20 ***	0,10	-0,04	0,00	0,37 ***
MAS	-0.01	0.13	-0.02	0.79 ***	0.12	0.19 *	0.17	0.15	-0.13		0,02	0,00	0,03	-0,06	0,13 *	0,07	0,10
NB	-0.25 **	-0.13	-0.19	-0.01	0.15	0.03	-0.10	-0.05	-0.12	0.02		0,44 ***	-0,18 **	-0,15 **	0,22 ***	-0,01	-0,03
NPB	-0.13	0.00	-0.01	-0.03	-0.14	-0.08	-0.07	0.01	-0.16	0.05	0.09		0,11	-0,18 **	0,08	-0,08	0,09
PM	0.13	0.05	-0.08	0.03	-0.10	0.02	-0.05	0.01	0.02	0.06	-0.26 **	0.14		-0,14 *	-0,06	0,03	-0,16 **
RH	0.19	-0.08	0.28 **	-0.23 *	-0.15	-0.31 **	0.20 *	-0.09	0.19	-0.20 *	-0.08	-0.17	-0.32 ***		-0,14 *	-0,32 ***	-0,05
TGW	-0.06	0.10	-0.25 *	-0.21 *	-0.19 *	-0.02	0.09	-0.37 ***	-0.20 *	-0.05	0.12	0.08	0.11	0.00		0,31 ***	0,18 *
YLD	0.01	0.21 *	-0.40 ***	0.03	0.16	-0.12	0.20 *	-0.27 **	0.04	0.02	0.13	-0.24 *	0.03	-0.08	0.39 ***		-0,49 **
P[*HSP*]	0.06	0.02	0.00	0.04	-0.01	-0.10	0.11	0.14	0.01	0.03	0.03	0.00	0.07	-0.12	0.03	0.07	

[1)] Abbreviation for traits: BS, Breaking of stem; BSP, Bending of spike; COD, Cold damage; EAR, Number of spikes; HEA, Days until heading; HEI, Plant Height; HI, Harvest index; LOH, Lodging at harvest; LR, Leaf rust; MAS, Biomass; NB, net blotch; NPB, Non-parasitic browning; PM, Powdery mildew; RH, leaf scald; TGW, Thousand-grain weight; YLD, Yield. The genetic correlation coefficients with grey background and white background were from C101and T101, respectively. Harvest index (HI) was only measured in T101. *, **, ***: Significant at 0.05, 0.01 and 0.001 levels, respectively P[*Hsp*]: Percentage of Hsp alleles per line.

3.2 The effect of cold damage on other traits

In this chapter, the effect of cold damage during the winter 2002/03 on other agronomic traits, pathogen resistances and non-parasitic browning will be presented by means of ANOVA and correlation analysis.

3.2.1 Analysis of variance for cold damage in 2002/03

In the season 2002/03, a considerable number of lines from C101 and T101 were seriously damaged by extremely low-temperatures in all environments. Figure 2 shows the distribution of COD in both populations. The COD scores of each line were averaged by the least square means option across all environments. Though the graphic shapes of the COD distributions were different in both populations, the statistical parameters were the same or similar. For instance, in C101 the mean of COD was 4.3 with a minimum by 2.4 and a maximum by 8.2 and the mean of COD was 4.3 with a minimum by 2.7 and a maximum by 8.1 in T101. In order to reveal whether the tolerance against low-temperature were different among lines with different exotic donor segments, the ANOVA was performed for COD based on all environments in 2002/03 season. The results of ANOVA indicated that the variations of COD among lines, environments and the interaction between lines and environment were highly significant ($P < 0.001$) in both populations (Table 8). In other words, the cold tolerance was significantly different between lines, which carried different wild alleles.

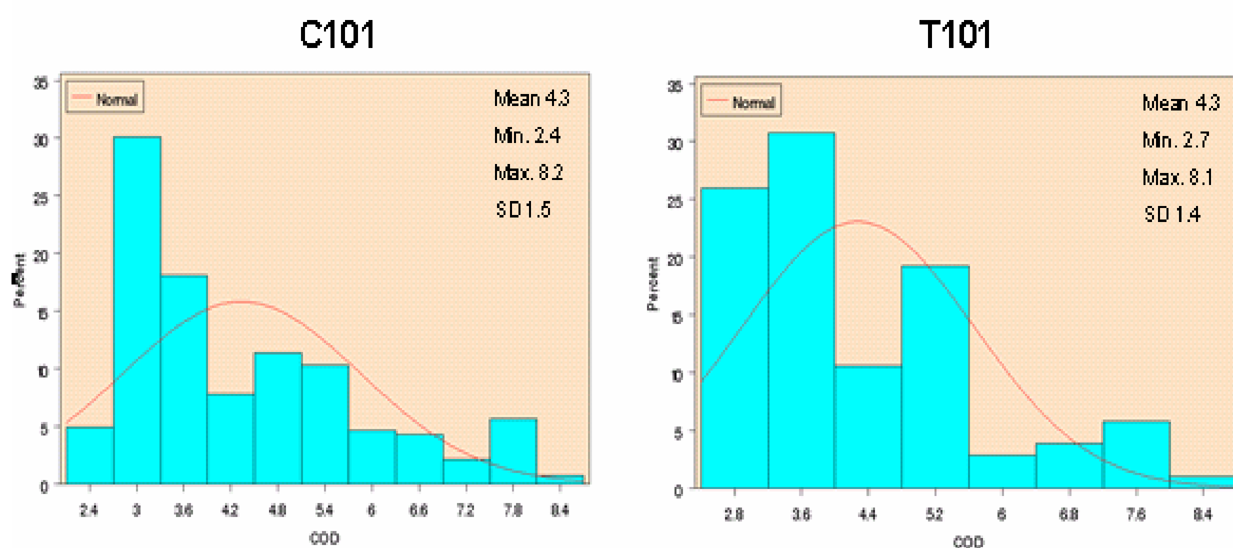


Figure 2: Distribution of cold damage scores (LSMeans) in two populations in 2002/03 across five environments. C101 and T101 consist of 282 and 104 BC_2DH lines, respectively.

Table 7: Analysis of variance for COD in 2002/03 in C101 and T101 applying model (3)

	Source[1)]	DF	MS	F	P
C101	Line	286	17.22	7.42	< 0.001
	Error	1195.5402	2.32		
	E	4	2128.72	881.15	< 0.001
	Error	1161.30	2.42		
	Line*E	1129	2.52	3.96	< 0.001
	Error: MS(Error)	1924	0.64		
T101	Line	108	13.74	5.34	< 0.001
	Error	431.23	2.57		
	E	4	1117.89	446.73	< 0.001
	Error	438.13	2.50		
	Line*E	422	2.68	4.82	< 0.001
	Error: MS(Error)	783	0.56		

[1)] E: Environment.

3.2.2 Analysis of the effects of seriously cold-damaged plots on their neighbouring plots in 2002/03

The effect of seriously cold-damaged plots on their neighbouring plots will be presented by means of ANOVA and comparison of means between normal plots, seriously cold-damaged plots and their neighbouring plots. Simultaneously, the effects of COD on other traits will be analyzed by means of analysis of correlation.

3.2.3 Correlation analysis between COD and other traits in C101 and T101 in 2002/03

The results of correlation analysis between COD and other traits (BS, BSP, EAR, HEA, HEI, HI, LOH, LR, MAS, NB, NPB, PM, RH, TGW, YLD and P[*Hsp*] are shown in Table 9.

In C101, COD showed positive and moderate correlations with RH and P[*Hsp*]. Negative and moderate correlation was observed for COD with BSP and NB. COD was strongly and negatively correlated with YLD.

In T101, COD displayed positive and moderate correlations with BS, HI and LOH. A negative and strong correlation was obtained between COD and YLD.

Table 8: Pearson's correlation coefficients (r) between COD and other quantitative traits[1)] in C101 and T101 in 2002/03

	C101		T101	
Trait	**COD**	**P**	**COD**	**P[3)]**
BS	0.22	***	0.26	*
BSP	-0.38	***	-0.03	ns
EAR	-0.06	ns	-0.21	*
HEA	-0.03	ns	0.17	ns
HEI	-0.15	**	-0.22	*
HI	n.a		0.33	***
LOH	0.18	**	0.28	**
LR	-0.04	ns	0.16	ns
MAS	0.05	ns	-0.05	ns
NB	-0.30	***	-0.22	*
NPB	0.01	ns	-0.05	ns
PM	0.19	**	-0.13	ns
RH	0.28	***	0.16	ns
TGW	-0.15	*	-0.18	ns
YLD	-0.68	***	-0.51	***
P[*Hsp*][2)]	0.27	***	0.01	ns

[1)] Abbreviation of traits: BS, Breaking of stem; BSP, Bending of spike; COD, Cold damage; EAR, Number of spikes; HEA, Days until heading; HEI, Plant Height; HI, Harvest index; LOH, Lodging at harvest; LR, Leaf rust; MAS, Biomass; NB, net blotch; NPB, Non-parasitic browning; PM, Powdery mildew; RH, leaf scald; TGW, Thousand-grain weight; YLD, Yield. [2)] P[*Hsp*]: *Hsp* % in line. [3)] *, **, ***: Significant at 0.05, 0.01 and 0.001 levels, respectively. ns: not significant. n.a: not analyzed.

3.2.3.1 Analysis of variance for normal plots, seriously cold-damaged plots and their neighboring plots in 2002/03

The results of ANOVA for C101 and T101 between normal plots (N = 0), seriously cold-damaged plots (N = 1, in the following termed ‘cold-damaged plot’) and their neighboring plots (N = 2, hereafter termed ‘neighbour plot’) are presented in Table 10 and Table 11. In C101 (Table 10), the variation between normal plots, cold-damaged plots and neighbouring plots was at least significant ($P < 0.05$) for BS, BSP, HEI, LOH, LR, NB, RH, TGW and YLD.

The results of ANOVA for normal plots, cold-damaged plots and neighbouring plots in T101 (Table 11) were slightly different from C101. The variation between normal plots, cold-damaged plots and neighbouring plots was at least significant ($P < 0.05$) for BS, HEA, HEI, HI, LOH, LR, NB, RH, TGW and YLD.

Table 9: Analysis of variance for all traits between normal plots, seriously cold-damaged plots and their neighbour plots in C101 in season 2002/03 [applying model (4)]

Trait[1)]	Source	DF	SS	MS	F	P[2)]
BS	Model	2	66.02	33.01	5.46	< 0.01
	Error	707	4273.03	6.04		
BSP	Model	2	69.96	34.98	7.35	< 0.001
	Error	701	3334.91	4.76		
EAR	Model	2	18242.08	9121.04	0.45	ns
	Error	299	6121516.12	20473.30		
HEA	Model	2	449.20	224.60	2.85	ns
	Error	902	71097.57	78.82		
HEI	Model	2	5023.45	2511.72	5.12	< 0.01
	Error	828	406360.54	490.77		
LOH	Model	2	58.36	29.18	4.02	< 0.05
	Error	813	5904.54	7.26		
LR	Model	2	11.00	5.50	5.82	< 0.01
	Error	954	901.77	0.95		
MAS	Model	2	1276.76	638.38	1.02	ns
	Error	298	186916.36	627.24		
NB	Model	2	34.93	17.47	6.93	< 0.01
	Error	954	2405.35	2.52		
NPB	Model	2	11.79	5.90	2.28	ns
	Error	954	2469.14	2.59		
PM	Model	2	16.19	8.10	2.28	ns
	Error	954	3380.43	3.54		
RH	Model	2	154.23	77.11	16.98	< 0.001
	Error	954	4332.82	4.54		
TGW	Model	2	426.04	213.02	6.79	< 0.01
	Error	866	27168.57	31.37		
YLD	Model	2	1978048.80	989024.40	22.15	< 0.001
	Error	862	38488275.65	44649.97		

[1)] Abbreviation for traits: BS, Breaking of stem; BSP, Bending of spike; COD, Cold damage; EAR, Number of spikes; HEA, Days until heading; HEI, Plant Height; HI: Harvest index; LOH, Lodging at harvest; LR, Leaf rust; MAS, Biomass; NB, net blotch; NPB, Non-parasitic browning; PM, Powdery mildew; RH, leaf scald; TGW, Thousand-grain weight; YLD, Yield. [2)] ns: not significant.

Table 10: Analysis of variance for all traits between normal plots, seriously cold-damaged plots and their neighbour plots in T101 in season 2002/03 [applying model (4)]

Trait[1)]	Source	DF	SS	MS	F	P[2)]
BS	Model	2	31.51	15.76	6.23	< 0.01
	Error	194	490.99	2.53		
BSP	Model	2	12.59	6.30	2.30	ns
	Error	207	565.81	2.73		
EAR	Model	2	28294.22	14147.11	0.67	ns
	Error	110	2307073.71	20973.40		
HEA	Model	2	507.35	253.68	4.76	< 0.01
	Error	338	17998.41	53.25		
HEI	Model	2	10041.02	5020.51	9.13	< 0.001
	Error	336	184759.79	549.88		
HI	Model	2	0.02	0.01	3.46	< 0.05
	Error	110	0.27	0.00		
LOH	Model	2	134.97	67.48	9.46	< 0.001
	Error	326	2325.26	7.13		
LR	Model	2	48.91	24.45	10.42	< 0.001
	Error	397	931.53	2.35		
MAS	Model	2	1276.98	638.49	1.06	ns
	Error	110	66182.03	601.65		
NB	Model	2	10.08	5.04	3.42	< 0.05
	Error	397	585.40	1.47		
NPB	Model	2	1.47	0.74	0.27	ns
	Error	398	1097.72	2.76		
PM	Model	2	23.44	11.72	1.99	ns
	Error	397	2336.40	5.89		
RH	Model	2	34.15	17.08	3.96	< 0.05
	Error	397	1712.29	4.31		
TGW	Model	2	324.92	162.46	5.11	< 0.01
	Error	325	10325.90	31.77		
YLD	Model	2	489625.11	244812.56	8.76	< 0.001
	Error	325	9084544.39	27952.44		

[1)] Abbreviation for traits: BS, Breaking of stem; BSP, Bending of spike; COD, Cold damage; EAR, Number of spikes; HEA, Days until heading; HEI, Plant Height; HI, Harvest index; LOH, Lodging at harvest; LR, Leaf rust; MAS, Biomass; NB, net blotch; NPB, Non-parasitic browning; PM, Powdery mildew; RH, leaf scald; TGW, Thousand-grain weight; YLD, Yield. [2)] ns: not significant.

3.2.3.2 Comparisons of means between normal plots, seriously cold-damaged plots and their neighbour plots in C101 and T101

The results of mean comparisons between normal plots, cold-damaged plots and neighbour plots for traits, which were significant in for C101 and T101 are shown in Table 12 and Table 13.

Table 11: Comparison of means averaged across five environments in season 2002/03 between normal plots, seriously cold-damaged plots and their neighbour plots in C101 by means of a Duncan test

Trait[1)]	Method	Significant[2)]	Mean	Number of plots	Level[3)]
BS	Duncan	A	4.24	41	1
		B	3.42	549	0
		B	2.84	120	2
BSP	Duncan	A	5.16	123	2
		A	4.66	539	0
		B	3.69	42	1
HEI	Duncan	A	105.82	85	1
		A	105.18	136	2
		B	99.88	610	0
LOH	Duncan	A	4.98	55	1
		B	3.97	622	0
		B	3.81	139	2
LR	Duncan	A	1.31	769	0
		B	1.13	68	1
		B	1.00	120	2
NB	Duncan	A	2.52	120	2
		B	2.04	769	0
		B	1.68	68	1
RH	Duncan	A	4.25	68	1
		A	3.97	120	2
		B	3.07	769	0
TGW	Duncan	A	42.02	142	2
		A	41.04	669	0
		B	38.80	58	1
YLD	Duncan	A	827.56	141	2
		B	719.96	666	0
		C	630.79	58	1

[1)] Abbreviation for traits: BS, Breaking of stem; BSP, Bending of spike; COD, Cold damage; EAR, Number of spikes; HEA, Days until heading; HEI, Plant Height; HI, Harvest index; LOH, Lodging at harvest; LR, Leaf rust; MAS, Biomass; NB, net blotch; NPB, Non-parasitic browning; PM, Powdery mildew; RH, leaf scald; TGW, Thousand-grain weight; YLD, Yield. [2)] Significant at 0.05 level. [3)] Level: 1 represents seriously cold-damaged plots; 2 represents neighbouring plots of seriously cold-damaged plots; 0 represents normal plots in 2003/03.

In C101 (Table 12): 1 (cold-damaged plots) were increased relative to 0 (normal plots) and 2 (neighbouring plots) for BS and LOH and decreased relative to 0 and 2 for BSP and TGW; 1 and 2 were increased relative to 0 for HEI and RH and decreased for LR; 2 was increased relative to 0 and 1 for NB; 2 was increased relative to 0 and 0 was increased relative to 1 for YLD.

Table 12: Comparison of means averaged across five environments in season 2002/03 between normal plots, seriously cold-damaged plots and their neighbour plots in T101 by means of a Duncan test

Trait[1]	Method	Significant[2]	Mean	Number of plots	Level[3]
BS	Duncan	A	4.33	6	1
		B	2.30	158	0
		B	1.85	33	2
HEA	Duncan	A	64.12	26	1
		B	60.86	42	2
		B	59.62	273	0
HEI	Duncan	A	112.19	42	2
		A	109.27	26	1
		B	97.58	271	0
HI	Duncan	A	0.58	11	1
		B	0.56	19	2
		B	0.54	83	0
LOH	Duncan	A	6.14	14	1
		A	5.71	273	0
		B	3.83	42	2
LR	Duncan	A	2.00	321	0
		B	1.20	25	1
		B	1.09	54	2
YLD	Duncan	A	845.83	42	2
		B	731.35	272	0
		B	715.76	14	1

1) Abbreviation for traits: BS, Breaking of stem; HEA, Days until heading; HEI, Plant Height; HI, Harvest index; LOH, Lodging at harvest; LR, Leaf rust; YLD, Yield. 2) Significant at 0.05 level. 3) Level: 1 represents seriously cold-damaged plots; 2 represents neighbouring plots of seriously cold-damaged plots; 0 represents normal plots in 2003/03.

In T101 (Table 13): Level 1 was increased relative to 0 and 2 for BS, HEA and HI; 1 and 2 were increased relative to 0 for HEI and decreased relative to 0 for LR; 2 increased relative to 1 and 0 for YLD and decreased relative to 0 and 1 for LOH.

3.3 Analysis of variance for all traits including data from 2002/03 and 2003/04 in both BC_2DH populations

In order to detect if the lines, COD and N (neighbouring plots) effects were significant, the analyses of variance were performed for all traits including data from 2002/03 and 2003/04 in both populations. The results of ANOVA performed by means of models (1) – (4) for all traits including data from 2002/03 and 2003/04 seasons in C101 and T101 were showed in Appendix 1 and 2.

3.3.1 Analysis of variance for all traits in C101 in seasons 2002/03 and 2003/04

In C101 (Appendix 1), the variations for BS, BSP, COD, HEA, LOH, NB, NPB, PM, TGW and YLD were highly significant among lines, environments and the interaction between line and environment. For EAR and MAS, no significant variation was observed among lines and both co-variables COD and N. Highly significant variations were obtained for HEI and LR among lines and environments, while the interaction between line and environment did not reach the significant level at $P < 0.05$. The effect of N was significant on HEI and RH at the level $P < 0.05$. The effect of COD on LR was significant at $P < 0.001$. For both co-variables N and COD, no significant variation was observed for other evaluated traits except for HEI, LR and RH.

3.3.2 Analysis of variance for all traits in T101 in seasons 2002/03 and 2003/04

In T101 (Appendix 2), the variations for BSP, HEA, LOH, NPB, PM and TGW were highly significant among lines, environments, and the variation of the interaction between line and environments also reached the significant level of $P < 0.05$ or more. For BS and NB, the variations of lines were not significant, however, the variations of the interaction between line and environments were significant, and the variations of environments were highly significant. No significant variation was obtained for EAR among lines, environments, the interaction between line and environment and both co-variables COD and N. For HEI, HI and RH, the variations were highly significant among lines and environments, while the variations were not significant among COD, N and the interaction between line and environment. The variation of lines for LR did not reach the significant level at $P < 0.05$, but the variation of the interaction between line and environment was significant at $P < 0.01$. Simultaneously, the effect of COD on LR was significant at $P < 0.01$. For MAS, only the variation of environments was highly significant. The variations for YLD were highly significant among lines, environments and the interaction between line and environment. The effect of N on YLD was significant at $P < 0.01$. No significant effect of COD was observed for all traits except for LR, while a significant effect of N was only obtained for YLD.

In both populations, the effect of COD on LR, and the effect of the co-variable N on YLD were significant. In addition, the effect of N on HEI and RH was significant in C101. No significant effect on EAR was observed in both populations. For MAS, only a significant effect in T101 was observed.

3.4 Genotyping of two BC_2DH populations

Eighty-two and 78 polymorphic SSR markers were successfully genotyped in C101 and T101, respectively (Table 13 Table 14 and Figure 3). The software program Graphical Genotypes (GGT, Van Berloo 1999) was used to illustrate the graphical genotypes from the BC_2DH population. Linkage distances between SSR markers were taken from von Koff et al. (2004). The genotyped markers were distributed over all seven chromosomes and covered 1,225 cM of the barley genome in both populations (Figure 3). The average distance between markers was 14.9 cM in C101, but 16.3 cM in T101. However, the distribution of SSR markers on individual chromosomes was uneven. In C101, the distribution of markers ranged from 9 – 14 SSRs with an average of 11.7, but in T101 from 8 – 16 SSRs with an average of 11.1. In addition, distinct clusters of markers and gaps (> 30 cM) were observed on chromosome. In C101, the gaps were observed: one gap was observed on chromosome of 1H, 2H, 3H and 7H and two gaps were observed on chromosomes 4H, 5H and 6H, respectively. In T101, eleven gaps were observed: one gap was observed on chromosomes 1H, 3H, 4H and 7H, two gaps were discovered on chromosomes 2H and 6H and three were present on chromosome 5H.

Among the BC_2DH lines, the percentage of *Hsp* genome ranged from 0 to 32.5% with an average of 13.2% in C101, but from 1.3 to 30.8% with an average of 13.7% in T101. This fits with the expected donor introgression of 12.5% in a BC_2DH population.

Table 13: Number of genotyped markers in C101

Chromosome	Number of mapped markers	Genome coverage (cM)	Marker density (cM per mapped marker)	Number of gaps (> 30 cM)
1H	11	175	15.9	1
2H	10	150	15.0	1
3H	14	190	13.6	1
4H	14	190	13.6	2
5H	11	187	17.0	2
6H	9	155	17.2	2
7H	13	178	13.7	1
Total	82	1225	106.0	10
Mean	11.7	175.0	14.9	1.4

Table 14: Number of genotyped markers in T101

Chromosome	Number of mapped markers	Genome coverage (cM)	Marker density (cM per mapped marker)	Number of gaps (> 30 cM)
1H	11	175	15.9	1
2H	8	150	18.8	2
3H	12	190	15.8	1
4H	16	190	11.9	1
5H	10	187	18.7	3
6H	8	155	19.4	2
7H	13	178	13.7	1
Total	78	1225	114.2	11
Mean	11.1	175.0	16.3	1.6

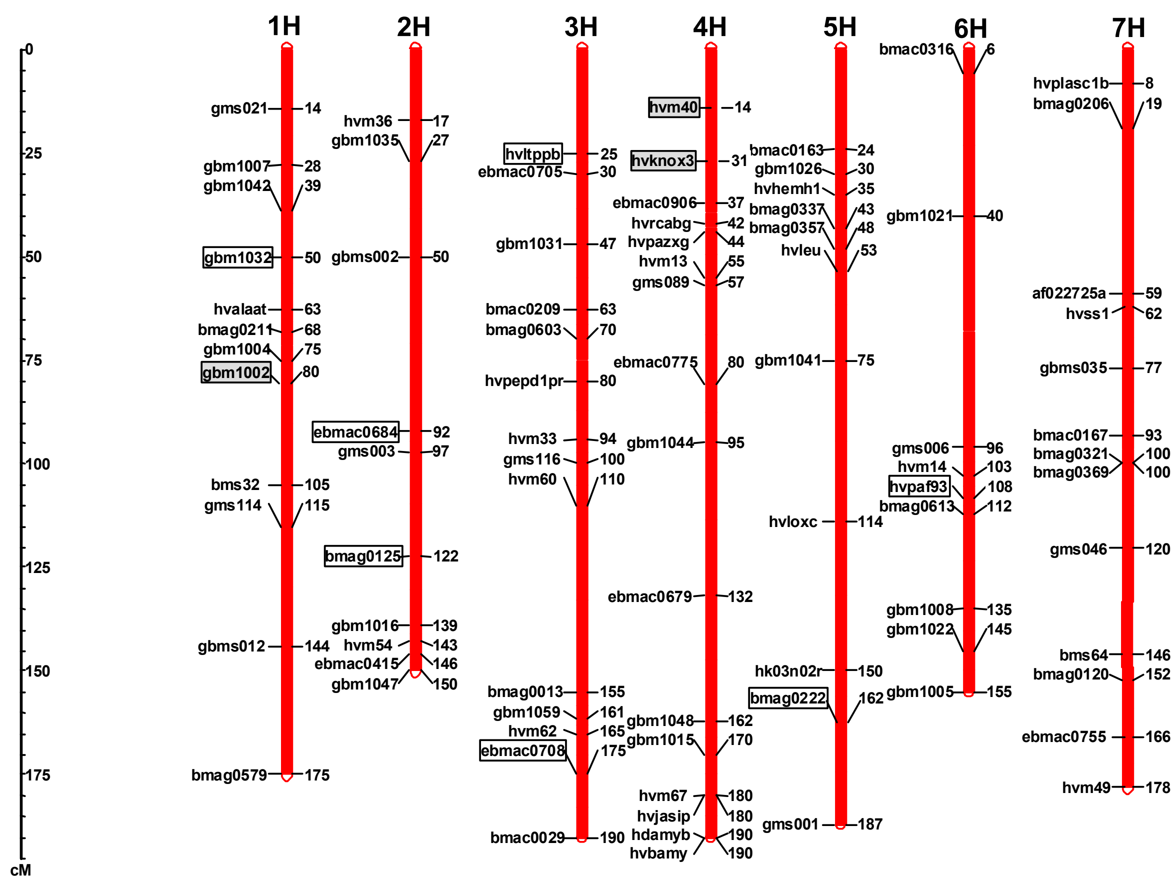


Figure 3: Linkage map from the two BC$_2$DH winter barley populations C101 and T101. The map contains 85 polymorphic SSR markers, which were genotyped in both populations. The framed seven markers with white background were only polymorphic in C101; the framed three markers with grey background were only polymorphic in T101. The SSR marker order is based on von Korff et al. (2004), Ramsay et al. (2000) and on calculation with MAPMARKER software (Lander et al. 1987).

3.5 Results of the AB-QTL analysis in two BC_2DH winter barley populations

A single-point analysis by means of a multi-factorial ANOVA (split plot mixed model) rather than interval mapping was used for QTLs analysis because data from multiple environments should be integrated.

Putative QTLs for each trait are listed in Table 17 and Table 19 and their map positions are shown in Fig. 4. As stated in the methods section, the presence of a stable QTL in the vicinity of a marker locus was accepted, if the marker main effect was significant with $P < 0.01$. Adjacent markers (≤ 20 cM) which showed the same effect were considered as a single QTL. In addition, the presence of an environment-dependent QTL was accepted, if the M×E interaction was significant with $P < 0.01$. Adjacent markers (≤ 20 cM) which showed the same effect were also considered as a single QTL. The complete list of significant marker main effects and M×E interactions detected in C101 and T101 are shown in Appendix 3 (C101) and Appendix 4 (T101).

In this study, the QTL effects were divided into three groups: **favorable QTL effects**, where the marker main effect or M×E interaction effect of the *Hsp* genotype improves the trait in regard to the breeding goal across all environments; **unfavorable QTL effects**, where the marker main effect or M×E interaction effect of the *Hsp* genotype deteriotes the trait in regard to the breeding goal across all environments; **crossover interaction QTL effects**, where the M×E interaction reveals a crossover interaction where the *Hsp* genotype is favorable in some environments but unfavorable in other environments (Table 17, Table 19, Appendix 6 and Appendix 7). In total, 268 putative QTLs for eleven agronomic traits, four pathogen resistances and one syndrome were detected among 2,478 marker × trait combinations in both BC_2DH populations (Table 15, Table 16 and Figure 4). At 93 putative QTLs, the marker main effect and at 207 putative QTLs, the M × E interactions were significant at $P < 0.01$ (Table 17, Table 18 and Table 19). In 32 cases, both effects were significant. Among these putative QTLs, 48 (17.9 %) exotic favorable QTL effects were identified. Although the two populations shared the same donor, the number of detected QTLs and favorable exotic alleles for agronomic traits, pathogen resistances and non-parasitic browning were very different between the two populations.

Much more putative QTLs and favorable exotic QTL alleles were detected in C101 than in T101. In C101, 82 polymorphic SSR markers revealed in total 183 putative QTLs of which 115 putative QTLs were associated with agronomic traits and 68 putative QTLs were associated with disease resistances and non-parasitic browning. Thirty-five (19.1 %) favorable QTL effects were identified among the 183 putative QTLs in C101 of which 22 favorable QTL effects were for agronomic traits and 13 favorable QTLs for pathogen resistances and non-parasitic browning. However, 85 putative QTLs were detected by 78 polymorphic SSRs in T101 of which 67 putative

QTLs were associated with agronomic traits and 18 putative QTLs were for pathogen resistances and non-parasitic browning. Only 13 (15.3 %) favorable exotic QTL alleles were identified from 85 putative QTLs of which all of 13 favorable QTL effects were associated with agronomic traits and no favourable exotic QTL alleles for disease resistances and non-parasitic browning.

The putative QTLs and favorable exotic QTL alleles were unevenly distributed over the chromosomes in both populations (Table 15 and Table 17). The great majority of putative QTLs were located on chromosome 1H, 5H, 6H and 7H in C101, but on 1H, 3H, 4H and 6H in T101. For favorable exotic QTL alleles, 25 (71.4 %) favorable exotic QTL alleles were detected on 1H, 2H, 3H and 7H in C101; however, almost 50 % favorable exotic QTL alleles were located on chromosome 1H in T101.

Among the seven chromosomes, 1H carried the highest number of putative QTLs, while the highest number of favorable exotic QTL alleles were detected on chromosome 2H in C101, for instance, 34 (18.8 %) putative QTLs and 7 (20.0 %) favorable exotic QTL alleles were located on chromosome 1H and 7H, respectively. However, the highest number of putative QTLs 28 (32.9 %) and favorable exotic QTL alleles 6 (46.2 %) were simultaneously detected on chromosome 1H in T101. No favorable QTL effect was detected on chromosomes 2H and 3H in T101.

Table 15: Number of putative QTLs and favorable exotic alleles for agronomic traits and pathogen resistances in C101

Chr[1)]	Number of putative QTLs	Number of favorable exotic QTL alleles	Number of QTLs for AT[2)]	Number of favorable exotic QTL alleles for AT	Number of QTLs for PS[3)]	Number of favorable exotic QTL alleles for PS
1H	34	6	22	6	12	0
2H	21	7	11	4	10	3
3H	15	6	9	4	6	2
4H	18	4	13	4	5	0
5H	33	3	23	1	10	2
6H	34	3	18	1	16	2
7H	28	6	19	2	9	4
Total	183	35	115	22	68	13
Mean	26.1	5.0	16.4	3.1	9.7	1.9

[1)] Chromosome. [2)] AT: agronomic trait. [3)] PS: pathogen resistances and syndrome.

The distribution of putative QTLs among the 85 genotyped SSR markers in both populations was also uneven (Table 17, Table 18, Table 19 and Figure 4). Marker $GBM1041_{[5H]}$ showed putative QTL effects on ten traits (BS, BSP, COD, HEA, HEI, LOH, NB, PM, TGW and YLD) in C101, and marker $GBM1002_{[1H]}$ was associated with six traits (BSP, HEA, HEI, HI, NB and NPB) in T101. The marker interval BMS32-GMS114 on chromosome 1H showed putative QTL effects

on eight traits (BS, COD, LOH, LR, NB, RH, TGW and YLD) in C101. However, markers GMS003$_{[2H]}$, GBM0125$_{[2H]}$ and Ebmac0775$_{[4H]}$ were not associated with any QTL effect. In the following, the detected putative QTLs are described in both populations separately.

Table 16: Number of putative QTLs and favorable exotic alleles for agronomic traits and pathogen resistances in T101

Chr[1)]	Number of putative QTLs	Number of favorable exotic QTL alleles	Number of QTLs for AT[2)]	Number of favorable exotic QTL alleles for AT	Number of QTLs for PS[3)]	Number of favorable exotic QTL alleles for PS
1H	28	6	23	6	5	0
2H	3	0	3	0	0	0
3H	12	0	8	0	4	0
4H	17	2	15	2	2	0
5H	9	1	7	1	2	0
6H	12	2	8	2	4	0
7H	4	2	3	2	1	0
Total	85	13	67	13	18	0
Mean	12.1	1.9	9.6	1.9	2.6	0.0

[1)] Chromosome. [2)] AT: agronomic trait. [3)] PS: pathogen resistances and syndrome.

3.5.1 Detection of QTLs for all of evaluated traits in C101

In this study, the QTL-analysis was performed for the ten agronomic traits breaking of stem (BS), bending of spike (BSP), cold damage (COD), days until heading (HEA), plant height (HEI), lodging at harvest (LOH), biomass (MAS), number of spikes per square metre (EAR), thousand-grain weight (TGW) and yield (YLD) and for the four pathogen resistances leaf rust (LR), net blotch (NB), powdery mildew (PM) and leaf scald (RH) and for non-parasitic browning (NPB) in population C101. Altogether, 35 (19.1 %) favorable QTL effects were identified from 183 putative QTLs for ten agronomic traits, four pathogen resistances and one syndrome (Table 17, Table 18 and Figure 4). At these loci, the homozygous *Hsp* genotype was associated with an improvement of the trait compared to the homozygous *Hv* genotype. The detailed results of QTL-analysis for agronomic traits and pathogen resistances are described in the following.

3.5.1.1 Detection of QTLs for agronomic traits in C101

For eight agronomic traits, 115 putative QTLs were detected in C101. Among these loci, 22 favorable QTL effects were identified. Most of putative QTLs were located on chromosomes 1H, 5H, 6H and 7H. Favorable QTL effects were mainly detected on chromosomes 1H, 2H, 3H and 7H. In the following, the detected QTLs are described for each trait.

Breaking of stem (BS)

Altogether, 15 putative QTLs were located for BS on all chromosomes except for 3H. All loci showed significant M×E interaction at $P < 0.01$ except for *QbsC101-1Hb*, where the marker main effect was significant at Bmag0211$_{[1H]}$ and the M×E interaction was significant at the adjacent locus GBM1004$_{[1H]}$. At five QTLs, which were detected at Ebmac0684$_{[2H]}$, Bmag0613$_{[6H]}$, GBM1008$_{[6H]}$, HvSS1$_{[7H]}$ and Ebmac0755$_{[7H]}$, the *Hsp* allele exhibited crossover interaction on BS. At these loci, the presence of the *Hsp* allele was associated with a decreased BS of up to 18.5 % (GBM1008$_{[6H]}$). Most of the *Hsp* alleles showed unfavorable effects on BS. They were detected on all chromosomes except for 3H and 6H. Especially on chromosome 1H, 4H and 5H, the introgressed exotic alleles could lead to an increase in BS. At these loci, the presence of the *Hsp* allele was associated with an increased breaking of stem of up to 23.8 % (GBM1048-HvBAMY$_{[4H]}$).

Bending of spike (BSP)

Five putative QTLs were located for BSP on chromosomes 1H, 5H and 6H. Four loci showed significant M×E interaction and at HvLOXC$_{[5H]}$ a significant marker main effect was found. Only at GMS114$_{[1H]}$, the crossover interaction of the *Hsp* allele showed a decreased BSP of 4.1 %. However, at the remaining QTLs, the *Hsp* allele showed unfavorable effects on BSP. At these loci, the presence of the *Hsp* allele could lead to an increased bending of spike of up to 14.8 % (HvLOXC$_{[5H]}$). The highest portion of the genetic variance was explained by HvLOXC$_{[5H]}$ (1.7 %).

Cold damage (COD)

Fifteen putative QTLs were located for COD on all chromosomes. At seven QTLs, a significant marker main effect was obtained. The interaction between marker and environment was significant at eleven loci. In six cases, the marker main effect as well as the interaction was significant. At two QTLs, which were located at EBmac0684$_{[2H]}$ with marker main effect and at GBM1008$_{[6H]}$ with interaction effect, the presence of the *Hsp* allele was associated with a reduced cold damage score of up to 31.3 % (EBmac0684$_{[2H]}$). In addition, four crossover interaction effects were detected at Bmag0579$_{[1H]}$, GBM1016-EBmac0415$_{[2H]}$, HvLEU$_{[5H]}$ and EBmac0755$_{[7H]}$. At these loci, the average effects aross all environments could led to a reduced COD of up to 9.5 % at GBM1016-EBmac0415$_{[2H]}$. At the remaining QTLs, the *Hsp* allele was associated with an increased cold damage score of up to 63.4 % (HvLOXC$_{[5H]}$). The explained genetic variance reached a maximum with 35.4 % at GBM1041$_{[5H]}$.

Days until heading (HEA)

Altogether, 19 putative QTLs were located for HEA on all chromosomes. Among these QTLs, seven loci showed a significant marker main effect and 17 loci exhibited a significant M×E interaction. Both, the marker main effect as well as the interaction was significant at five loci. For nine QTLs, a favorable effect of *Hsp* allele on HEA was observed. At these loci, which were located on all chromosomes except for 6H, the presence of the *Hsp* allele was associated with a reduced HEA of up to 6.4 % (Ebmac0679$_{[4H]}$). Six favorable exotic QTL alleles with significant marker main effects or marker main and interaction effects on HEA were located at BMS32$_{[1H]}$, GBMS012$_{[1H]}$, Bmag0579$_{[1H]}$, Ebmac0679$_{[4H]}$, GBM1048$_{[4H]}$ and HVM49$_{[7H]}$, respectively. On chromosomes 1H and 4H, all *Hsp* QTL alleles at the loci of detected QTLs for HEA showed favorable effects on HEA. At four QTLs, which were detected at GBMS002$_{[2H]}$, GBM1016-GBM1047$_{[2H]}$, GBM1041$_{[5H]}$ and HvLOXC$_{[5H],}$ a crossover interaction effect could lead to a reduced HEA of up to 1.5 % at GBM1016-GBM1047$_{[2H]}$. At the remaining QTLs, the presence of the *Hsp* allele was associated with an increased heading time of up to 1.1 % at marker interval HvLTPPB-EBmac0705$_{[3H]}$. A maximum explained genetic variance was found at Bmag0579$_{[1H]}$ with 7.8 %.

Plant height (HEI)

Eighteen putative QTLs were located for HEI on all chromosomes. At ten loci, a significant marker main effect was obtained. The interaction between marker and environment was significant at nine loci. In one case, the marker main effect as well as the interaction was significant. For eight QTLs, the *Hsp* alleles showed favorable effects on HEI. At these loci, the presence of the *Hsp* allele was associated with a reduced plant height of up to 5.9 % (HVM49$_{[7H]}$). The favorable effects of the *Hsp* alleles for HEI were detected on all chromosomes except for 5H and 6H. In addition, five crossover interaction effects, which were located at Bmag0579$_{[1H]}$, HvPAZXG$_{[4H]}$, HvLEU$_{[5H]}$, GBM1041$_{[5H]}$ and GMS006-HVM14$_{[6H]}$, could lead to a reduced HEI of up to 2.2 % at HvLEU$_{[5H]}$. At the remaining QTLs, the presence of the *Hsp* allele was associated with an increased HEI of up to 5.8 % (Bmag0013-Bmac0029$_{[3H]}$). The highest portion of genetic variance was explained by marker interval Bmag0013-Bmac0029$_{[3H]}$ with 11.8 %.

Lodging at harvest (LOH)

For lodging at harvest (LOH), 16 putative QTLs were located on all chromosomes except for 2H. All loci exhibited significant M×E interactions. No significant marker main effect was obtained. Only one favorable *Hsp* allele was detected at GMS116-HVM60$_{[3H]}$ which led to a LOH

reduction of 20.5 %. At GMS046$_{[7H]}$ and BMS64-Bmag0120$_{[7H]}$, the crossover interaction effects were associated with a LOH reduction of up to 7.7 % (BMS64-Bmag0120$_{[7H]}$). However, at most QTLs the presence of the *Hsp* allele showed negative effects on LOH. The *Hsp* allele with the strongest negative effect on LOH was detected on chromosome 4H in marker interval Ebmac0906-GMS089, which was associated with an increased LOH of 44.5 %.

Biomass (MAS)

No QTLs were detected for biomass in C101.

Number of spike per square metre (EAR)

No QTLs were detected for EAR in C101.

Thousand-grain weight (TGW)

Ten putative QTLs were located for TGW chromosomes 1H, 3H, 4H, 5H and 6H. Three loci showed a significant marker main effect. Eight loci exhibited a significant M×E interaction. In marker interval GBM1007-GBM1004$_{[1H]}$, a significant marker main effect and a significant interaction were observed. Only at locus Bmag0013$_{[3H]}$, a favorable effect of the *Hsp* allele on TGW was observed. At this locus the presence of the *Hsp* allele led to an increased TGW of 3.1 %. The *Hsp* allele with the strongest negative effect on TGW was detected on chromosome 1H in marker interval GBM1007-GBM1004$_{[1H],}$ where the presence of the *Hsp* allele was associated with a decreased TGW of 5.8%. The maximum explained genetic variance was found at GBM1007-GBM1004$_{[1H]}$ with 12.8 %.

Yield (YLD)

Sixteen putative QTLs were located for YLD on all chromosomes except for 2H. At six loci, a significant marker main effect was obtained. And at the remaining loci, the M×E interactions were significant. For three QTLs, which were detected as crossover interaction effects at HvLEU$_{[5H]}$, HvPAF93$_{[6H]}$ and marker interval GBM1008-GBM1005$_{[6H]}$, the presence of the *Hsp* allele resulted in an YLD increase of up to 2.9 % (GBM1008-GBM1005$_{[6H]}$. Much more unfavorable effects of *Hsp* alleles were detected, and these alleles were associated with a reduced yield of up to 9.6 % (BMS32-GMS114$_{[1H]}$). The genetic variance explained by a QTL reached a maximum with 17.2 % at BMS32-GMS114$_{[1H].}$

3.5.1.2 Detection of QTLs for pathogen resistance and non-parasitic browning in C101

In total, 68 putative QTLs for four pathogen resistances and one syndrome were detected in C101. Among these loci, at 13 loci favorable QTL effects were identified for leaf rust (LR), net blotch (NB), non-parasitic browning (NPB), powdery mildew (PM) and leaf scald (RH) (Table 17, Table 18 and Figure 4). The putative QTLs were mainly located on chromosomes 1H, 2H, 5H and 6H. No favorable effect of the *Hsp* alleles was detected for pathogen resistance and non-parasitic browning on chromosomes 1H and 4H. In the following, the detected QTLs are described for each trait.

Leaf rust (LR)

Ten putative QTLs were located for LR on chromosomes 1H, 2H, 3H, 4H and 6H. At two loci, the M×E interactions were significant. And at the remaining loci, a significant marker main effect was obtained. For two QTLs with marker main effect, which were located at GBMS002$_{[2H]}$ and HVM33–GMS116$_{[3H]}$, the presence of the *Hsp* allele resulted in a reduced LR symptom of up to 25.3 % GBMS002$_{[2H]}$. At the remaining loci, the presence of the *Hsp* allele were associated with an increased leaf rust infection of up to 52.8 % (EBmac0906–GMS089$_{[4H]}$). At this marker interval, the highest explained genetic variance was found with 3.1 %.

Net blotch (NB)

For NB, 16 putative QTLs were located on all chromosomes. All loci exhibited significant M×E interaction. For two QTLs, which were located at GBM1021$_{[6H]}$ and GBM1008-GBM1005$_{[6H]}$, a favorable effect of the *Hsp* allele on NB resistance was observed. At these loci, the presence of the *Hsp* allele was associated with a reduced NB infection of up to 20.8 % at GBM1008-GBM1005$_{[6H]}$. In addition, at eight QTLs with crossover interaction effects, the average effects of the *Hsp* alleles led to a reduced NB symptoms of up to 29.4 % (GMS006-Bmag0613$_{[6H]}$). At the remaining QTLs, the *Hsp* allele caused an increased NB infection of up to 27.0 % at GBM1044$_{[4H]}$.

Non-parasitic browning (NPB)

Nineteen putative QTLs were located for NPB on all chromosomes. Seven QTLs exhibited significant marker main effects, and other loci showed significant M×E interaction. At two loci (GBM1059-EBmac0708$_{[3H]}$ and Bmac0029$_{[3H]}$), a marker main effect as well as the M×E interaction was significant. Favorable QTL effects of the *Hsp* alleles on NPB were observed for three QTLs at GBM1047$_{[2H]}$, Bmac0163-HvLEU$_{[5H]}$ and HvSS1-GBMS035$_{[7H]}$. At these loci, the

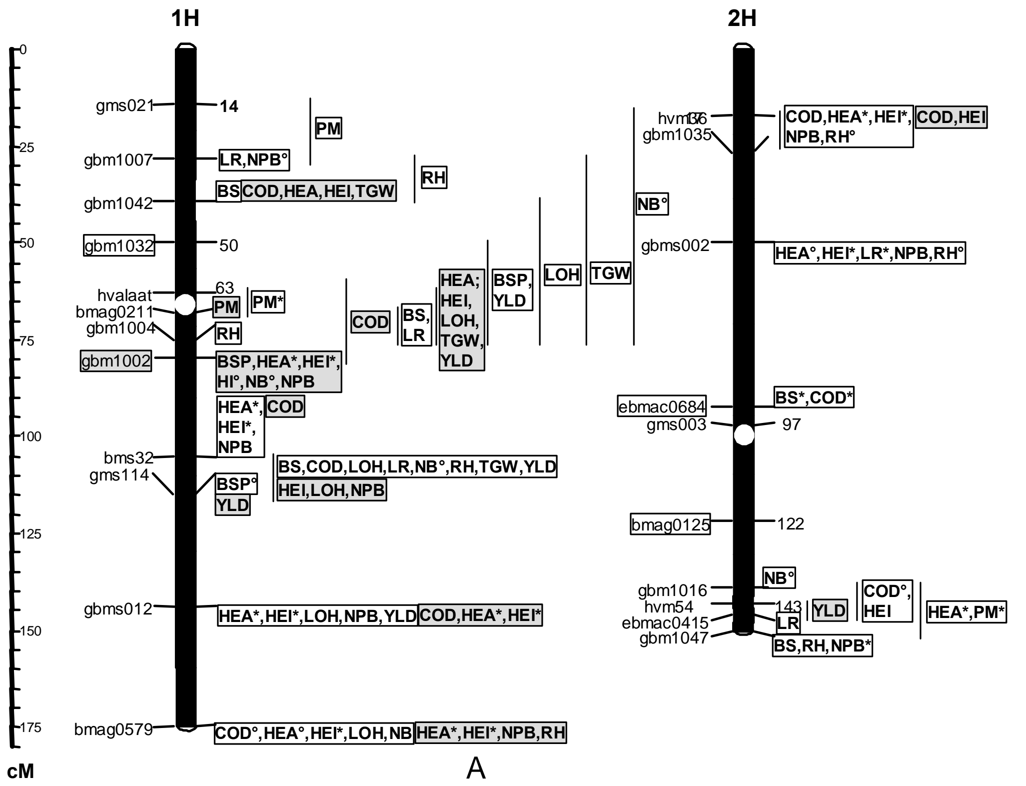
presence of the *Hsp* allele resulted in a NPB decrease of up to 17.2 % (EBmac0755$_{[7H]}$). For four QTLs with crossover interaction effects, which were located at GBM1007$_{[1H]}$, GMS006-Bmag0613$_{[6H]}$, GBM1008-GBM1022$_{[6H]}$ and GMS046$_{[7H]}$, the presence of the *Hsp* allele caused a NPB decrease of up to 19.9 % (GMS006-Bmag0613$_{[6H]}$). The negative effects of the *Hsp* alleles were associated with a NPB increase of up to 36.9 % at EBmac0679$_{[4H]}$. At locus GBM1059-EBmac0708$_{[3H]}$, the highest explained genetic variance was found (10.7 %).

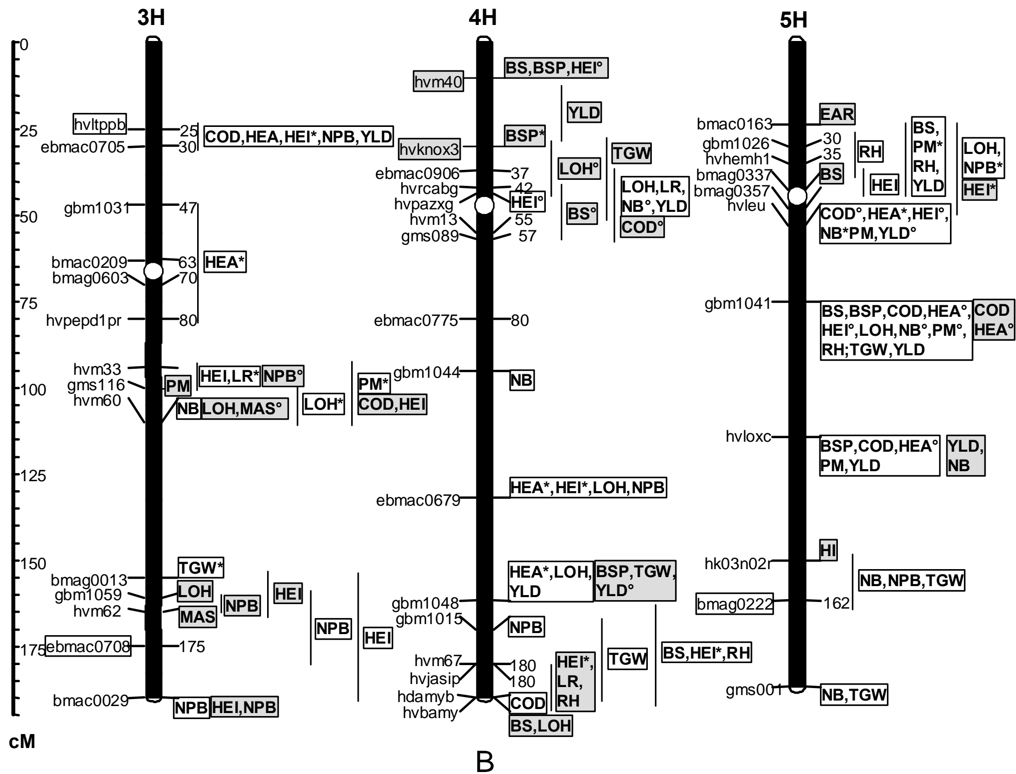
Powdery mildew (PM)

Eleven putative QTLs were located for PM on all chromosomes except for 4H. Six loci showed a significant marker main effect. Eight loci exhibited a significant M×E interaction. In marker interval AF022725A-GBMS035$_{[7H]}$, a significant marker main effect and a significant interaction were observed. For four QTLs, which were located on chromosomes 2H, 3H, 5H and 7H, the presence of the *Hsp* alleles led to a decreased PM infection of up to 17.8 % at marker interval GBM1016-GBM1047$_{[2H]}$. A crossover interaction effect, which was detected at GBM1041$_{[5H]}$, was associated with a reduced PM symptoms of 5.9 %. At the remaining QTLs, the *Hsp* alleles were associated with an increased PM infection of up to 30.7 % at GBM1008–GBM1005$_{[6H]}$. At this locus, the highest portion of the genetic variance was explained with 17.8 %.

Scald (RH)

For RH, 13 putative QTLs were located on all chromosomes except for 3H. Eight loci showed significant marker main effects. At the other loci, significant M×E interactions were observed. Favorable QTL effect of the *Hsp* alleles on RH resistance was only observed at Bmag0369$_{[7H.}$ At this locus, the presence of the *Hsp* allele resulted in a RH symptom decrease of 4.9 %. In addition, at five QTLs which were detected as crossover interaction effect, the presence of the *Hsp* allele led to a RH symptom decrease of 3.4 % at GBMS002$_{[2H]}$. At the remaining loci, the presences of the *Hsp* alleles were associated with an increased RH infection of up to 22.9 % at EBmac0755 - HVM49$_{[7H]}$. The genetic variance explained by a QTL reached a maximum with 7.5 % at GBM1005$_{[5H].}$





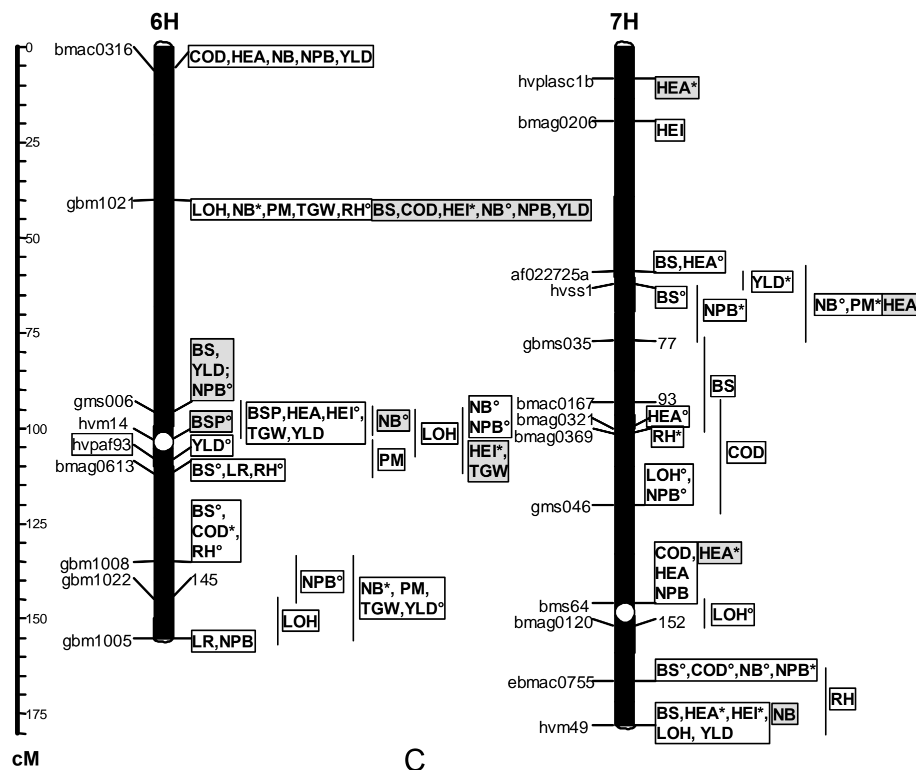


Figure 4: Linkage map containing 268 putative QTLs, which were detected for 16 traits in C101 and T101 (A, B, C). Map position of SSRs in cM: see Figure 3. Putative QTLs which revealed either a significant (P < 0.01) marker main effect or M×E interaction are written to the right of the SSR locus. The abbreviations of the quantitative traits follow Table 4: Trait abbreviations: BS, Breaking of stem; BSP, Bending of spike; COD, Cold damage; EAR, Number of spikes; HEA, Days until heading; HEI, Plant Height; HI, Harvest index; LOH, Lodging at harvest; LR, Leaf rust; MAS, Biomass; NB, net blotch; NPB, Non-parasitic browning; PM, Powdery mildew; RH, leaf scald; TGW, Thousand-grain weight; YLD, Yield. A favorable effect of the *Hsp* allele at a putative QTL is indicated by *. (°) QTL: where the M×E interaction reveals a cross interaction where the *Hsp* genotype is favorable in some environments but unfavorable in other environments. The QTLs with white background were detected in C101 and the QTLs with grey background were detected in T101. A vertical line represents the marker interval, where the QTL was located.

Table 17: List of 183 putative QTLs detected in C101

Trait[1)]	QTL[2)]	Marker Interval[3)]	Chr[4)]	Range[5)] (in cM)	Repr. Marker[6)]	Factor[7)]	Sign[8)]	LSM [*Hsp*][8)]	R^{2} [10)]$_G$ (%)	RP[*Hsp*][11)] (in %)	P/N[12)]
BS	QbsC101-1Ha	GBM1042	1H	39	GBM1042	M*E	**	3.74			°
	QbsC101-1Hb	Bmag0211-GBM1004	1H	68-75	GBM1004	M + M*E	**	4.01	5.48	19.57	-
	QbsC101-1Hc	BMS32-GMS114	1H	105-115	GMS114	M*E	***	3.87			°
	QbsC101-2Ha	EBmac0684	2H	80	EBmac0684	M*E	**	3.37			°
	QbsC101-2Hb	GBM1047	2H	150	GBM1047	M*E	**	3.92			°
	QbsC101-4H	GBM1048-HvBAMY	4H	162-190	HvJASIP	M*E	***	4.24			°
	QbsC101-5Ha	Bmac0163-Bmag0357	5H	24-48	GBM1026	M*E	**	3.82			°
	QbsC101-5Hb	GBM1041	5H	75	GBM1041	M*E	***	3.79			°
	QbsC101-6Ha	Bmag0613	6H	112	Bmag0613	M*E	**	3.34			°
	QbsC101-6Hb	GBM1008	6H	135	GBM1008	M*E	**	2.90			°
	QbsC101-7Ha	AF022725A	7H	59	AF022725A	M*E	***	3.49			°
	QbsC101-7Hb	HvSS1	7H	62	HvSS1	M*E	***	3.45			°
	QbsC101-7Hc	GBMS035-Bmag0369	7H	77-100	Bmag0321	M*E	***	3.62			°
	QbsC101-7Hd	EBmac0755	7H	166	EBmac0755	M*E	***	3.25			°
	QbsC101-7He	HVM49	7H	178	HVM49	M*E	***	3.57			°
BSP	QbspC101-1Ha	GBM1032-GBM1004	1H	50-75	HvALAAT	M*E	***	4.57			°
	QbspC101-1Hb	GMS114	1H	115	GMS114	M*E	**	4.30			°
	QbspC101-5Ha	GBM1041	5H	75	GBM1041	M*E	***	4.51			°
	QbspC101-5Hb	HvLOXC	5H	114	HvLOXC	M	**	5.05	1.68	14.77	-
	QbspC101-6H	GMS006-HVM14	6H	96-103	GMS006	M*E	**	4.63			°
COD	QcodC101-1Ha	BMS32-GMS114	1H	105-115	BMS32	M + M*E	***	4.90	10.05	28.26	-
	QcodC101-1Hb	Bmag0579	1H	175	Bmag0579	M*E	**	3.86			°
	QcodC101-2Ha	HVM36-GBM1035	2H	17-27	GBM1035	M + M*E	**	5.09	4.45	28.63	-
	QcodC101-2Hb	EBmac0684	2H	80	EBmac0684	M	**	2.81	4.22	-31.33	+
	QcodC101-2Hc	GBM1016-EBmac0415	2H	139-146	EBmac0415	M*E	**	3.72			°
	QcodC101-3H	HvLTPPB-EBmac0705	3H	25-30	EBmac0705	M + M*E	**	5.37	7.61	36.90	-
	QcodC101-4H	HDAMYB	4H	190	HDAMYB	M*E	**	4.68			°
	QcodC101-5Ha	HvLEU	5H	53	HvLEU	M*E	**	3.71			°

Table 17 (continued)

Trait[1)]	QTL[2)]	Marker Interval[3)]	Chr[4)]	Range[5)] (in cM)	Repr. Marker[6)]	Factor[7)]	Sign[8)]	LSM [*Hsp*][8)]	R^{2} [10)] $_G$ (%)	RP[*Hsp*][11)] (in %)	P/N[12)]
COD	QcodC101-5Hb	GBM1041	5H	75	GBM1041	M + M*E	**	5.26	35.37	49.49	-
	QcodC101-5Hc	HvLOXC	5H	114	HvLOXC	M + M*E	**	6.26	22.00	63.36	-
	QcodC101-6Ha	Bmac0316	6H	6	Bmac0316	M + M*E	***	5.14	9.51	32.70	-
	QcodC101-6Hb	GBM1008	6H	135	GBM1008	M*E	**	3.57	0.82	-12.23	+
	QcodC101-7Ha	Bmac0167-GMS046	7H	93-120	Bmag0321	M*E	***	4.40			°
	QcodC101-7Hb	BMS64	7H	146	BMS64	M*E	**	4.36			°
	QcodC101-7Hc	EBmac0755	7H	166	EBmac0755	M*E	***	3.72			°
HEA	QheaC101-1Ha	BMS32	1H	105	BMS32	M + M*E	**	57.04	6.86	-2.35	+
	QheaC101-1Hb	GBMS012	1H	144	GBMS012	M + M*E	**	57.18	4.55	-1.99	+
	QheaC101-1Hc	Bmag0579	1H	175	Bmag0579	M + M*E	***	56.88	7.80	-2.68	+
	QheaC101-2Ha	HVM36-GBM1035	2H	17-27	GBM1035	M*E	***	57.08		-2.08	+
	QheaC101-2Hb	GBMS002	2H	50	GBMS002	M*E	***	57.55			°
	QheaC101-2Hc	GBM1016-GBM1047	2H	139-150	GBM1047	M*E	***	57.44	1.14	-1.45	+
	QheaC101-3Ha	HvLTPPB-EBmac0705	3H	25-30	HvLTPPB	M*E	**	58.79			°
	QheaC101-3Hb	GBM1031-HVPEPD1PR	3H	47-80	Bmac0209	M*E	***	54.92		-5.66	+
	QheaC101-4Ha	EBmac0679	4H	132	EBmac0679	M	**	54.50	3.58	-6.38	+
	QheaC101-4Hb	GBM1048	4H	162	GBM1048	M + M*E	**	56.73	4.31	-2.70	+
	QheaC101-5Ha	HvLEU	5H	53	HvLEU	M + M*E	**	57.24	3.05	-1.88	+
	QheaC101-5Hb	GBM1041	5H	75	GBM1041	M*E	***	57.88			°
	QheaC101-5Hc	HvLOXC	5H	114	HvLOXC	M*E	***	57.54			°
	QheaC101-6Ha	Bmac0316	6H	6	Bmac0316	M*E	**	58.21			°
	QheaC101-6Hb	GMS006-HVM14	6H	96-103	HVM14	M*E	***	58.53			°
	QheaC101-7Ha	AF022725A	7H	59	AF022725A	M*E	**	57.98			°
	QheaC101-7Hb	Bmag0321	7H	100	Bmag0321	M*E	**	58.17			°
	QheaC101-7Hc	BMS64	7H	146	BMS64	M*E	**	58.35			°
	QheaC101-7Hd	HVM49	7H	178	HVM49	M	**	56.44	2.96	-3.08	+

Table 17 (continued)

Trait[1)]	QTL[2)]	Marker Interval[3)]	Chr[4)]	Range[5)] (in cM)	Repr. Marker[6)]	Factor[7)]	Sign[8)]	LSM [*Hsp*][8)]	$R^{2\ 10)}_G$ (%)	RP[*Hsp*][11)] (in %)	P/N[12)]
HEI	QheiC101-1Ha	BMS32	1H	105	BMS32	M	***	105.76	3.81	-3.27	+
	QheiC101-1Hb	GBMS012	1H	144	GBMS012	M*E	**	106.64	0.77	-2.27	+
	QheiC101-1Hc	Bmag0579	1H	175	Bmag0579	M*E	***	107.19			°
	QheiC101-2Ha	HVM36-GBM1035	2H	17-27	HVM36	M	**	104.55	3.12	-4.02	+
	QheiC101-2Hb	GBMS002	2H	50	GBMS002	M	**	104.11	3.36	-4.47	+
	QheiC101-2Hc	GBM1016-EBmac0415	2H	139-146	GBM1016	M*E	***	109.58			°
	QheiC101-3Ha	HVLTPPB-EBmac0705	3H	25-30	EBmac0705	M	**	105.04	2.66	-3.57	+
	QheiC101-3Hb	HVM33-GMS116	3H	94-100	HVM33	M	***	113.65	6.84	5.18	-
	QheiC101-3Hc	Bmag0013-Bmac0029	3H	155-190	Bmag0013	M	***	114.23	11.81	5.86	-
	QheiC101-4Ha	HvPAZXG	4H	44	HvPAZXG	M*E	**	107.76			°
	QheiC101-4Hb	EBmac0679	4H	132	EBmac0679	M	**	108.15	3.24	-0.65	+
	QheiC101-4Hc	GBM1048-HvBAMY	4H	162-190	GBM1015	M + M*E	**	103.36	6.62	-5.29	+
	QheiC101-5Ha	Bmag0337-Bmag0357	5H	43-48	Bmag0357	M*E	**	109.26			°
	QheiC101-5Hb	HvLEU	5H	53	HvLEU	M*E	***	106.53			°
	QheiC101-5Hc	GBM1041	5H	75	GBM1041	M*E	***	108.62			°
	QheiC101-6H	GMS006-HVM14	6H	96-103	HVM14	M*E	***	107.32			°
	QheiC101-7Ha	Bmag0206	7H	19	Bmag0206	M	**	112.01	3.57	3.46	-
	QheiC101-7Hb	HVM49	7H	178	HVM49	M	***	102.48	3.26	-5.91	+
LOH	QlohC101-1Ha	GBM1042-GBM1004	1H	39-75	GBM1004	M*E	***	4.53	3.59	23.82	-
	QlohC101-1Hb	BMS32-GMS114	1H	105-115	BMS32	M*E	***	4.75	4.72	28.05	-
	QlohC101-1Hc	GBMS012	1H	144	GBMS012	M*E	***	4.77	2.80	27.16	-
	QlohC101-1Hd	Bmag0579	1H	175	Bmag0579	M*E	***	4.17			°
	QlohC101-3H	GMS116-HVM60	3H	100-110	HVM60	M*E	***	3.12	2.37	-20.47	+
	QlohC101-4Ha	EBmac0906-GMS089	4H	37-57	HVM13	M*E	***	5.50	3.78	44.45	-
	QlohC101-4Hb	EBmac0679	4H	132	EBmac0679	M*E	***	5.40			°
	QlohC101-4Hc	GBM1048	4H	162	GBM1048	M*E	**	4.00			°
	QlohC101-5Ha	Bmac0163-HvLEU	5H	24-53	GBM1026	M*E	***	4.50			°
	QlohC101-5Hb	GBM1041	5H	75	GBM1041	M*E	**	4.32			°

Table 17 (continued)

Trait[1]	QTL[2]	Marker Interval [3]	Chr[4]	Range[5] (in cM)	Repr. Marker[6]	Factor[7]	Sign[8]	LSM [*Hsp*][8]	R^{2} [10] $_G$ (%)	RP[*Hsp*][11] (in %)	P/N[12]
LOH	QlohC101-6Ha	GBM1021	6H	40	GBM1021	M*E	***	4.49			°
	QlohC101-6Hb	GMS006-HvPAF93	6H	96-108	HVM14	M*E	***	4.46			°
	QlohC101-6Hc	GBM1022-GBM1005	6H	145-155	GBM1022	M*E	***	4.82		26.73	-
	QlohC101-7Ha	GMS046	7H	120	GMS046	M*E	***	3.74			°
	QlohC101-7Hb	BMS64-Bmag0120	7H	146-152	BMS64	M*E	***	3.67			°
	QlohC101-7Hc	HVM49	7H	178	HVM49	M*E	**	4.25			°
LR	QlrC101-1Ha	GBM1007	1H	28	GBM1007	M	**	2.48	1.52	21.73	-
	QlrC101-1Hb	Bmag0211-GBM1004	1H	68-75	Bmag0211	M*E	**	2.25			°
	QlrC101-1Hc	BMS32-GMS114	1H	105-115	GMS114	M*E	**	2.36		19.04	-
	QlrC101-1Hd	Bmag0579	1H	175	Bmag0579	M	**	2.49	2.11	23.94	-
	QlrC101-2Ha	GBMS002	2H	50	GBMS002	M	**	1.59	1.09	-25.32	+
	QlrC101-2Hb	EBmac0415	2H	146	EBmac0415	M	**	2.44	1.37	19.26	-
	QlrC101-3H	HVM33-GMS116	3H	94-100	HVM33	M	***	1.59	1.74	-23.95	+
	QlrC101-4H	EBmac0906-GMS089	4H	37-57	HvRCABG	M	**	2.96	3.62	52.75	-
	QlrC101-6Ha	Bmag0613	6H	112	Bmag0613	M	***	2.62	3.00	30.28	-
	QlrC101-6Hb	GBM1005	6H	155	GBM1005	M	***	2.98	5.00	48.35	-
NB	QnbC101-1Ha	GMS021-GBM1004	1H	14-75	GBM1007	M*E	**	2.74			°
	QnbC101-1Hb	BMS32-GMS114	1H	105-115	BMS32	M*E	***	2.88			°
	QnbC101-1Hc	Bmag0579	1H	175	Bmag0579	M*E	**	3.06			°
	QnbC101-2H	GBM1016	2H	139	GBM1016	M*E	**	2.91			°
	QnbC101-3H	HVM60	3H	110	HVM60	M*E	***	3.16			°
	QnbC101-4Ha	EBmac0906-GMS089	4H	37-57	HvPAZXG	M*E	***	2.57			°
	QnbC101-4Hb	GBM1044	4H	95	GBM1044	M*E	**	3.86			°
	QnbC101-5Ha	GBM1041	5H	75	GBM1041	M*E	***	3.01			°
	QnbC101-5Hb	MGB318-Bmag0222	5H	150-162	Bmag0222	M*E	**	3.25			°
	QnbC101-5Hc	GMS001	5H	187	GMS001	M*E	**	3.39			°
	QnbC101-6Ha	Bmac0316	6H	6	Bmac0316	M*E	***	3.30			°

Table 17 (continued)

Trait[1)]	QTL[2)]	Marker Interval[3)]	Chr[4)]	Range[5)] (in cM)	Repr. Marker[6)]	Factor[7)]	Sign[8)]	LSM [*Hsp*][8)]	R^{2} [10)] $_G$ (%)	RP[*Hsp*][11)] (in %)	P/N[12)]
NB	QnbC101-6Hb	GBM1021	6H	40	GBM1021	M*E	***	2.61		-15.92	+
	QnbC101-6Hc	GMS006-Bmag0613	6H	96-112	HVM14	M*E	***	2.23			°
	QnbC101-6Hd	GBM1008-GBM1005	6H	135-155	GBM1022	M*E	***	2.45		-20.77	+
	QnbC101-7Ha	AF022725A-GBMS035	7H	59-77	HvSS1	M*E	***	2.97			°
	QnbC101-7Hb	EBmac0755	7H	166	EBmac0755	M*E	***	2.74			°
NPB	QnpbC101-1Ha	GBM1007	1H	28	GBM1007	M*E	**	3.52			°
	QnpbC101-1Hb	GBMS012	1H	144	GBMS012	M + M*E	**	3.64	1.51	3.30	-
	QnpbC101-2Ha	HVM36-GBM1035	2H	17-27	GBM1035	M*E	***	4.49		29.56	-
	QnpbC101-2Hb	GBMS002	2H	50	GBMS002	M	**	4.47	5.88	27.51	-
	QnpbC101-2Hc	GBM1047	2H	150	GBM1047	M	**	3.10	3.68	-14.47	+
	QnpbC101-3Ha	HvLTPPB-EBmac0705	3H	25-30	HvLTPPB	M*E	***	4.73		37.11	-
	QnpbC101-3Hb	GBM1059-EBmac0708	3H	161-169	GBM1059	M + M*E	***	4.13	10.66	22.16	-
	QnpbC101-3Hc	Bmac0029	3H	190	Bmac0029	M + M*E	**	4.09	5.23	18.55	-
	QnpbC101-4H	EBmac0679	4H	132	EBmac0679	M*E	**	4.83			°
	QnpbC101-5Ha	Bmac0163-HvLEU	5H	24-53	HvHEMH1	M*E	***	3.13		-14.86	+
	QnpbC101-5Hb	MGB318-Bmag0222	5H	150-162	Bmag0222	M*E	**	3.70			°
	QnpbC101-6Ha	Bmac0316	6H	6	Bmac0316	M*E	***	3.70			°
	QnpbC101-6Hb	GMS006-Bmag0613	6H	96-112	HVM14	M*E	***	2.91			°
	QnpbC101-6Hc	GBM1008-GBM1022	6H	135-145	GBM1008	M*E	***	3.22			°
	QnpbC101-6Hd	GBM1005	6H	155	GBM1005	M*E	**	3.55			°
	QnpbC101-7Ha	HvSS1-GBMS035	7H	62-77	HvSS1	M	**	3.30	2.76	-9.67	+
	QnpbC101-7Hb	GMS046	7H	120	GMS046	M*E	**	3.46			°
	QnpbC101-7Hc	BMS64	7H	146	BMS64	M*E	***	3.56			°
	QnpbC101-7Hd	EBmac0755	7H	166	EBmac0755	M	**	2.97	3.35	-17.24	+
PM	QpmC101-1H	GMS021-GBM1007	1H	14-28	GMS021	M	***	4.93	5.97	14.50	-
	QpmC101-2H	GBM1016-GBM1047	2H	139-150	GBM1047	M*E	***	3.69		-17.81	+
	QpmC101-3H	HVM33-HVM60	3H	94-110	GMS116	M*E	***	3.98		-10.62	+

Table 17 (contnued)

Trait[1)]	QTL[2)]	Marker Interval[3)]	Chr[4)]	Range[5)] (in cM)	Repr. Marker[6)]	Factor[7)]	Sign[8)]	LSM [*Hsp*][8)]	$R^{2\ 10)}_G$ (%)	RP[*Hsp*][11)] (in %)	P/N[12)]
PM	QpmC101-5Ha	Bmac0163-Bmag0357	5H	24-48	GBM1026	M	**	4.11	4.02	-8.53	+
	QpmC101-5Hb	HvLEU	5H	53	HvLEU	M	***	5.01	4.33	16.49	-
	QpmC101-5Hc	GBM1041	5H	75	GBM1041	M*E	***	4.21			°
	QpmC101-5Hd	HvLOXC	5H	114	HvLOXC	M*E	***	4.47			°
	QpmC101-6Ha	GBM1021	6H	40	GBM1021	M*E	**	4.91			°
	QpmC101-6Hb	GMS006-Bmag0613	6H	96-112	Bmag0613	M	***	5.15	11.98	20.60	-
	QpmC101-6Hc	GBM1008-GBM1005	6H	135-155	GBM1005	M	***	5.58	17.75	30.69	-
	QpmC101-7H	AF022725A-GBMS035	7H	59-77	AF022725A	M + M*E	***	3.91	5.83	-13.25	+
RH	QrhC101-1Ha	GBM1004	1H	75	GBM1004	M	**	4.12	2.79	8.44	-
	QrhC101-1Hb	BMS32-GMS114	1H	105-115	GMS114	M	**	4.29	4.64	11.79	-
	QrhC101-2Ha	HVM36-GBM1035	2H	17-27	GBM1035	M*E	**	3.79			°
	QrhC101-2Hb	GBMS002	2H	50	GBMS002	M*E	**	3.77			°
	QrhC101-2Hc	GBM1047	2H	150	GBM1047	M	**	4.32	4.66	12.97	-
	QrhC101-4H	GBM1048-HvBAMY	4H	162-190	GBM1048	M	**	4.52	5.55	17.53	-
	QrhC101-5Ha	Bmac0163-GBM1022	5H	24-48	GBM1026	M	***	4.13	3.71	8.73	-
	QrhC101-5Hb	GBM1005	5H	75	GBM1005	M	**	4.25	7.46	13.37	-
	QrhC101-6Ha	GBM1021	6H	40	GBM1021	M*E	**	3.81			°
	QrhC101-6Hb	Bmag0613	6H	112	Bmag0613	M*E	**	3.85			°
	QrhC101-6Hc	GBM1008	6H	135	GBM1008	M*E	**	3.90			°
	QrhC101-7Ha	Bmag0369	7H	100	Bmag0369	M	**	3.77	1.41	-4.90	+
	QrhC101-7Hb	EBmac0755-HVM49	7H	166-178	HVM49	M	***	4.75	5.04	22.93	-
TGW	QtgwC101-1Ha	GBM1007-GBM1004	1H	28-75	GBM1004	M*E	**	38.74		-5.78	-
	QtgwC101-1Hb	BMS32-GMS114	1H	105-115	GMS114	M*E	***	39.27			°
	QtgwC101-3Hc	Bmag0013	3H	155	Bmag0013	M	**	41.70	2.28	3.05	+
	QtgwC101-4H	GBM1015-HvBAMY	4H	170-190	GBM1015	M	**	38.80	4.14	-4.87	-
	QtgwC101-5Ha	GBM1041	5H	75	GBM1041	M*E	***	40.58			°
	QtgwC101-5Hb	MGB318-Bmag0222	5H	150-162	MGB318	M*E	***	39.41			°

Table 17 (continued)

Trait[1)]	QTL[2)]	Marker Interval[3)]	Chr[4)]	Range[5)] (in cM)	Repr. Marker[6)]	Factor[7)]	Sign[8)]	LSM [*Hsp*][8)]	R^{2} [10)] $_G$ (%)	RP[*Hsp*][11)] (in %)	P/N[12)]
TGW	QtgwC101-5Hc	GMS001	5H	187	GMS001	M*E	***	39.37			°
	QtgwC101-6Ha	GBM1021	6H	40	GBM1021	M*E	***	39.16		-4.22	-
	QtgwC101-6Hb	GMS006-HVM14	6H	96-103	HVM14	M*E	***	39.23			°
	QtgwC101-6Hc	GBM1008-GBM1022	6H	135-145	GBM1008	M*E	***	39.59			°
YLD	QyldC101-1Ha	GBM1032-GBM1004	1H	50-75	GBM1032	M	***	703.89	9.62	-7.02	-
	QyldC101-1Hb	BMS32-GMS114	1H	105-115	BMS32	M	***	687.95	17.18	-9.62	-
	QyldC101-1Hc	GBMS012	1H	144	GBMS012	M	***	704.89	7.62	-6.66	-
	QyldC101-3H	HvLTPPB-EBmac0705	3H	25-30	EBmac0705	M*E	***	697.58		-7.08	-
	QyldC101-4Ha	EBmac0906-GMS089	4H	37-57	HvPAZXG	M*E	***	707.32			°
	QyldC101-4Hb	GBM1048	4H	162	GBM1048	M	**	708.47	2.80	-5.61	-
	QyldC101-5Ha	Bmac0163-Bmag0357	5H	24-48	Bmag0337	M*E	***	711.87		-6.34	-
	QyldC101-5Hb	HvLEU	5H	53	HvLEU	M*E	***	752.59			°
	QyldC101-5Hc	GBM1041	5H	75	GBM1041	M*E	***	700.04		-8.57	-
	QyldC101-5Hd	HvLOXC	5H	114	HvLOXC	M*E	***	706.73			°
	QyldC101-6Ha	Bmac0316	6H	6	Bmac0316	M*E	***	704.41		-6.40	-
	QyldC101-6Hb	GMS006-HVM14	6H	96-103	HVM14	M*E	**	741.55			°
	QyldC101-6Hc	HvPAF93	6H	108	HvPAF93	M*E	**	763.19			°
	QyldC101-6Hd	GBM1008-GBM1005	6H	135-155	GBM1005	M*E	***	766.76			°
	QyldC101-7Ha	AF022725A-HvSS1	7H	59-62	AF022725A	M	**	715.62	4.80	-5.20	-
	QyldC101-7Hb	HVM49	7H	178	HVM49	M	**	676.76	4.52	-9.78	-

[1)] Trait abbreviations: BS, Breaking of stem; BSP, Bending of spike; COD, Cold damage; HEA, Days until heading; HEI, Plant Height; HI, Harvest index; LOH, Lodging at harvest; LR, Leaf rust; NB, net blotch; NPB, Non-parasitic browning; PM, Powdery mildew; RH, leaf scald; TGW, Thousand-grain weight; YLD, Yield. [2)] Name of **QTLs** contains the prefix 'Q' (QTL), abbreviation of trait, abbreviation of population, chromosomal location and the ordinal number of QTLs on chromosome. [3)] Marker exhibiting significant QTL effects. [4)] Chromosomal assignment of SSR. [5)] Position of marker in cM derived from von Koff et al. (2004). [6)] For each group of linked markers with a significant QTL effect only the marker with the highest F statistics is listed. [7)] Factor M or M*E significant in QTL analysis. [8)] Level of significance of the marker main effect or the MxE interaction, with **: $P < 0.01$, ***: $P < 0.001$; if there were more than one significant marker effect in the QTL interval, then the highest level of significance was taken. [9)] The least square mean across all tested environments for homozygous *Hsp* genotypes at the given marker locus. [10)] The portion of genetic variance which is explained by marker main effect (R^2_G). [11)] Relative performance of *Hsp* genotype: RP[*Hsp*] = ([*Hsp*]-[*Hv*]) x 100 / [*Hv*], where [*Hsp*] and [*Hv*] are the least square means of the homozygous *Hsp* and *Hv* genotypes, respectively, calculated across all environments tested; if there were more than one significant marker effect in the QTL interval, then the highest RP[*Hsp*] was taken. [12)] (+) QTL where the marker main effect or M×E interaction effect of the *Hsp* genotype is favorable across all environments; (–) QTL where the marker main effect or M×E interaction effect of the *Hsp* genotype is unfavorable across all environments; (°) QTL where the M×E interaction reveals a cross interaction where the Hsp genotype is favorable in some environments but unfavorable in other environments. For details, see Appendix 6 and Appendix 7.

Table 18: The relative performance of homozygous *Hsp* genotypes at 183 putative QTLs detected in C101

Chr	Range (in cM)	Marker Interval	BS	BSP	COD	HEA	HEI	LOH	LR	NB	NPB	PM	RH	TGW	YLD	No. of QTLs
1H	28	GBM1007							21,73		-0,53					2
	39	GBM1042	9,81													1
	75	GBM1004											8,44			1
	105	BMS32				-2,35	-3,27									2
	115	GMS114		-4,11												1
	144	GBMS012				-1,99	-2,27	27,16			3,30				-6,66	5
	175	Bmag0579			-4,45	-2,68	-1,53	8,71	23,94	0,80						6
	105-115	BMS32-GMS114	13,69		28,26			28,05	19,04	-6,30			11,79	-4,72	-9,62	8
	14-28	GMS021-GBM1007										14,50				1
	14-75	GMS021-GBM1004								-12,40						1
	28-75	GBM1007-GBM1004												-5,78		1
	39-75	GBM1042-GBM1004						23,82								1
	50-75	GBM1032-GBM1004		2,23											-7,02	2
	68-75	Bmag0211-GBM1004	19,57						9,28							2
2H	50	GBMS002				-1,10	-4,47		-25,32		27,51		-3,37			5
	80	EBmac0684	-3,48		-31,33											2
	139	GBM1016								-5,29						1
	146	EBmac0415							19,26							1
	150	GBM1047	14,22								-14,47		12,97			3
	139-146	GBM1016-EBmac0415			-9,54		1,10									2
	139-150	GBM1016-GBM1047				-1,45						-17,81				2
	17-27	HVM36-GBM1035			28,63	-2,08	-4,02				29,56		-3,25			5
3H	110	HVM60								4,41						1
	155	Bmag0013												3,05		1
	190	Bmac0029									18,55					1
	100-110	GMS116-HVM60						-20,47								1
	155-190	Bmag0013-Bmac0029					5,86									1
	161-169	GBM1059-EBmac0708									22,16					1
	25-30	HvLTPPB-EBmac0705			36,90	1,13	-3,57				37,11				-7,08	5
	47-80	GBM1031-HvPEPD1PR				-5,66										1
	94-100	HVM33-GMS116					5,18		-26,15							2
	94-110	HVM33-HVM60										-10,62				1

Table 18 (continued)

Chr	Range (in cM)	Marker Interval	BS	BSP	COD	HEA	HEI	LOH	LR	NB	NPB	PM	RH	TGW	YLD	No. of QTLs
4H	44	HvPAZXG					-0,95									1
	95	GBM1044								26,98						1
	132	EBmac0679				-6,38	-0,65	39,20			36,94					4
	162	GBM1048				-2,70		2,94							-5,61	3
	190	HDAMYB			18,73											1
	162-190	GBM1048-HvBAMY	23,81				-5,29						17,53			3
	170-190	GBM1015-HvBAMY												-4,87		1
	37-57	EBmac0906-GMS089						44,45	52,75	-16,05					-5,62	4
5H	53	HvLEU			-8,51	-1,88	-2,24					16,49			0,75	5
	75	GBM1005											13,37			1
		GBM1041	12,65	1,69	49,49	-0,71	-0,03	15,23		-1,13		-5,89		-0,16	-8,57	10
	114	HvLOXC		14,77	63,36	-1,20						1,93			-5,95	5
	187	GMS001								12,07				-3,31		2
	150-162	MGB318-Bmag0222								7,64	4,58			-3,28		3
	24-48	Bmac0163-Bmag0357	14,64									-8,53			-6,34	3
		Bmac0163-GBM1022											8,73			1
	24-53	Bmac0163-HvLEU						23,72			-14,86					2
	43-48	Bmag0337-Bmag0357					0,79									1
6H	6	Bmac0316			32,70	0,06				9,91	4,98				-6,40	5
	40	GBM1021						17,93		-15,92		13,72	-2,72	-4,22		5
	108	HvPAF93													2,48	1
	112	Bmag0613	-5,16						30,28				-1,34			3
	135	GBM1008	-18,47		-12,23								-0,04			3
	155	GBM1005							48,35		0,21					2
	135-145	GBM1008-GBM1022									-10,01			-2,84		2
	135-155	GBM1008-GBM1005								-20,77		30,69			2,88	3
	145-155	GBM1022-GBM1005						26,73								1
	96-103	GMS006-HVM14		4,47		0,69	-1,37							-3,91	-0,84	5
	96-108	GMS006-HvPAF93						16,98								1
	96-112	GMS006-Bmag0613								-29,37	-19,85	20,60				3
7H	19	Bmag0206					3,46									1
	59	AF022725A	0,48			-0,43										2

Table 18 (continued)

Chr	Range (in cM)	Marker Interval	BS	BSP	COD	HEA	HEI	LOH	LR	NB	NPB	PM	RH	TGW	YLD	No. of QTLs
7H	62	HvSS1	-1,51													1
	100	Bmag0321				-0,02										1
		Bmag0369											-4,90			1
	120	GMS046						-5,96			-3,49					2
	146	BMS64			11,72	0,39					0,57					3
	166	EBmac0755	-8,12		-8,09					-10,66	-17,24					4
	178	HVM49	2,19			-3,08	-5,91	9,96							-9,78	5
	146-152	BMS64-Bmag0120						-7,68								1
	166-178	EBmac0755-HVM49											22,93			1
	59-62	AF022725A-HvSS1													-5,20	1
	59-77	AF022725A-GBMS035								-3,95		-13,25				2
	62-77	HvSS1-GBMS035									-9,67					1
	77-100	GBMS035-Bmag0369	6,03													1
	93-120	Bmac0167-GMS046			15,11											1
No. of QTLs			15	5	15	19	18	16	10	16	19	11	12	10	16	**183**

Relative performance of *Hsp* genotype: The relative performance of the exotic genotype is defined as: (*Hsp*-*Hv*)*100/*Hv*), where *Hv* and *Hsp* are the Lsmeans of lines with the elite and exotic genotype, respectively, at a given marker locus. **Chr:** Chromosomal assignment of SSR. **Range (in cM):** Position of marker in cM derived from von Koff et al. (2004). **Trait abbreviations (from BS to YLD)**: BS, Breaking of stem; BSP, Bending of spike; COD, Cold damage; HEA, Days until heading; HEI, Plant Height; HI, Harvest index; LOH, Lodging at harvest; LR, Leaf rust; NB, net blotch; NPB, Non-parasitic browning; PM, Powdery mildew; RH, leaf scald; TGW, Thousand-grain weight; YLD, Yield.

3.5.2 Detection of QTLs for all traits evaluated in T101

In this study, QTL-analysis was performed for 11 agronomic traits (BS, BSP, COD, HEA, HEI, HI, LOH, MAS, EAR, TGW and YLD), four pathogen resistances (LR, NB, PM and RH) and one syndrome (NPB) in population T101. In total, 85 putative QTLs were detected for agronomic traits, pathogen resistance and non-parasitic browning (Table 19, Table 20, and Figure 4). Among these QTLs, at 13 (19.4 %) loci out of 67 putative QTLs for agronomic traits, the presence of the *Hsp* alleles led to an improvement of the trait compared to the *Hv* allele for 11 agronomic traits. No favorable QTL was detected for pathogen resistances and non-parasitic browning. The detailed results of the QTL-analysis for agronomic traits, pathogen resistances and non-parasitic browning are described in the following.

3.5.2.1 Detection of QTLs for agronomic traits in T101

Altogether, 67 putative QTLs were detected for 11 agronomic traits (BS, BSP, COD, HEA, HEI, HI, LOH, MAS, NOS, TGW and YLD) in T101 (Table 19, Table 20 and Figure 4). Among these loci, 13 (19.4 %) favorable QTL effects were detected. Most putative QTLs were located on chromosomes 1H, 3H, 4H and 6H. However, most favorable effects of the *Hsp* alleles were detected on chromosomes 1H. In the following, the detected QTLs are described for each trait.

Breaking of stem (BS)

Six putative QTLs were located for BS on chromosomes 4H, 5H and 6H. All loci exhibited significant M×E interaction. Among the detected QTLs, only at marker interval HvRCABG-GMS089$_{[4H]}$, the *Hsp* allele resulted in a decreased BS of 23.0 %. However, the *Hsp* allele showed crossover interaction effect on BS at this QTL. At the remaining QTLs, the presence of the *Hsp* allele was associated with an increased BS of up to 37.7 % (HDAMYB$_{[4H]}$).

Bending of spike (BSP)

Five putative QTLs were located for BSP on chromosomes 1H, 4H and 6H. Four loci showed significant M×E interactions. At HvKNOX3$_{[4H]}$ the marker main effect was significant. The favorable QTL effect of the *Hsp* allele was observed at HvKNOX3$_{[4H]}$. At this locus, the *Hsp* allele resulted in a reduced BSP of 19.3 %. A crossover interaction effect, which was associated with a reduction of BSP of 4.7 %, was detected at HVM14$_{[6H]}$. At three loci, the presence of the *Hsp* allele caused an increased BSP of up to 5.4 % at HVM40$_{[4H]}$. The genetic variance was explained by HvKNOX3$_{[4H]}$ with 8.8 %.

Cold damage (COD)

For COD, nine putative QTLs were located on all chromosomes except for 7H. All loci exhibited significant M×E interaction except for GBM1041$_{[5H]}$ where the marker main effect was significant. At EBmac0906-GMS089$_{[4H]}$, where the crossover interactioneffect was detected for COD, the presence of the *Hsp* allele was associated with a decreased COD level of 19.4 %. However, at the other loci, unfavorable effects of the *Hsp* alleles on COD were observed. At these loci, the *Hsp* allele resulted in an increased COD level of up to 64.3 % at HVM33-HVM60$_{[3H].}$ The explained genetic variance reached 37.3 % at GBM1041$_{[5H]}$.

Number of spikes per square metre (EAR)

Only one putative QTL for EAR was detected as significant M×E interaction on 5H. At Bmac0613$_{[5H],}$ the presence of the *Hsp* allele was associated with a reduced EAR of 0.8 %.

Days until heading (HEA)

Nine putative QTLs were located for HEA on chromosomes 1H, 5H and 7H. Six loci showed significant marker main effects, while five loci exhibited a significant M×E interaction. In addition, the marker main effects as well as the interaction effect were significant at loci GBM1002$_{[1H]}$ and GBMS012$_{[1H]}$. For five QTLs, the presence of the *Hsp* alleles caused HEA reductions with a maximum of 4.8 % at HvPLSC1B$_{[7H]}$. A crossover interaction effect, which was detected at GBM1041$_{[5H]}$, resulted in a decreased HEA of 0.8 %. At the remaining loci, the presence of the *Hsp* allele was associated with an increased HEA of up to 2.9 % (GBM1042$_{[1H]}$). The maximum explained genetic variance was found at GBM1002$_{[1H]}$ with 28.0 %.

Plant height (HEI)

Fifteen Putative QTLs were located for HEI on all chromosomes expect for 7H. At eleven loci, the marker main effects were significant, while 13 loci showed significant M×E interactions. In nine cases, both, the marker main effect as well as the interaction were significant. More marker main effects were detected for HEI than for other traits in this study. And most favorable QTL effects of *Hsp* alleles on HEI showed marker main effects. For seven QTLs, which were located on chromosome 1H, 4H, 5H and 6H, the favorable effect of the *Hsp* allele was associated with a decreased HEI of up to 7.3 % at GBMs012$_{[1H].}$ At HVM40$_{[4H]}$, the crossover interaction effect resulted in a decreased HEI of 1.5 %. On the other hand, seven negative QTL effects of *Hsp* alleles caused HEI increases with a maximum 9.5 % in marker interval HVM33-HVM60$_{[3H].}$ The genetic variance explained by a QTL reached its maximum with 31.2 % at GBMs012$_{[1H].}$

Harvest index (HI)

Only two putative QTLs for HI were located on chromosomes 1H and 5H. Both QTLs, at GBM1002$_{[1H]}$ and MGB318$_{[5H]}$ exhibited significant M×E interactions. Both QTLs showed crossover interaction effects on HI. At GBM1002$_{[1H],}$ the presence of the *Hsp* allele resulted in an increased HI of 3.3 %. However, the *Hsp* allele caused a reduced HI of 4.9 % at MGB318$_{[5H].}$

Lodging at harvest (LOH)

A total of six putative QTLs were located for LOH on chromosomes 1H, 3H and 4H. While four loci exhibited a significant marker main effect, the other loci showed a significant M×E interaction. The detected marker main effects exhibited very strong unfavorable effect on LOH. At these loci, the unfavorable effect of the *Hsp* allele led to an increased LOH of up to 62.3 % at HVM60$_{[3H]}$. Only at marker interval HvKNOX3-HvPAXG$_{[4H],}$ a crossover interaction affect of the *Hsp* allele was observed. At this locus, the presence of the *Hsp* allele resulted in a LOH reduction of 14.7 %. The maximum explained genetic variance was reached with 26.7 % at marker interval BMS32-GMS114$_{[1H]}$.

Biomass (MAS)

As in the case of HI, two putative QTLs were located for MAS on chromosomes 3H. Both QTLs showed significant M×E interactions. The two QTLs exhibited crossover interaction effects. At HVM60$_{[3H]}$, the *Hsp* allele caused MAS increase of 5.8 % while At HVM62$_{[6H]}$, the crossover interaction effect of the *Hsp* allele on MAS led to a MAS reduction of 2.4 %.

Thousand-grain weight (TGW)

For TGW, five putative QTLs were located on chromosomes 1H, 4H and 6H. Two loci showed significant marker main effects. At the other loci, a significant M×E interaction was observed. In addition, the marker main effect as well as the interaction effect was significant at GMS006-Bmag0613$_{[6H]}$. No *Hsp* allele with a favorable effect on TGW was detected. The *Hsp* alleles resulted in TGW reductions of up to 7.3 % at GBM1048$_{[4H]}$. The genetic variance was explained by GBM1042$_{[1H]}$ with 7.0 %.

Yield (YLD)

Seven putative QTLs were located for yield on all chromosomes except for 3H and 7H. At three loci, a significant marker main effect was observed, while six loci showed significant M×E interactions. In two cases, the marker main effect and the interaction were significant. Only at

GBM1048$_{[4H]}$, where a crossover interaction effect was detected for YLD, the presence of the *Hsp* allele led to an YLD increase of 0.3 %. At the remaining loci, the *Hsp* allele was associated with a reduced YLD of up to 8.4 % at marker interval HVM40-HvKNOX3$_{[4H]}$. At this locus, the explained genetic variance reached its maximum with 13.8 %.

3.5.2.2 Detection of QTLs for pathogen resistances and non-parasitic browning in T101

In T101, a total of 18 putative QTLs for four pathogen resistances and non-parasitic browning were located on all chromosomes except for 2H. Among these QTLs, no favorable QTL effect was identified for pathogen resistances and non-parasitic browning (NPB) (Table 22, Table 23 and Figure 4). The putative QTLs were mainly located on chromosomes 1H, 3H and 6H. In the following, the detected QTLs are described for each trait.

Leaf rust (LR)

Only one putative QTL for LR was detected as significant M×E interaction on 4H. At HVM67-HvBAMY$_{[4H]}$, the presence of the *Hsp* allele was associated with an increased LR symptom of 29.0 %.

Net blotch (NB)

Five putative QTLs were located for NB on chromosomes 1H, 5H, 6H and 7H. All QTLs were detected as significant M×E interaction. For three QTLs, which were detected as crossover interaction effects at GBM1002$_{[1H]}$ GBM1021$_{[6H]}$ and GMS006-HVM14$_{[6H]}$, the presence of the *Hsp* allele resulted in a reduced NB infection of up to 10.1 % at GBM1002$_{[1H]}$. However, at HvLOXC$_{[5H]}$ and HVM49$_{[7H]}$, the *Hsp* allele led to an increased NB infection of up to 36.4 % (HvLOXC$_{[5H]}$).

Non-parasitic browning (NPB)

Altogether, eight putative QTLs were located for NPB on chromosomes 1H, 3H and 6H. All loci exhibited significant M×E interaction. At HVM33-GMS116$_{[3H]}$ and GMS006$_{[6H]}$, where the crossover interaction effects on NPB were observed, the *Hsp* allele was associated with a reduced NPB symptoms of up to 7.8 % (GMS006$_{[6H]}$). At the remaining loci, the presence of the *Hsp* allele caused a NPB increase with a maximum 11.2 % at GBM1002$_{[1H]}$.

Powdery mildew (PM)

As in the case of LR, only one putative QTL for PM was detected as significant M×E interaction on 3H. At GMS116$_{[3H],}$ the presence of the *Hsp* allele was associated with an increased PM symptom of 9.1 %.

Scald (RH)

Three putative QTLs were located for RH on chromosomes 1H, 4H and 5H. At GBM1026-Bmag0337$_{[5H]}$, a significant marker main effect was observed, while the other two loci exhibited significant M×E interactions. No favorable effect of the *Hsp* allele on RH was observed. On the other hand, the presence of the *Hsp* allele was associated with an increased RH infection of up to 40.3 % at HVM67-HvBAMY$_{[4H].}$ The genetic variance explained by GBM1026-Bmag0337$_{[5H]}$ with 4.0 %.

Table 19: List of 85 putative QTLs detected in T101

Trait[1]	QTL[2]	Marker Interval[3]	Chr[4]	Range[5] (in cM)	Repr. Marker[6]	Factor[7]	Sign[8]	LSM [*Hsp*][8]	R^{2}[10] $_G$ (%)	RP[*Hsp*][11] (in %)	P/N[12]
BS	QbsT101-4Ha	HVM40	4H	14	HVM40	M*E	**	2.84			°
	QbsT101-4Hb	HvRCABG-GMS089	4H	42-57	HvPAZXG	M*E	**	2.32			°
	QbsT101-4Hc	HDAMYB	4H	190	HDAMYB	M*E	***	3.78			°
	QbsT101-5H	Bmag0337	5H	43	Bmag0337	M*E	**	3.49			°
	QbsT101-6Ha	GBM1021	6H	40	GBM1021	M*E	***	3.50			°
	QbsT101-6Hb	GMS006	6H	96	GMS006	M*E	**	3.33			°
BSP	QbspT101-1H	GBM1002	1H	80	GBM1002	M*E	***	3.51			°
	QbspT101-4Ha	HVM40	4H	14	HVM40	M*E	**	3.58			°
	QbspT101-4Hb	HvKNOX3	4H	31	HvKNOX3	M	***	2.86	8.79	-19.34	+
	QbspT101-4Hc	GBM1048	4H	162	GBM1048	M*E	**	3.44			°
	QbspT101-6H	HVM14	6H	103	HVM14	M*E	**	3.33			°
COD	QcodT101-1Ha	GBM1042	1H	39	GBM1042	M*E	**	3.47			°
	QcodT101-1Hb	HvALAAT-GBM1002	1H	63-80	GBM1002	M*E	***	4.35		46.21	-
	QcodT101-1Hc	BMS32	1H	105	BMS32	M*E	**	3.44			°
	QcodT101-1Hd	GBMS012	1H	144	GBMS012	M*E	***	3.98			°
	QcodT101-2H	GBM1035	2H	27	GBM1035	M*E	**	4.40			°
	QcodT101-3H	HVM33	3H	94-110	HVM60	M*E	***	5.33			°
	QcodT101-4H	EBmac0906-GMS089	4H	37-57	GMS089	M*E	***	2.77			°
	QcodT101-5H	GBM1041	5H	75	GBM1041	M	**	4.80			°
	QcodT101-6H	GBM1021	6H	40	GBM1021	M*E	**	3.81			°
EAR	QearT101-5H	Bmac0163	5H	24	Bmac0163	M*E	**	655.20			°

Table 19 (continued)

Trait[1]	QTL[2]	Marker Interval[3]	Chr[4]	Range[5] (in cM)	Repr. Marker[6]	Factor[7]	Sign[8]	LSM [*Hsp*][8]	R^{2} [10] $_{G}$ (%)	RP[*Hsp*][11] (in %)	P/N[12]
HEA	QheaT101-1Ha	GBM1042	1H	39	GBM1042	M	**	60.69	7.74	2.87	-
	QheaT101-1Hb	HvALAAT-GBM1004	1H	63-75	GBM1004	M	***	60.34	11.90	2.64	-
	QheaT101-1Hc	GBM1002	1H	80	GBM1002	M + M*E	**	57.44	28.00	-3.76	+
	QheaT101-1Hd	GBMS012	1H	144	GBMS012	M + M*E	**	57.62	14.68	-3.05	+
	QheaT101-1He	Bmag0579	1H	175	Bmag0579	M	***	56.57	15.36	-4.68	+
	QheaT101-5H	GBM1041	5H	75	GBM1041	M*E	***	58.78			°
	QheaT101-7Ha	HvPLASC1B	7H	8	HVPLASC1B	M	**	56.39	7.25	-4.82	+
	QheaT101-7Hb	AF022725A-GBMS035	7H	59-77	AF022725A	M*E	***	59.25			°
	QheaT101-7Hc	BMS64	7H	146	BMS64	M*E	***	58.21		-1.85	+
HEI	QheiT101-1Ha	GBM1042	1H	39	GBM1042	M	**	112.29	8.13	5.37	-
	QheiT101-1Hb	HvALAAT-GBM1004	1H	63-75	HvALAAT	M + M*E	***	113.28	29.67	7.55	-
	QheiT101-1Hc	GBM1002	1H	80	GBM1002	M + M*E	**	101.14	31.19	-7.26	+
	QheiT101-1Hd	BMS32-GMS114	1H	105-115	GMS114	M + M*E	***	111.91	27.74	6.50	-
	QheiT101-1He	GBMS012	1H	144	GBMS012	M + M*E	**	101.46	18.38	-6.27	+
	QheiT101-1Hf	Bmag0579	1H	175	Bmag0579	M	**	100.35	9.46	-6.75	+
	QheiT101-2H	HVM36-GBM1035	2H	17-27	HVM36	M*E	***	113.08		6.12	-
	QheiT101-3Ha	HVM33-HVM60	3H	94-110	HVM60	M + M*E	***	116.75	10.79	9.47	-
	QheiT101-3Hb	Bmag0013-HVM62	3H	155-165	Bmag0013	M + M*E	**	114.69	16.43	8.08	-
	QheiT101-3Hc	Bmac0029	3H	190	Bmac0029	M*E	**	110.11			°
	QheiT101-4Ha	HVM40	4H	14	HVM40	M*E	***	105.84			°
	QheiT101-4Hb	HvJASIP-HvBAMY	4H	180-190	HvBAMY	M*E	**	101.07		-5.97	+
	QheiT101-5H	Bmac0163-HVLEU	5H	24-53	HvHEMH1	M + M*E	***	104.15	11.07	-4.34	+
	QheiT101-6Ha	GBM1021	6H	40	GBM1021	M + M*E	**	102.15	16.74	-5.67	+
	QheiT101-6Hb	GMS006-Bmag0613	6H	96-112	Bmag0613	M + M*E	**	102.04	10.05	-5.17	+
HI	QhiT101-1H	GBM1002	1H	80	GBM1002	M*E	**	0.55			°
	QhiT101-5H	MGB318	5H	150	MGB318	M*E	**	0.51			°

Table 19 (continued)

Trait[1)]	QTL[2)]	Marker Interval[3)]	Chr[4)]	Range[5)] (in cM)	Repr. Marker[6)]	Factor[7)]	Sign[8)]	LSM [*Hsp*][8)]	$R^{2\ 10)}_G$ (%)	RP[*Hsp*][11)] (in %)	P/N[12)]
LOH	QlohT101-1Ha	HvALAAT-GBM1004	1H	63-75	Bmag0211	M	***	6.16	26.72	42.76	-
	QlohT101-1Hb	BMS32-GMS114	1H	105-115	BMS32	M	**	5.46	10.50	25.46	-
	QlohT101-3Ha	HVM60	3H	110	HVM60	M	**	7.43	8.36	62.31	-
	QlohT101-3Hb	GBM1059	3H	161	GBM1059	M	**	5.64	6.61	24.10	-
	QlohT101-4Ha	HvKNOX3-HvPAZXG	4H	31-44	HvKNOX3	M*E	**	4.11			°
	QlohT101-4HB	HDAMYB	4H	190	HDAMYB	M*E	**	4.74			°
LR	QlrT101-4H	HVM67-HvBAMY	4H	180-190	HvBAMY	M*E	**	4.5			°
MAS	QmasT101-3Ha	HVM60	3H	110	HVM60	M*E	**	131.84			°
	QmasT101-3Hb	HVM62	3H	165	HVM62	M*E	**	121.95			°
NB	QnbT101-1H	GBM1002	1H	80	GBM1002	M*E	**	1.51			°
	QnbT101-5H	HvLOXC	5H	114	HvLOXC	M*E	**	2.20			°
	QnbT101-6Ha	GBM1021	6H	40	GBM1021	M*E	***	1.51			°
	QnbT101-6Hb	GMS006-HVM14	6H	96-103	GMS006	M*E	***	1.52			°
	QnbT101-7H	HVM49	7H	178	HVM49	M*E	**	1.91			°
NPB	QnpbT101-1Ha	GBM1002	1H	80	GBM1002	M*E	**	3.57			°
	QnpbT101-1Hb	BMS32-GMS114	1H	105-115	BMS32	M*E	***	3.41			°
	QnpbT101-1Hc	Bmag0579	1H	175	Bmag0579	M*E	**	3.32			°
	QnpbT101-3Ha	HVM33-GMS116	3H	94-100	HVM33	M*E	**	3.15			°
	QnpbT101-3Hb	GBM1059-HVM62	3H	161-165	HVM62	M*E	**	3.41			°
	QnpbT101-3Hc	Bmac0029	3H	190	Bmac0029	M*E	***	3.54			°
	QnpbT101-6Ha	GBM1021	6H	40	GBM1021	M*E	**	3.38			°
	QnpbT101-6Hb	GMS006	6H	96	GMS006	M*E	**	3.10			°
PM	QpmT101-3H	GMS116	3H	100	GMS116	M*E	**	3.97			°
RH	QrhT101-1H	Bmag0579	1H	175	Bmag0579	M*E	**	3.44			°
	QrhT101-4H	HVM67-HVBAMY	4H	180-190	HVM67	M*E	**	4.03			°
	QrhT101-5H	GBM1026-Bmag0337	5H	30-43	HvHEMH1	M	**	3.40	4.00	20.50	-

Table 19 (continued)

Trait[1)]	QTL[2)]	Marker Interval [3)]	Chr[4)]	Range[5)] (in cM)	Repr. Marker[6)]	Factor[7)]	Sign[8)]	LSM [*Hsp*][8)]	$R^{2\ 10)}_G$ (%)	RP[*Hsp*][11)] (in %)	P/N[12)]
TGW	QtgwT101-1Ha	GBM1042	1H	39	GBM1042	M	**	39.79	7.00	-5.43	-
	QtgwT101-1Hb	HvALAAT-GBM1002	1H	63-80	GBM1004	M*E	***	39.90			°
	QtgwT101-4Ha	HvKNOX3-HVM13	4H	31-55	HvKNOX3	M*E	**	39.90		-5.50	-
	QtgwT101-4Hb	GBM1048	4H	162	GBM1048	M*E	**	39.12		-7.28	-
	QtgwT101-6H	GMS006-Bmag0613	6H	96-112	Bmag0613	M + M*E	***	39.17	10.66	-7.01	-
YLD	QyldT101-1Ha	HvALAAT-GBM1002	1H	63-80	HvALAAT	M + M*E	***	733.13	9.75	-7.77	-
	QyldT101-1Hb	GMS114	1H	115	GMS114	M	**	752.81	9.36	-5.28	-
	QyldT101-2H	HVM54-EBmac0415	2H	143-146	HVM54	M*E	**	752.85		-5.22	-
	QyldT101-4Ha	HVM40-HvKNOX3	4H	14-31	HvKNOX3	M + M*E	***	724.97	13.80	-8.35	-
	QyldT101-4Hb	GBM1048	4H	162	GBM1048	M*E	**	784.14			°
	QyldT101-5H	HvLOXC	5H	114	HvLOXC	M*E	***	739.87			°
	QyldT101-6Hb	GMS006	6H	96	GMS006	M*E	***	742.60			°

[1)] Trait abbreviations: BS, Breaking of stem; BSP, Bending of spike; COD, Cold damage; EAR, Number of spikes; HEA, Days until heading; HEI, Plant Height; HI, Harvest index; LOH, Lodging at harvest; LR, Leaf rust; MAS, Biomass; NB, net blotch; NPB, Non-parasitic browning; PM, Powdery mildew; RH, leaf scald; TGW, Thousand-grain weight; YLD, Yield. [2)] Name of **QTLs** contains the prefix 'Q' (QTL), abbreviation of trait, abbreviation of population, chromosomal location and the ordinal number of QTLs on chromosome. [3)] Marker exhibiting significant QTL effects. [4)] Chromosomal assignment of SSR. [5)] Position of marker in cM derived from von Koff et al. (2004). [6)] For each group of linked markers with a significant QTL effect only the marker with the highest F statistics is listed. [7)] Factor M or M*E significant in QTL analysis. [8)] Level of significance of the marker main effect or the MxE interaction, with **: $P < 0.01$, ***: $P < 0.001$; if there were more than one significant marker effect in the QTL interval, then the highest level of significance was taken. [9)] The least square mean across all tested environments for homozygous *Hsp* genotypes at the given marker locus. [10)] The portion of genetic variance which is explained by marker main effect (R^2_G). [11)] Relative performance of *Hsp* genotype: RP[*Hsp*] = ([*Hsp*]-[*Hv*]) x 100 / [*Hv*], where [*Hsp*] and [*Hv*] are the least square means of the homozygous *Hsp* and *Hv* genotypes, respectively, calculated across all environments tested; if there were more than one significant marker effect in the QTL interval, then the highest RP[*Hsp*] was taken. [12)] (+) QTL where the marker main effect or M×E interaction effect of the *Hsp* genotype is favorable across all environments; (–) QTL where the marker main effect or M×E interaction effect of the *Hsp* genotype is unfavorable across all environments; (°) QTL where the M×E interaction reveals a cross interaction where the Hsp genotype is favorable in some environments but unfavorable in other environments. For details, see Appendix 6 and Appendix 7.

Table 20: The relative performance of homozygous *Hsp* genotypes at 85 putative QTLs detected in T101

Chr	Range (in cM)	Marker Interval	BS	BSP	COD	EAR	HEA	HEI	HI	LOH	LR	MAS	NB	NPB	PM	RH	TGW	YLD	No. of QTLs
1H	39	GBM1042			6,30		2,87	5,37									-5,43		4
	80	GBM1002		3,44			-3,76	-7,26	3,32				-10,05	11,23					6
	105	BMS32			6,80														1
	115	GMS114																-5,28	1
	144	GBMS012			33,79		-3,05	-6,27											3
	175	Bmag0579					-4,68	-6,75						0,58		18,88			4
	105-115	BMS32-GMS114						6,50		25,46				4,64					3
	63-75	HvALAAT-GBM1004					2,64	7,55		42,76									3
	63-80	HvALAAT-GBM1002			46,21												-6,39	-7,77	3
2H	27	GBM1035			40,70														1
	143-146	HVM54-EBmac0415																-5,22	1
	17-27	HVM36-GBM1035						6,12											1
3H	100	GMS116													9,11				1
	110	HVM60								62,31		5,81							2
	161	GBM1059								24,10									1
	165	HVM62										-2,42							1
	190	Bmac0029						3,35						8,86					2
	155-165	Bmag0013-HVM62						8,08											1
	161-165	GBM1059-HVM62												4,08					1
	94-100	HVM33-GMS116												-4,77					1
	94-110	HVM33-HVM60			64,28			9,47											2
4H	14	HVM40	0,97	5,41				-1,54											3
	31	HvKNOX3		-19,34															1
	162	GBM1048		1,33													-7,28	0,30	3
	190	HDAMYB	37,68							3,34									2
	14-31	HVM40-HvKNOX3																-8,35	1
	180-190	HvJASIP-HvBAMY						-5,97											1
		HVM67-HvBAMY									28,95					40,28			2
	31-44	HvKNOX3-HvPAZXG								-14,73									1
	31-55	HvKNOX3-HVM13															-5,50		1
	37-57	EBmac0906-GMS089			-19,42														1
	42-57	HvRCABG-GMS089	-22,96																1

Table 20 (continued)

Chr	Range (in cM)	Marker Interval	BS	BSP	COD	EAR	HEA	HEI	HI	LOH	LR	MAS	NB	NPB	PM	RH	TGW	YLD	No. of QTLs
5H	24	Bmac0163				-0,81													1
	43	Bmag0337	27,83																1
	75	GBM1041			72,28		-0,82												2
	114	HvLOXC											36,38					-5,60	2
	150	MGB318							-4,48										1
	24-53	Bmac0163-HvLEU						-4,34											1
	30-43	GBM1026-Bmag0337														20,50			1
6H	40	GBM1021	28,71		20,68			-5,67					-9,75	2,86					5
	96	GMS006	24,14											-7,77				-6,59	3
	103	HVM14		-4,65															1
	96-103	GMS006-HVM14											-9,64						1
	96-112	GMS006-Bmag0613						-5,17									-7,01		2
7H	8	HvPLASC1B					-4,82												1
	146	BMS64					-1,85												1
	178	HVM49											17,97						1
	59-77	AF022725A-GBMS035					0,17												1
No. of QTLs			6	5	9	1	9	15	2	6	1	2	5	8	1	3	5	7	**85**

Relative performance of *Hsp* genotype: The relative performance of the exotic genotype is defined as: (*Hsp*-*Hv*)*100/*Hv*), where *Hv* and *Hsp* are the Lsmeans of lines with the elite and exotic genotype, respectively, at a given marker locus. **Chr:** Chromosomal assignment of SSR. **Range (in cM):** Position of marker in cM derived from von Koff et al. (2004). **Trait abbreviations from BS to YLD**: BS, Breaking of stem; BSP, Bending of spike; COD, Cold damage; EAR, Number of spikes; HEA, Days until heading; HEI, Plant Height; HI, Harvest index; LOH, Lodging at harvest; LR, Leaf rust; MAS, Biomass; NB, net blotch; NPB, Non-parasitic browning; PM, Powdery mildew; RH, leaf scald; TGW, Thousand-grain weight; YLD, Yield.

4. Discussion

In this study the AB-QTL analysis strategy was applied to map QTLs for 11 agronomic traits, four pathogen resistances and one syndrome in two BC_2DH winter barley populations (C101 and T101), which shared the barley accession ISR101-23 as the donor for exotic QTL alleles. The goal of the present work was to detect favorable QTL alleles from the wild donor, which may lead to an improvement of quantitative characteristics in the two populations. The minimum number of QTLs which are involved in the inheritance of a quantitative trait and of favorable QTL effects of the *Hsp* alleles were estimated for both populations. In the following, the results of QTL mapping in both winter barley populations will be discussed; afterwards a comparison of the methods of QTL mapping between classical QTL analysis and AB-QTL analysis will be conducted.

4.1 Comparison of the AB-QTL analysis between C101 and T101

In this section the results of the AB-QTL analysis in C101 are compared with T101. The two winter barley varieties Carola and Theresa are related by descent because they share the parent, Franka in their pedigree. Carola originated from the cross (SG402085 × Franka) × GW1307, introduced in 1998 by Nordsaat, Germany, and Theresa was from the cross (Franka × 943/77) × Carona, introduced in 1994 by Secobra, Germany. Both populations share the donor ISR101-23. The two populations were investigated in adjacent fields and under identical field conditions during the 2002/03 and 2003/04 seasons. However, the size of the populations differs: C101 consists of 282 BC_2DH lines, whereas the number of T101 individual drops to 104. The number of informative markers was slightly different between C101 and T101. C101 was genotyped with 82 polymorphic SSR markers, while 78 informative SSR markers were successfully genotyped in T101. Both populations shared 75 SSR markers. The genotyped polymorphic SSR markers covered 1,125 cM in C101 as well as in T101. According to the comprehensive consensus maps (Qi et al. 1996; Thiel et al. 2003), the total genetic length of the barley genome is approximately 1,060 cM. The first SSR map for the barley genome included 299 SSRs and covered 1,173 cM (Ramsay et al. 2000), while the SSR map of Pillen et al. (2003) contained 67 SSRs and covered 852 cM of the barley genome. However, the distribution of SSR markers on chromosomes was uneven and distinct clusters of markers and gaps (> 30 cM) were observed on every chromosome in both populations (Figure 3). Especially on chromosome 6H, two adjacent gaps covered over 90 cM in both populations. The clusters and gaps of SSR markers were also observed in previous studies (Ramsay et al. 2000; Li et al. 2003; Pillen et al. 2003, 2004). Our attempts to fill in gaps, for instance on chromosome 5H and 6H, failed since no polamorphic SSR was found for that particular chromosomal region. The same

15 quantitative traits were investigated in both populations with the exception of harvest index (HI) which was only phenotyped in T101.

4.1.1 Comparison of the detected putative QTLs in both populations

Whereas 183 (14.9 %) putative QTLs were detected among 1,230 marker×trait combinations in C101 (Table 17 and Table 19), 85 (6.8 %) putative QTLs were detected among 1,248 marker×trait combinations in T101 (Table 18 and Table 20). However, 345 (28.0 %) and 137 (11.0 %) significant marker main effects and M×E interactions were identified in C101 and T101 (Appendix 3 and 4), respectively. It is obvious that the rate of QTL detection and the number of significant marker effects and M×E interactions are notable difference between the two populations. The percentage of favorable QTL alleles was also considerable different in both populations. The QTL alleles of *Hsp* revealed much more favorable effects in C101, where 35 (19.1 %) favorable QTL alleles of the *Hsp* genome were identified, than in T101, where only 13 (15.3 %) favorable QTL alleles were detected. These differences may be caused by several reasons. The first reason might be the difference of the population size. Huang et al. (2004) detected 40 putative QTLs with a population size of 72 BC_2F_2 individuals in wheat. Eighty-six and 108 putative QTLs were detected by Pillen et al. (2003, 2004) in 136 and 164 BC_2F_2 spring barley plants, respectively. In this study, much more QTLs were detected in bigger population (C101) than smaller population (T101). Thus, the number of detected QTLs increased with the increase in population size. The second reason for these differences might be the number of the BC_1 plants, which the two populations originated. C101 consists of 282 BC_2DH lines from eight BC_1 plants and 104 BC_2DH lines of T101 were generated from seven BC_1 plants. However, Cox (1984) demonstrated that the additive genetic variance depends on the number of F_1 plants backcrossed in each previous generation rather than on the size of the derived population analysed and increasing the number of BC_1F_1 beyond 12 individuals produced little change of additive genetic variance in BC_1F_1 derived lines. The third reason might be the difference of genetic similarity (GS) between the elite varieties and the wild donor (here, the genetic similarity is only inferred based on 85 polymorphic SSR markers in both populations). Eighty-two (96.5 %) polymorphic SSR markers were found in C101, while 78 (91.0 %) SSR markers among 85 polymorphic SSR markers in both populations were polymorphic in T101 (Table 21). It suggested that the genetic distance is relatively closer between Theresa and ISR101-23 than between Carola and ISR101-23. Thus, the relatively close genetic distance between the barley wild form ISR101-23 and Theresa might have reduced the number of detectable putative QTLs. A further reason may be the use of the different statistic models in both populations for some

traits due to the inclusion of cold damage (COD) and neighbouring plots of (N) in the QTL analysis. For instance, N was used as a co-variable for QTL analysis of YLD in T101, but not in C101.

Table 21: Comparison of polymorphic and monomorphic markers between the elite varieties and wild donor in both populations

	ISR101-23		
	Monomorph	**Polymorph**	**∑**
Carola	3 (3.5%)	82 (96.5 %)	85 (100.0 %)
Theresa	7 (9.0 %)	78 (91.0 %)	85 (100.0 %)

The detected putative QTLs were clearly localized in clusters on some chromosomes in both populations, but most clusters were observed in different regions in both populations (Figure 4). In C101, the distribution of detected QTLs was relatively even on chromosomes 1H, 5H, 6H and 7H; on chromosome 2H, the putative QTLs mainly gathered in two regions, from HVM36 to GBMS002 and from GBM1016 to GBM1047; on chromosome 3H, three clusters were observed from HvLTPPB to EBmac0705, from HVM33 to HVM60 and from Bmag0013 to Bmac0029; one QTL cluster was observed in the region from Ebmac0679 to HvBAMY on chromosome 4H. In T101, little QTLs were detected on chromosomes 2H and 7H; putative QTLs exhibited an even distribution on chromosomes 1H and 5H; On chromosome 3H, putative QTLs only gathered on the long arm from HVM33 to HVM60 and from Bmag0013 to Bmac0029; two QTL clusters were observed from HVM40 to GMS89 and from GBM1048 to HvBAMY on chromosome 4H and two clusters were observed at GBM1021 and from GMS006 to Bmag0613 on chromosome 6H. The QTL clusters did not match with the marker clusters in both populations, for instance, ten QTLs were detected at $GBM1041_{[5H]}$ in C101 and only one QTL was located for YLD at GBM1016-$GBM1047_{[2H]}$ in T101.

4.1.1.1 Comparison of the significant effects detected by 75 shared markers in C101 and T101

In order to compare both populations further, the amount of potentially identical effects of the *Hsp* allele in both populations were investigated. For this, the polymorphic markers were reduced to those markers that were shared in both populations. In addition, the traits used for QTL analysis were reduced to 13 traits (BS, BSP, COD, HEA, HEI, LOH, LR, NB, NPB, PM, RH, TGW and YLD) measured in both populations.

To reveal the difference between C101 and T101, first of all, the significant effects detected by 75 shared polymorphic markers for 13 traits should be compared between both populations

because a lot of QTLs were defined within marker intervals so that the detected putative QTLs could not clearly show the difference between both populations. Table 22 shows the data of the significant marker main effects and M×E interaction detected by 75 shared markers for 13 traits in both populations. In total, 60 significant marker main effects and M×E interactions were common between both populations. The rates of significant effects, which were detected for 13 traits, were 33.1 % (323) in C101 and 12.2 % (119) in T101. Both values are not notably different from the overall significant effect rates of 28.0 % and 11.0 %. The number of loci with favorable effects were also much higher in C101 (64) than in T101 (21). The percentage (**R1**) of significant effects per chromosome among all marker×trait combinations, calculated by the formula: significant effects / [marker×trait combinations (75 × 13 = 975)], was higher on each chromosome in C101 than in T101. The percentage (**R2**) of significant effects per chromosome among the marker×trait combinations on a single chromosome, calculated by the formula: significant effects / [marker×trait combinations (n × 13, where n is the polymorphic markers per chromosome in both populations)], was profoundly higher on each chromosome in C101 than T101 except for 3H, for instance, 54 (51.9 %) effects on chromosome 6H were significant in C101, while 15 (14.4 %) effects were significant in T101. Sixty significant effects were verified in both populations. This number is equal to 50 % of the significant effect in T101 and 20 % of the significant effects in C101 which could be verified in the sister populations. Most of the verified effects were gathered on chromosomes 1H (19), 3H (11) and 5H (10). Comparison of the significant loci between 13 traits indicated that the significant loci were clearly more in C101 than in T101 for all traits except for COD and HEI.

Table 22: The list of significant marker main effects and M×E interactions detected for 13 traits by 75 shared markers in C101 and T101

	Chr	Pop	BS	BSP	COD	HEA	HEI	LOH	LR	NB	NPB	PM	RH	TGW	YLD	∑	CE	R1 (%)	R2 (%)
Significant effects	1H	C101	5	4	3	3(3)*	3(2)	8	6	9	2	2	3	7	6	61(5)	19	6.26	46.92
		T101	0	0	7	6(2)	8(2)	5	0	1	4	0	1	4	4	40(4)	19	4.10	30.77
	2H	C101	1	0	4(1)	7(2)	5(3)	0	2(1)	1	4(1)	4(4)	4	0	0	32(12)	3	3.28	30.77
		T101	0	0	1	0	2	0	0	0	0	0	0	0	2	5	3	0.51	4.81
	3H	C101	0	0	1	5(4)	7(2)	2(2)	2(2)	1	4	3(3)	0	1(1)	1	27(14)	11	2.77	17.31
		T101	0	0	2	0	7	2	0	0	5(2)	1	0	0	0	17(2)	11	1.74	10.90
	4H	C101	6	0	1	2(2)	8(7)	7	3	6	1	0	5	5	6	50(9)	7	5.13	27.47
		T101	4	1	4	0	3(3)	2	2	0	0	0	2	3	1	22(3)	7	2.26	12.09
	5H	C101	6	2	3	3(2)	4	7	0	3	6(4)	7(4)	6	3	8	58(10)	10	5.95	44.62
		T101	1	0	2	1	6(6)	0	0	1	0	0	3	0	1	15(6)	10	1.54	11.54
	6H	C101	2	2	2(1)	3	2	5	2	8(2)	7(3)	7	3	5	6	54(6)	8	5.54	51.92
		T101	2	1(1)	1	0	3(3)	0	0	3	2	0	0	2	1	15(4)	8	1.54	14.42
	7H	C101	8	0	6(1)	4(1)	2(1)	4	0	4	5(2)	2(2)	3(1)	0	3	41(8)	2	4.21	24.26
		T101	0	0	0	4(2)	0	0	0	1	0	0	0	0	0	5(2)	2	0.51	2.96
∑		C101	28	8	20(3)	27(14)	31(15)	33(2)	15(3)	32(2)	29(10)	25(13)	24(1)	21(1)	30	323(64)	60	33.13	X=34.75
		T101	7	2(1)	17	11(4)	29(14)	9	2	6	11(2)	1	6	9	9	119(21)	60	12.53	X=12.50
CE		C101	2	1	3	5	18	7	0	3	4	1	4	5	7	60			
		T101	2	1	3	5	18	7	0	3	4	1	4	5	7	60			

Chr: chromosome. **Pop**: population. **BS** to **YLD:** abbreviations of traits: BS, Breaking of stem; BSP, Bending of spike; COD, Cold damage; HEA, Days until heading; HEI, Plant Height; LOH, Lodging at harvest; LR, Leaf rust; NB, net blotch; NPB, Non-parasitic browning; PM, Powdery mildew; RH, leaf scald; TGW, Thousand-grain weight; YLD, Yield. ***** The number under each trait represents the significant loci at $P < 0.01$; and the number in brackets represents favorable effect of the *Hsp* alleles. **CE:** the number of identified significant effects ($P < 0.01$) in both populations among total significant effects in every population. **R1**: the percentage of significant effects per chromosome among all marker×trait combinations, calculated by the formula: significant effects / (marker×trait combinations (75 × 13 = 975)). **R2**: the percentage of significant effects per chromosome among the marker×trait combinations on a single chromosome, calculated by the formula: significant effects / (marker×trait combinations (n × 13, where n is the polymorphic markers per chromosome in both populations)). **X**: mean of **R2.**

4.1.1.2 Comparison of the putative QTLs detected by 75 shared markers in C101 and T101

In total, 179 and 74 putative QTLs were detected by 75 shared markers for 13 traits in C101 and T101, respectively (Table 23). In total, 39 QTLs in C101 matched to 40 QTLs in T101. The detected putative QTLs were notably different on chromosomes 1H, 2H, 5H and 7H. At 27 loci (GMS021$_{[1H]}$, GBM1007$_{[1H]}$, GBMS002$_{[2H]}$, EBmac0684$_{[2H]}$, GBM1016$_{[2H]}$, GBM1047$_{[2H]}$, HvLTPPB$_{[3H],}$ EBmac0705$_{[3H]}$, GBM1031$_{[3H],}$ Bmac0209$_{[3H]}$, Bmag0603$_{[3H]}$, HvPEPD1PR$_{[3H]}$, GBM1044$_{[4H]}$, EBmac0679$_{[4H]}$, GBM1015$_{[4H]}$, GMS001$_{[5H],}$ Bmac0613$_{[6H]}$, GBM1008$_{[6H]}$, GBM1022$_{[6H]}$, GBM1005$_{[6H]}$, Bmag0206$_{[7H]}$, Bmac0167$_{[7H]}$, Bmag0321$_{[7H]}$, BMAG0369$_{[7H]}$, GMS046$_{[7H]}$, Bmag0120$_{[7H]}$ and EBmac0755$_{[7H]}$), the putative QTLs were only detected in C101, while one putative QTL for HEA at HvPLASC1B$_{[7H]}$ was only detected in T101 (Fig. 4). No QTL was associated with GMS003$_{[2H]}$, Bmag0125$_{[2H]}$ and EBmac0775$_{[4H]}$ in both populations. The number of detected putative QTLs showed no clear difference for BSP, COD and HEI between both populations, while much more putative QTLs were detected in C101 than in T101 for the remaining traits.

Most of the verified putative QTL effects gathered on chromosome 1H (11 QTLs in C101 and 12 QTLs in T101), while little putative QTLs were verified on chromosomes 2H (2) and 7H (2). This result indicated that most of the QTL alleles on chromosome 1H from Carola and Theresa exhibit similar effects and that these effects are significantly different in their ISR101-23 counterpart, but the results turned out contrary on chromosomes 2H and 7H. The majority of verified QTL effects were found for HEI (10), HEA (5), LOH (4) and YLD (4). However, no putative QTL effects were verified for LR. This finding indicated that a lot of the QTL alleles for HEI, HEA, LOH and YLD from Carola and Theresa exhibit similar effects and that these effects are significantly different from the donor ISR101-23. In nine cases (*QbspC101-6H* or *QbspT101-6H*, *QheaC101-7Ha* or *QheaT101-7Hb*, *QheaC101-7Hc* or *QheaT101-7Hc*, *QheiC101-1Ha* or *QheiT101-1Hd*, *QheiC101-2Ha QheiT101-2H*, *QheiC101-5Ha* or *QheiT101-3Hb*, *QlohC101-3H* or *QlohT101-3Ha*, *QlohC101-4Ha* or *QlohT101-4Ha* and *QpmC101-3H* or *QpmT101-3H*), the *Hsp* alleles are associated with contrary QTL effects in C101 and T101. The highest numbers of QTLs detected in both populations were found at GMS006-Bmag0613$_{[6H]}$. This marker interval was associated with common effects on BSP, HEI, NB, TGW and YLD and only for BSP the *Hsp* allele had opposite effects in C101 and T101. Likewise, four common QTLs were detected for COD, HEI, LOH and YLD at BMS32-GMS114$_{[1H]}$ in both populations and opposite effects of the *Hsp* allele were only found for HEI. In addition, at GBMS012$_{[1H]}$, GBM1041$_{[5H]}$ and GBM1048-HvBAMY$_{[4H]}$ the *Hsp* alleles had common effects on corresponding traits in both populations. In summary, 19.8

% putative QTL effects of *Hsp* alleles (i.e. 50 common QTLs/253 QTLs investigated in C101 and T101, Table 24) were reproducible with the same effects between the two genetic backgrounds of Carola and Theresa. For 7 % of the QTLs investigated, the *Hsp* alleles had opposite effects in C101 and T101. The remaining 73 % of putative QTLs were not reproducible between the two populations. Consequently, it is difficult to predict the performance of a favorable exotic QTL allele in a new genomic background. Similar results were reported by Pillen et al. (2004) for the two spring barley populations H101 and A101, which shared the same donor (ISR101-23) with C101 and T101. The preponderance of non-reproducible QTLs between the two related backcross populations indicates a high degree of epistatic genetic interaction between the detected QTLs and the genomic background (Pillen et al. 2004).

Table 23: The list of QTLs detected for 13 traits by 75 shared markers in C101 and T101

	Chr	Pop	BS	BSP	COD	HEA	HEI	LOH	LR	NB	NPB	PM	RH	TGW	YLD	∑	CQ	R3(%)
Detected QTLs	1H	C101	3	2	2	3(3)*	3(2)	4	4	3	2	1	2	2	3	34(5)	11	18.99
		T101	0	0	5	4(2)	5(2)	2	0	0	2	0	1	2	2	23(4)	12	31.08
	2H	C101	1	0	2(1)	3(2)	3(2)	0	2(1)	1	3(1)	1(1)	3	0	0	19(8)	2	10.61
		T101	0	0	1	0	1	0	0	0	0	0	0	0	1	3	2	4.05
	3H	C101	0	0	1	2(1)	3(1)	1(1)	1(1)	1	3	1(1)	0	1(1)	1	15(6)	6	8.38
		T101	0	0	1	0	3	2	0	0	3	1	0	0	0	10	7	13.51
	4H	C101	1	0	1	2(2)	3(2)	3	1	2	1	0	1	1	2	18(4)	4	10.06
		T101	2	1(1)	1	0	1(1)	2	1	0	0	0	1	2	1	12(2)	4	16.22
	5H	C101	2	2	3	3(1)	3	2	0	3	2(1)	4(1)	2	3	4	33(3)	7	18.44
		T101	1	0	1	1	1(1)	0	0	1	0	0	1	0	1	7(1)	6	9.46
	6H	C101	2	1	1(1)	2	1	3	2	4(2)	4	3	3	3	3	32(3)	7	17.88
		T101	2	1	2	0	2(2)	0	0	2	2	0	0	1	2	14(2)	7	18.92
	7H	C101	5	0	3	4(1)	2(1)	3	0	2	4(2)	1(1)	2(1)	0	2	28(6)	2	15.64
		T101	0	0	1	3(2)	0	0	0	1	0	0	0	0	0	5(2)	2	6.76
∑		C101	14	5	13(2)	19(10)	18(8)	16(1)	10(2)	16(2)	19(4)	11(4)	13(1)	10(1)	15	179(35)	39	X=14.28
		T101	5	2(1)	12	8(4)	13(6)	6	1	4	7	1	3	5	7	74(11)	40	X=14.28
CQ		C101	2	1	3	5	10	4	0	2	3	1	2	2	4	39		
		T101	2	1	3	5	10	4	0	2	3	1	2	3	4	40		

Chr: chromosome. **Pop**: population. **BS** to **YLD:** abbreviations of traits: BS, Breaking of stem; BSP, Bending of spike; COD, Cold damage; HEA, Days until heading; HEI, Plant Height; LOH, Lodging at harvest; LR, Leaf rust; NB, net blotch; NPB, Non-parasitic browning; PM, Powdery mildew; RH, leaf scald; TGW, Thousand-grain weight; YLD, Yield. ***** The number under each trait represents the detected QTLs; and the number in brackets represents favorable effect of the *Hsp* alleles. **CQ**: the number of common QTLs in both populations. **R3**: the percentage of detected QTLs per chromosome among total QTLs in each population.

Table 24: Validation of the QTLs in C101 and T101

Trait[1)]	QTL[2)]	Repr. Marker[3)]	Chr[4)]	Range[5)] (in cM)	Factor[6)]	Sign[7)]	LSM [*Hsp*][8)]	$R^{2\,9)}_{G}$ (%)	RP[*Hsp*][10)] (in %)	P/N[11)]	Pop[12)]
BS	QbsC101-4H	HvJASIP	4H	162-190	M*E	***	4.24		23.81	°	**C**
	QbsT101-4Hc	HDAMYB	4H	190	M*E	***	3.78		37.68	°	**T**
	QbsC101-5Ha	GBM1026	5H	24-48	M*E	**	3.82		14.64	°	**C**
	QbsT101-5H	Bmag0337	5H	43	M*E	**	3.49		27.83	°	**T**
BSP	QbspC101-6H	GMS006	6H	96-103	M*E	**	4.63		4.47	°	**C**
	QbspT101-6H	HVM14	6H	103	M*E	**	3.33		-4.65	°	**T**
COD	QcodT101-1Hc	BMS32	1H	105	M*E	**	3.44		6.80	°	**T**
	QcodC101-1Ha	BMS32	1H	105-115	M + M*E	***	4.90	10.05	28.26	-	**C**
	QcodT101-2H	GBM1035	2H	27	M*E	**	4.40		40.70	°	**T**
	QcodC101-2Ha	GBM1035	2H	17-27	M + M*E	**	5.09	4.45	28.63	-	**C**
	QcodT101-5H	GBM1041	5H	75	M	**	4.80	37.31	72.28	-	**T**
	QcodC101-5Hb	GBM1041	5H	75	M + M*E	**	5.26	35.37	49.49	-	**C**
HEA	QheaT101-1He	Bmag0579	1H	175	M	***	56.57	15.36	-4.68	+	**T**
	QheaC101-1Hc	Bmag0579	1H	175	M + M*E	***	56.88	7.80	-2.68	+	**C**
	QheaT101-1Hd	GBMS012	1H	144	M + M*E	**	57.62	14.68	-3.05	+	**T**
	QheaC101-1Hb	GBMS012	1H	144	M + M*E	**	57.18	4.55	-1.99	+	**C**
	QheaT101-5H	GBM1041	5H	75	M*E	***	58.78		-0.82	°	**T**
	QheaC101-5Hb	GBM1041	5H	75	M*E	***	57.88		-0.71	°	**C**
	QheaC101-7Ha	AF022725A	7H	59	M*E	**	57.98		-0.43	°	**C**
	QheaT101-7Hb	AF022725A	7H	59-77	M*E	***	59.25		0.17	°	**T**
	QheaT101-7Hc	BMS64	7H	146	M*E	***	58.21	4.44	-1.85	+	**T**
	QheaC101-7Hc	BMS64	7H	146	M*E	**	58.35		0.39	°	**C**
HEI	QheiT101-1Hf	Bmag0579	1H	175	M	**	100.35	9.46	-6.75	+	**T**
	QheiC101-1Hc	Bmag0579	1H	175	M*E	***	107.19	1.22	-1.53	+	**C**
	QheiC101-1Ha	BMS32	1H	105	M	***	105.76	3.81	-3.27	+	**C**
	QheiT101-1Hd	GMS114	1H	105-115	M + M*E	***	111.91	27.74	6.50	-	**T**
	QheiT101-1He	GBMS012	1H	144	M + M*E	**	101.46	18.38	-6.27	+	**T**
	QheiC101-1Hb	GBMS012	1H	144	M*E	**	106.64	0.77	-2.27	+	**C**
	QheiT101-2H	HVM36	2H	17-27	M*E	***	113.08	3.03	6.12	-	**T**
	QheiC101-2Ha	HVM36	2H	17-27	M	**	104.55	3.12	-4.02	+	**C**

Table 24 (continued)

Trait[1)]	QTL[2)]	Repr. Marker [3)]	Chr[4)]	Range[5)] (in cM)	Factor[6)]	Sign[7)]	LSM [*Hsp*][8)]	$R^{2\ 9)}_G$ (%)	RP[*Hsp*][10)] (in %)	P/N[11)]	Pop[12)]
HEI	QheiT101-3Hc	Bmac0029	3H	190	M*E	**	110.11		3.35	°	**T**
	QheiC101-3Hc	Bmag0013	3H	155-190	M	***	114.23	11.81	5.86	-	**C**
	QheiT101-3Hb	Bmag0013	3H	155-165	M + M*E	**	114.69	16.43	8.08	-	**T**
	QheiC101-3Hb	HVM33	3H	94-100	M	***	113.65	6.84	5.18	-	**C**
	QheiT101-3Ha	HVM60	3H	94-110	M + M*E	***	116.75	10.79	9.47	-	**T**
	QheiC101-4Hc	GBM1015	4H	162-190	M + M*E	**	103.36	6.62	-5.29	+	**C**
	QheiT101-4Hb	HvBAMY	4H	180-190	M*E	**	101.07	2.34	-5.97	+	**T**
	QheiT101-5H	HvHEMH1	5H	24-53	M + M*E	***	104.15	11.07	-4.34	+	**T**
	QheiC101-5Hb	HvLEU	5H	53	M*E	***	106.53		-2.24	°	**C**
	QheiC101-5Ha	Bmag0357	5H	43-48	M*E	**	109.26		0.79	°	**C**
	QheiT101-6Hb	Bmag0613	6H	96-112	M + M*E	**	102.04	10.05	-5.17	+	**T**
	QheiC101-6H	HVM14	6H	96-103	M*E	***	107.32		-1.37	°	**C**
LOH	QlohT101-1Hb	BMS32	1H	105-115	M	**	5.46	10.50	25.46	-	**T**
	QlohC101-1Hb	BMS32	1H	105-115	M*E	***	4.75	4.72	28.05	-	**C**
	QlohC101-1Ha	GBM1004	1H	39-75	M*E	***	4.53	3.59	23.82	-	**C**
	QlohT101-1Ha	Bmag0211	1H	63-75	M	***	6.16	26.72	42.76	-	**T**
	QlohC101-3H	HVM60	3H	100-110	M*E	***	3.12	2.37	-20.47	+	**C**
	QlohT101-3Ha	HVM60	3H	110	M	**	7.43	8.36	62.31	-	**T**
	QlohC101-4Ha	HVM13	4H	37-57	M*E	***	5.50	3.78	44.45	-	**C**
	QlohT101-4Ha	HVKNOX3	4H	31-44	M*E	**	4.11		-14.73	°	**T**
NB	QnbC101-6Hb	GBM1021	6H	40	M*E	***	2.61	6.05	-15.92	+	**C**
	QnbT101-6Ha	GBM1021	6H	40	M*E	***	1.51	18.24	-9.75	°	**T**
	QnbC101-6Hc	HVM14	6H	96-112	M*E	***	2.23		-29.37	°	**C**
	QnbT101-6Hb	GMS006	6H	96-103	M*E	***	1.52		-9.64	°	**T**
NPB	QnpbC101-3Hb	GBM1059	3H	161-169	M + M*E	***	4.13	10.66	22.16	-	**C**
	QnpbT101-3Hb	HVM62	3H	161-165	M*E	**	3.41		4.08	°	**T**
	QnpbC101-6Hb	HVM14	6H	96-112	M*E	***	2.91		-19.85	°	**C**
	QnpbT101-6Hb	GMS006	6H	96	M*E	**	3.10		-7.77	°	**T**
	QnpbC101-3Hc	Bmac0029	3H	190	M + M*E	**	4.09	5.23	18.55	-	**C**
	QnpbT101-3Hc	Bmac0029	3H	190	M*E	***	3.54		8.86	°	**T**

Table 24 (continued)

Trait[1)]	QTL[2)]	Repr. Marker[3)]	Chr[4)]	Range[5)] (in cM)	Factor[6)]	Sign[7)]	LSM [*Hsp*][8)]	$R^{2\,9)}_G$ (%)	RP[*Hsp*][10)] (in %)	P/N[11)]	Pop[12)]
PM	QpmC101-3H	GMS116	3H	94-110	M*E	***	3.98	2.46	-10.62	+	**C**
	QpmT101-3H	GMS116	3H	100	M*E	**	3.97		9.11	°	**T**
RH	QrhC101-5H	GBM1026	5H	24-75	M	***	4.25	7.46	13.37	-	**C**
	QrhT101-5H	HvHEMH1	5H	30-43	M	**	3.40	4.00	20.50	-	**T**
	QrhC101-4H	GBM1048	4H	162-190	M	**	4.52	5.55	17.53	-	**C**
	QrhT101-4H	HVM67	4H	180-190	M*E	**	4.03	3.78	40.28	-	**T**
TGW	QtgwC101-1Ha	GBM1004	1H	28-75	M*E	**	38.74	15.20	-5.78	-	**C**
	QtgwT101-1Ha	GBM1042	1H	39	M	**	39.79	7.65	-5.43	-	**T**
	QtgwT101-1Hb	GBM1004	1H	63-80	M*E	***	39.90	11.79	-6.39	-	**T**
	QtgwT101-6H	Bmag0613	6H	96-112	M + M*E	***	39.17	11.65	-7.01	-	**T**
	QtgwC101-6Hb	HVM14	6H	96-103	M*E	***	39.23		-3.91	°	**C**
YLD	QyldC101-1Hb	BMS32	1H	105-115	M	***	687.95	25.83	-9.62	-	**C**
	QyldT101-1Hb	GMS114	1H	115	M	**	752.81	11.53	-5.28	-	**T**
	QyldC101-1Ha	GBM1032	1H	50-75	M	***	703.89	14.47	-7.02	-	**C**
	QyldT101-1Ha	HvALAAT	1H	63-80	M + M*E	***	733.13	12.02	-7.77	-	**T**
	QyldT101-5H	HvLOXC	5H	114	M*E	***	739.87	6.37	-5.60	-	**T**
	QyldC101-5Hd	HvLOXC	5H	114	M*E	***	706.73	6.96	-5.95	-	**C**
	QyldT101-6Hb	GMS006	6H	96	M*E	***	742.60		-6.59	°	**T**
	QyldC101-6Hb	HVM14	6H	96-103	M*E	**	741.55		-0.84	°	**C**

[1)] Trait abbreviations: BS, Breaking of stem; BSP, Bending of spike; COD, Cold damage; HEA, Days until heading; HEI, Plant Height; LOH, Lodging at harvest; LR, Leaf rust; NB, net blotch; NPB, Non-parasitic browning; PM, Powdery mildew; RH, leaf scald; TGW, Thousand-grain weight; YLD, Yield. [2)] Name of **QTLs** contains the prefix 'Q' (QTL), abbreviation of trait, abbreviation of population, chromosomal location and the ordinal number of QTLs on chromosome. [3)] For each group of linked markers with a significant QTL effect only the marker with the highest F statistics is listed. [4)] Chromosomal assignment of SSR. [5)] Position of marker in cM derived from von Koff et al. (2004). [6)] Factor M or M*E significant in QTL analysis. [7)] Level of significance of the marker main effect or the MxE interaction, with **: P < 0.01, ***: P < 0.001; if there were more than one significant marker effect in the QTL interval, then the highest level of significance was taken. [8)] The least square mean across all tested environments for homozygous *Hsp* genotypes at the given marker locus. [9)] The portion of genetic variance which is explained by marker main effect (R_G) or by M×E interaction (R_{GI}). [10)] Relative performance of *Hsp* genotype: RP[*Hsp*] = ([*Hsp*]-[*Hv*]) x 100 / [*Hv*], where [*Hsp*] and [*Hv*] are the least square means of the homozygous *Hsp* and *Hv* genotypes, respectively, calculated across all environments tested; if there were more than one significant marker effect in the QTL interval, then the highest RP[*Hsp*] was taken. [11)] (+) QTL where the marker main effect or M×E interaction effect of the *Hsp* genotype is favorable across all environments; (–) QTL where the marker main effect or M×E interaction effect of the *Hsp* genotype is favorable across all environments; (°) QTL where the M×E interaction reveals a cross interaction where the Hsp genotype is favorable in some environments but unfavorable in other environments. For details, see Appendix 6 and Appendix 7. [12)] Pop: C = C101; T = T101.

4.1.2 Comparison of putative QTL effects with other AB populations in barley

The use of shared markers and donors allows to compare the populations C101 and T101 with the populations A101, derived from the cross Apex×ISR101-23 (Pillen et al. 2003), and H101, derived from the cross Harry×ISR101-23 (Pillen et al. 2004). In order to find consistency of the exotic QTL effects in different genetic backgrounds, the putative QTL effects were compared by shared markers for all new population-pairs between the populations C101, T101, A101 and H101. Finally, the comparison of putative QTL effects was performed across all four populations.

Between C101 and H101, 21 shared markers revealed 74 putative QTLs for five traits in both populations and 14 (37.8 %) QTLs were detected simultaneously in both populations (Table 25). However, only eight (21.6 %) QTLs had the same effect in both populations. The majority of QTLs with the same effect were for HEA (3) and HEI (2) and the remaining for TGW (1) and YLD (1).

Table 25: Comparison of putative QTL effects between C101 and H101 (Harry ×ISR101-23, Pillen et al. 2004)

			HEA		HEI		LOH		TGW		YLD	
Chr	**Pos**	**Marker**	**C**	**H**	**C**	**H**	**C**	**H**	**C**	**H**	**C**	**H**
1H	63	HvALAAT		-			-		-	-	-	
2H	17	HVM36	+	+				+		+		-
	97	GMS003		+		+		+		+		-
	143	HVM54	+	-								
	146	EBmac0415	+	-								
3H	30	EBmac0705	-	-	+	-					-	
	63	Bmac0209	+	+						+		
	94	HVM33			-		+			+		
	110	HVM60		+			+			+		-
	155	Bmag0013		+	-				+	-		
4H	57	GMS089		-			-				-	
	80	EBmac0775										-
	132	EBmac0679	+	-	+		-					+
	180	HVM67		-	+				-			
	190	HvBAMY			+	+			-			-
5H	43	Bmag0337		-	-		-				-	
	114	HvLOXC	+	+							-	-
	187	GMS001							-			-
6H	96	GMS006	-	+	+	+	-		-		-	
7H	62	HvSS1		-							+	
	166	EBmac0755		-								
∑			8	17	8	4	7	2	6	7	7	8

Chr: Chromosome. Pos: Position in cM. **HEA to YLD** are the abbreviations of traits: HEA: Days until heading; HEI: Plant Height; LOH: Lodging at harvest; TGW: Thousand-grain weight; YLD: Yield. **C:** C101. **H:** H101 = Harry ×ISR101-23 (Pillen et al. 2004). Putative QTL effects of *Hsp* alleles are either favorable with respect to breeding goal (+) or unfavorable with respect to breeding goal (-). Common QTLs are shaded. Identical QTL effects of the Hsp alleles are framed.

Sixty putative QTLs were detected for five traits by 22 shared SSRs markers between T101 and H101. All five (16.7 %) common QTLs exhibited identical QTL effects in both populations (Table 26). Among the reproducible putative QTL effects, only one favorable QTL effect of the exotic allele was detected for HEI and the other exotic QTL alleles had unfavorable effects on HEA (2), TGW (1) and YLD (1).

Table 26: Comparison of putative QTL effects between T101 and H101 (Harry ×ISR101-23, Pillen et al. 2004)

			HEA		HEI		LOH		TGW		YLD	
Chr	**Pos**	**Marker**	**T**	**H**	**T**	**H**	**T**	**H**	**T**	**H**	**T**	**H**
1H	63	HvALAAT	-	-	-		-		-	-	-	
2H	17	HVM36		+	-			+		+		-
	97	GMS003		+		+		+		+		-
	143	HVM54		-							-	
	146	EBmac0415		-							-	
3H	30	EBmac0705		-		-						
	63	Bmac0209		+	-					+		
	94	HVM33		+			-			+		
	110	HVM60		+	-		-			+		-
	155	Bmag0013		+	-					-		
4H	14	HVM40			+							
	57	GMS089		-								
	80	EBmac0775										-
	132	EBmac0679		-								-
	180	HVM67		-	+							
	190	HvBAMY			+	+	-					-
5H	43	Bmag0337		-	+							
	114	HvLOXC		+							-	-
	187	GMS001										-
6H	96	GMS006		+		+					-	
7H	62	HvSS1	-	-								
	166	EBmac0755		-								
∑			2	18	9	4	4	2	1	7	5	8

Chr: Chromosome. **Pos:** Position in cM. **HEA** to **YLD** are the abbreviations of traits: HEA: Days until heading; HEI: Plant Height; LOH: Lodging at harvest; TGW: Thousand-grain weight; YLD: Yield. **T:** T101. **H:** H101 = Harry ×ISR101-23 (Pillen et al. 2004). Putative QTL effects of *Hsp* alleles are either favorable with respect to breeding goal (+) or unfavorable with respect to breeding goal (-). Common QTLs are shaded. Identical QTL effects of the Hsp alleles are framed.

In total, 67 putative QTLs were detected for five traits by 23 shared markers between C101 and A101. Five (14.9 %) QTLs were simultaneously detected in both populations (Table 27). However, only one (3.0 %) QTL effect for HEI was reproducible in both populations. The other QTLs had opposite effects in C101 and A101.

Table 27: Comparison of putative QTL effects between C101 and A101 (Apex ×ISR101-23, Pillen et al. 2003)

			HEA		HEI		LOH		TGW		YLD	
Chr	**Pos**	**Marker**	**C**	**A**	**C**	**A**	**C**	**A**	**C**	**A**	**C**	**A**
1H	14	GMs021		-								-
	63	HvALAAT		+		+	-	+	-		-	
	68	Bmag0211		+		+	-	+	-		-	
2H	97	GMS003		+				-		+		
	143	HVM54	+	-	-							-
	146	EBmac0415	+		-							-
3H	30	EBmac0705	-		+						-	
	100	GMS116			-		+					
	155	Bmag0013			-				+			
	190	Bmac0029			-							
4H	44	HvPAZXG			+		-				-	
	57	GMS089					-		+		-	
	180	HVM67		-	+				-			
	190	HvBAMY			+	+	-		-			
5H	43	Bmag0337			-		-			-	-	
	187	GMS001		-		+				-		
6H	6	Bmac0316	-								-	
	96	GMS006	-		+		-		-		-	
7H	62	HvSS1	-									
	100	Bmag0321										
	120	GMS046		-								
	146	BMS64	+	-		-						
7H	166	EBmac0755		-		-						-
∑			7	10	11	6	8	3	7	3	8	4

Chr: Chromosome. **Pos:** Position in cM. **HEA** to **YLD** are the abbreviations of traits: HEA: Days until heading; HEI: Plant Height; LOH: Lodging at harvest; TGW: Thousand-grain weight; YLD: Yield. **C:** C101. **A:** Apex ×ISR101-23 (Pillen et al. 2003). Putative QTL effects of *Hsp* alleles are either favorable with respect to breeding goal (+) or unfavorable with respect to breeding goal (-). Common QTLs are shaded. Identical QTL effects of the Hsp alleles are framed.

Between T101 and A101, 53 QTLs were detected for five traits by 24 informative markers in both populations (Table 28). Ten (37.7 %) QTLs were simultaneously detected in both populations. Among these QTLs, three (11.3 %) putative QTL effects (one for HEI and two for YLD) were identical in both populations.

When all four populations were compared simultaneously, the shared markers were reduced to 12, whereas the shared traits still were five (Table 29). Altogether, 69 putative QTLs were detected for five traits by 12 informative markers across the four populations. Only one (5.8 %) QTL was simultaneously detected in all four populations (HEI at HvBAMY$_{[4H]}$). At this locus, the *Hsp* allele had favorable effect on HEI in C101, T101 and H101, but a negative effect in A101. Five (21.7 %) QTLs were simultaneously detected in three populations. Only one (4.3 %) QTLs (TGW at HvALAAT$_{[1H]}$) were reproducible in all three populations. Fourteen (40.6 %) QTLs were

simultaneously detected in two populations. Among these QTLs, twelve (34.8 %) putative QTL effects were identical in two populations.

Table 28: Comparison of putative QTL effects between T101 and A101 (Apex ×ISR101-23, Pillen et al. 2003)

			HEA		HEI		LOH		TGW		YLD	
Chr	**Pos**	**Marker**	**T**	**A**	**T**	**A**	**T**	**A**	**T**	**A**	**T**	**A**
1H	14	GMs021		-								-
	63	HvALAAT	-	+	-	+	-	+	-		-	
	68	Bmag0211	-	+	-	+	-	+	-		-	
2H	97	GMS003		+				-		+		
	143	HVM54		-							-	-
	146	EBmac0415									-	-
3H	30	EBmac0705										
	100	GMS116			-							
	155	Bmag0013			-							
	190	Bmac0029			-							
4H	14	HVM40			+						-	+
4H	44	HvPAZXG					+		-			
	57	GMS089										
	180	HVM67		-	+							
	190	HvBAMY			+	+	-					
5H	43	Bmag0337			+					-		
	187	GMS001		-		+				-		
6H	6	Bmac0316										
	96	GMS006			+				-		-	
7H	62	HvSS1										
	100	Bmag0321										
	120	GMS046		-								
	146	BMS64		-		-						
7H	166	EBmac0755		-		-						-
∑			2	10	10	6	4	3	4	3	6	5

Chr: Chromosome. **Pos:** Position in cM. **HEA** to **YLD** are the abbreviations of traits: HEA: Days until heading; HEI: Plant Height; LOH: Lodging at harvest; TGW: Thousand-grain weight; YLD: Yield. **T:** T101. **A:** Apex ×ISR101-23 (Pillen et al. 2003). Putative QTL effects of *Hsp* alleles are either favorable with respect to breeding goal (+) or unfavorable with respect to breeding goal (-). Common QTLs are shaded. Identical QTL effects of the Hsp alleles are framed.

Pillen et al. (2004) reported that 26% of the putative QTL effects of the ISR101-23 alleles were reproducible between the two genetic backgrounds of the spring barley varieties Harry and Apex. Between two winter barley populations C101 and T101, 23 % of putative QTL effects of ISR101-23 alleles were reproducible. Thus, the portion of reproducible putative QTL effects of the ISR101-23 alleles is similar in spring barley and winter barley populations. However, the reproduction of QTL effects of exotic alleles was notably lower between winter and spring barley populations than within spring barley populations or winter barley populations. For instance, the reproducable QTL effects ranged from 3 % (between C101 and A101) to 21.6 % (between C101 and H101) with an average of 14.1 % between winter and spring barley populations.

Table 29: Comparison of putative QTL effects between C101, T101, A101 and H101

			HEA				HEI				LOH				TGW				YLD			
Chr	**Pos**	**Marker**	**C**	**T**	**A**	**H**	**C**	**T**	**A**	**H**	**C**	**T**	**A**	**H**	**C**	**T**	**A**	**H**	**C**	**T**	**A**	**H**
1H	14	GMS021			+																-	
	63	HvALAAT		-	+	-		-	+		-	-	+		-	-		-	-	-		
2H	97	GMS003			+	+				+				+			+	+				-
	143	HVM54	+		-	-	-													-	-	
	146	EBmac0415	+			-	-													-	-	
3H	30	EBmac0705	-			-	+			+									-			
4H	57	GMS089				-															+	
	180	HVM67			-	-	+	+							-							
	190	HvBAMY			-		+	+	-	+		-			-			-				-
5H	43	Bmag0337				-	-	+		+	-						-		-			
	187	GMS001			-										-		-					-
7H	166	EBmac0755			-	-			-												-	
∑			3	1	8	9	6	4	3	4	2	2	1	1	4	1	3	3	3	3	5	3

Chr: Chromosome. **Pos:** Position in cM. **HEA** to **YLD** are the abbreviations of traits: HEA: Days until heading; HEI: Plant Height; LOH: Lodging at harvest; TGW: Thousand-grain weight; YLD: Yield. **C:** C101. **T:** T101. **A:** Apex ×ISR101-23 (Pillen et al. 2003). **H:** H101 = Harry ×ISR101-23 (Pillen et al. 2004). Putative QTL effects of *Hsp* alleles are either favorable with respect to breeding goal (+) or unfavorable with respect to breeding goal (-). Common QTLs are shaded.

The number of common QTLs between the population-pairs also clearly showed that the reproduction of QTL effects of exotic alleles was lower between winter and spring barley populations than within spring barley populations or winter barley populations (Table 30). For instance, eleven favorable exotic QTL effects out of 30 common QTLs were reproducable between C101 and T101 and eight favorable QTL effects out of 13 common QTLs could be simultaneously detected in H101 and A101. Between winter and spring barley populations, however, only one common QTL was found between C101 and A101 and the highest number of common QTLs was reached with eight between C101 and H101. This indicated that on one hand, a high degree of genetic difference exists between winter barley and spring barley; on the other hand, a high degree of epistatic genetic interaction exists between detected QTLs and the genomic background. Fulton et al. (1997) reported a similar result in tomato. When they compared AB-QTL results from three different wild species accessions which were backcrossed with a single tomato cultivar—only 19 % of the QTLs found in the *Lycopersicon peruvianum* cross could be confirmed in at least one of the two additional crosses. This suggests that only a portion of the QTL effects of a donor can be transferred from one recipient to the next. The same conclusion was drawn by Thomas et al. (1995) and Mather et al. (1997) from classical QTL analyses in barley. Both studies emphasized that only a few QTLs were conserved between the barley crosses Blenheim×E224/3, Harrington×TR306 and Steptoe×Morex. Therefore, the utilization of exotic germplasm faces the challenge of low reproduction of favorable QTL effects between different genetic backgrounds.

Table 30: Common QTLs and identical QTL effects between four populations

Type	Pop	C101	T101	A101	H101
Winter	C101		11(19)	1(0)	5(3)
Winter	T101	30 (23 %)		1(2)	1(4)
Spring	A101	1 (3.0 %)	3 (11.3 %)		8(5)
Spring	H101	8 (21.6 %)	5 (16.7 %)	13 (26 %)	

C101: Carola×ISR101-23. **T101:** Theresa×ISR101-23. **A101:** Apex ×ISR101-23 (Pillen et al. 2003). **H101:** Harry ×ISR101-23 (Pillen et al. 2004). The number below the diagonal with light dark grey background represents common QTLs between two populations. The number above the diagonal with light grey background represents identical QTL effects between two populations (the number out of brackets represents favorable effects and the number in brackets represents unfavorable QTL effects).

4.2 Comparison of the AB-QTL analysis in C101 and T101 with classical QTL analyses in barley

Classical QTL analyses were conducted in early, balanced generations like doubled haploids (DH) and F_2, while AB-QTL analysis was based on advanced backcrossed populations (Pillen et al. 2003). In this study, the AB-QTL analysis was based on two BC_2DH winter barley populations. The use of advanced backcross generations was necessary since the barley progenitor *Hsp* was used as the donor of potentially favorable QTL alleles in our study. The genome portion of *Hsp* was reduced by backcrossing to mean P[*Hsp*] values of 13.2 % and 13.7 % in C101 and T101, respectively. It is assumed that masking negative side effects of linked and unlinked *Hsp* alleles on quantitative traits are reduced by this strategy (Tanksley and Nelson 1996). The overwhelming majority of the genetic diversity in *Oryza* and *Lycopersicon* is present in the wild species gene pool (Tanksley and McCouch 1997). Powell and Russell (2000) reported similar results in *Hordeum*. Based on these findings, it is likely that at least a portion of the identified favorable QTL alleles from *Hsp* are new alleles, so far not present in the barley elite gene pool (Pillen et al. 2003).

The selection of the statistical method exerts a major impact on the results of a QTL experiment (Pillen et al. 2003). The refined methods, such as the simple interval mapping (SIM, Haley and Knott 1992), composite interval mapping (CIM, Jansen and Stam 1994; Zeng 1994) and simplified CIM (sCIM, Tinker and Mather 1995b) were applied in classical QTL analyses. Based on these methods, several software programs have been written for detection of QTLs, e.g. **MAPMARKER/QTL** (Lander and Botstein 1989), **QTL-CARTOGRAPHER** (Basten et al. 1994), **MQTL** (Tinker and Mather 1995b) and **PLAB-QTL** (Utz and Melchinger 1996). Unfortunately, these programs are focused on the analysis of balanced populations which are used in classical QTL analyses. For unbalanced populations, which are used in AB-QTL studies, the program **QGENE** was written (Nelson 1997). However, **QGENE**, which operates with single marker regression as well as simple interval mapping for QTL detection, can not handle multiple

environments simultaneously (Pillen et al. 2003). Since our AB-QTL study was conducted in up to six separate environments and since we wanted to include the M×E interaction as a measure of the environmental stability of a QTL effect, we preferred to use a three-factorial ANOVA with the marker genotype, line (nested in marker or genotype) and the environment as factors. The factors line and environment were used in order to reduce the residual variance of the experiment and to increase the probability of detecting a QTL effect. Simultaneously, a three-factorial model allowed us to differentiate between a QTL significant as a marker main effect, which is considered to be stable across the tested environments, and a QTL significant as a M×E interaction where the effect is considered to depend on a particular environment (Pillen et al. 2003). In addition, cold damage (COD) or neighbouring plots (N) of seriously cold-damaged plots were used as co-variables for some traits, which were significantly affected by COD or N during the winter 2002/03

For comparison between AB-QTL analysis and classical QTL analysis with respect to common QTL effects, we use the indirect comparison from Pillen et al. (2003, 2004) by means of the current Steptoe × Morex map (hereafter abbreviated with 'BIN map'), published by A. Kleinhofs (http://barleygenomics.wsu.edu/databases/databases.html) because the classical barley studies have been conducted with RFLPs and, to a lesser extend, with AFLPs, whereas our AB-QTL study is exclusively based on SSR markers. The BIN map integrates RFLP, AFLP and SSR markers, which are mapped in independent linkage studies, by allocating them to 99 evenly spaced BIN groups. The QTL comparison was mainly carried out by means of an up-to-date compilation of mapped barley QTLs from P. Hayes (http://www.css.orst.edu/#barley/nabgmp/qtlsum.htm), which is based on the Steptoe × Morex BIN classification. A possible common QTL was assumed, if the BIN groups of two independently detected QTLs were identical or, at least, overlapped. In the following, the comparison was carried out for agronomic traits, pathogen resistances and for non-parasitic browning.

4.2.1 Comparison of the AB-QTL analysis in C101 and T101 with classical QTL and linkage analyses for agronomic traits in barley

In barley, classical QTL analysis was conducted very early because scientists intended to find QTLs, which were associated with the traits of agronomic importance such as yield and yield components. However, the classical QTL analysis was focused on the elite gene pool. The AB-QTL analysis was used to find favorable exotic alleles from wild accessions and to broaden the genetic base of barley. The comparison of the QTL effects detected between AB-QTL analysis and classical QTL analysis will show us if the wild progenitor (*Hsp*) carries new favorable QTL alleles for important of agronomic traits in barley. In the following, the comparison is described for each agronomic trait studied (List of comparisons in Appendix 5).

Breaking of stem (BS)

Altogether, 21 putative QTLs were detected for BS in C101 (15) and T101 (6) and six crossover interaction effects were detected on chromosomes 2H, 4H, 6H and 7H in both populations (Table 17 and Table 19). Only one common QTL was found for BS by comparison of BIN groups (Appendix 5). This common QTL was associated with HvRVABG-GMS089$_{[4H]}$ in T101. Backes et al. (1995) located a QTL for BS in marker interval MWG921-MWG880$_{[4H]}$ in Igri×Danilo. Both, HvRVABG$_{[4H]}$ and MWG880$_{[4H]}$ were mapped in the same BIN 7.

Bending of spike (BSP)

For BSP, ten QTLs were detected in both populations, five QTLs from C101 and other five QTLs from T101. Three corossover interaction effects of the *Hsp* alleles were located at GMS114$_{[1H]}$ (in C101), HvKNOX3$_{[4H]}$ (in T101) and HVM14$_{[6H]}$ (in T101). Up to now, no classical QTL was associated with BSP.

Cold damage (COD)

In total, 24 putative QTLs and two favorable QTL effects of the *Hsp* alleles were detected for COD in both populations. Two favorable exotic alleles were located at EBmac0684$_{[2H]}$ and GBM1008$_{[6H]}$ in C101. No classical QTL matched the favorable COD QTLs by comparison of BIN groups. However, five Dehydrin (*Dhn*) genes, *Dhn3, Dhn4, Dhn5, Dhn7* and *Dhn8*, were mapped as a cluster on the long arm of chromosome 6H by Choi et al. (1999) and matched the favorable exotic QTL allele detected at GBM1008$_{[6H]}$ in C101. *Dhn* genes are associated with tolerance to or response to the onset of low temperature or dehydration (Choi et al. 1999). In addition, two frost tolerance QTLs were mapped in marker intervals HvCBF4-OPAL17a and *Dhn1*-Hv635P2.4 on the long arm of chromosome 5H in the cross Nure × Tremois (winter × spring barley) by Francia et al. (2004). These two QTLs are flanked by markers Bmag0223 and Bmag0222. Simultaneously, HvCBF3 and HvCBF8 (C-repeat building factor) which respond to drought and low temperature (Baker et al. 1994; Yamaguchi-Shinozaki and Shinozaki 1994) and the vernalization response gene *Vrn-H1* were mapped in this region (Choi et al. 2002; von Zitzewitz et al. 2003; Francia et al. 2004). Within marker interval Bmag0223-Bmag0222, two very strong and unfavorable exotic QTL effects were detected at GBM1041$_{[5H]}$ (in both populations) and HvLOXC$_{[5H]}$ (in C101). Though the marker Bmag0223 was monomorphic in C101 and T101, it was mapped within marker interval Bmag0357-GBM1041$_{[5H]}$ (von Korff et al. 2004). The two favorable QTL alleles at HvCBF4-OPAL17a and *Dhn1*-Hv635P2.4 for frost tolerance were inherited from winter barley 'Nure' in Nure × Tremois, like our two favorable QTL alleles were inherited from winter barley elite parents.

It suggested that the elite winter barleys carried a frost tolerance gene in the region Bmag0223-Bmag0222$_{[5H]}$, and when this allele is substituted by the *Hsp* allele, the frost tolerance is reduced.

In barley, QTLs controlling traits associated with winter-hardiness, such as field winter survival and crown fructan content, were mapped in the Dicktoo × Morex (winter × spring barley) cross only on the long arm of chromosome 5H (Hayes et al. 1993a; Pan *et al.* 1994). The authors found evidence for a multilocus cluster of linked QTLs in this region rather than a single QTL with pleiotropic effects. No other genomic regions exceeded the threshold of significance (Cattivelli et al. 2002). Nine freezing tolerance QTLs were detected and mapped on chromosomes 2H, 3H, 6H and 5H in the cross Arda × Opale (winter × winter barley) by Tuberosa et al. (1997). However, these QTLs could not be used to compare with our AB-QTLs because of their linkage with AFLP markers neither present in other maps, nor linked to anchor loci. Besides the examples described above, there are stress-related genes located clearly outside any stress tolerance QTLs. Although the barley cold-regulated genes *cor14b* (on chromosome 2H, Chauvin et al. 1993) and *cor tmc-ap3* (on chromosomes 1H, Baldi et al. 1999) are expressed at higher levels in frost-resistant than in susceptible cultivars, none of them maps on chromosome 5H where almost all cold tolerance QTLs have been localized (Crosatti *et al.* 1996; Baldi *et al.* 1999; Mastrangelo *et al.* 2000).

Days until heading (HEA)

Twenty-eight putative QTLs were detected for HEA in both populations. In C101, ten favorable QTL alleles of the *Hsp* were located on all chromosomes except 6H, while five favorable exotic alleles were detected on chromosomes 1H and 7H in T101. Nine out of 15 favorable QTL effects for HEA in both populations were verified in classical QTL and linkage analyses. In classical QTL analysis, more than 80 QTLs for heading date have been mapped up to now in different crosses (http://www.css.orst.edu/barley/nabgmp/qtlsum.htm), with a maximum of QTLs concentrated on chromosomes 2H (mostly: 19), 7H (17) and 5H (13). Often, heading date QTLs map to locations corresponding to previously known *Vrn, Ppd* or *Ea* genes. Pan et al. (1994) located a QTL associated with heading date at ipdg-BCD265c between BINs 12-13 on 1H. In this study, a favorable exotic QTL allele was detected at GBM1002$_{[1H]}$ in BIN 12 in T101 and this QTL also corresponds to the vernalization gene *Vrn-H3* (Cattivelli et al. 2002). On chromosome 1H, another QTL was detected for HEA at ABG195c-MWG912 in BIN 14 by Marquez-Cedillo et al. (2001), while a favorable exotic allele was detected in our study at GMS012$_{[1H]}$ (*QheaC101-1Hb* and *QheaT101-1Hd*), which was placed 2.6 cM north of anchor marker ABC261 of BIN 14, in both populations. According to the map from Cattivelli et al. (2002), *QheaC101-1Hb*, *QheaT101-1Hd* and the photoperiod response gene *Ppd-H2* which regulates flowering under short days, were in the same region, in the vicinity of marker ABC261 on chromosome 1H (Laurie et al. 1995). Two QTLs

QheaC101-2Ha and *QheaC101-2Hb* which were detected at HVM36-GBM1035$_{[2H]}$ and GBMS002$_{[2H]}$ in C101, matched the classical QTL detected at *Rbcs*-ABG2 between BIN 3-4 on chromosome 2H in Steptoe/Morex (Hayes et al. 1993b), MWG557-MWG769 between BIN 3-9 on chromosome 2H in Igri/Danino (Backes et al. 1995) and the photoperiod response gene *Ppd-H1* (Laurie et al. 1995), which regulates flowering under long days. The favorable exotic QTL allele detected at GBM1016-GBM1047$_{[2H]}$ in C101 was verified by a classical QTL, which was located at ABG14-Cgr3a between BIN 9-12 on chromosome 2H in Steptoe/Morex (Hayes et al. 1993b). The favorable exotic QTL allele detected at GBM1031-HvPEPD1PR$_{[3H]}$ in C101 was verified by classical QTL that was located at ABG396-ABG703A in BIN 6 in Steptoe/Morex (Hayes et al. 1993b). On chromosome 5H, the QTL allele with crossover interaction effect was detected at GBM1041$_{[5H]}$ in both populations and this QTL matched a classical QTL, which was located at ABC168-ABC717 between BIN 9-10 in Chevron/M69 (de la Pena et al. 1999). The favorable QTL effect for HEA at HVM49$_{[7H]}$ was also found in classical QTL study at MWG539-MWG929 between BIN 11-12 in Igri/Danilo (Backes et al. 1995).

Plant height (HEI)

In total, 33 putative QTLs were detected for HEI in both populations. Eight and seven favorable exotic QTL alleles were identified in C101 and T 101, respectively. Up to now, more than 50 putative QTLs were detected in classical QTL studies. By comparing BIN groups, 14 QTLs were verified by classical QTL and linkage analyses and nine favorable QTL effects correspond to the candidate genes or the QTLs detected in classical QTL. An unfavorable putative QTL effect on HEI was detected at HvALAAT-GBM1004$_{[1H]}$ between BIN 5-7 in C101. At the same BIN, a QTL was mapped at ABG452 by Marquez-Cedillo et al. (2001). At GBMS012$_{[1H]}$ in BIN 13-14, favorable QTL effects were detected for HEI in both populations, while two QTLs were located at MWG844c$_{[1H]}$ and MWG911-MWG514$_{[1H]}$ in the same BIN with GBMS012$_{[1H]}$ by Backes et al. (1995) and Zhu et al. (1999), respectively. The favorable putative QTL effect for HEI which was associated with HVM36-GBM1035$_{[2H]}$ in C101 was detected at *Rbcs*-ABG2 between BIN 3-4 in Steptoe/Morex (Hayes et al. 1993b) and this QTL (at *Rbcs*-ABG2) also corresponds to another favorable QTL effect which was detected at GBMS002$_{[2H]}$ in C101. On chromosome 3H, two unfavorable QTL effects were detected for HEI at HVM33-GMS116 and HVM33-HVM60 at BIN 7-8 in C101 and T101, respectively. At the same BIN, a QTL for HEI was located at E45M55-274-E40M32-397 in classical barley QTL analysis by Qi et al. (1998a). In the vicinity of HVM62, unfavorable QTL effects on HEI were detected in both populations (*QheiC101-3Hc* and *QheiC101-3Hb*). The *denso* gene for reduced plant height was mapped to the same region by Laurie et al. (1995). On chromosome 4H, two favorable exotic QTL alleles and two crossover interaction effects

were detected at GBM1048–HvBAMY$_{[4H]}$ (in C101), HvJASIP–HvBAMY$_{[4H]}$ (in T101) HVM40$_{[4H]}$ (in T101) and HvPAZXG$_{[4H]}$ (in C101) and these QTL effects matched the classical QTL effects for HEI which were associated with MWG880-MWG842 (at BIN 7-11, in Igri/Danilo, Backes et al. 1995), Bmy1 (at BIN 12-13, in Gerbel×Heroit, Hackett et al. 1992), int-c-Phy2 (at BIN 2-4, in Harrington/Morex, Marquez-Cedillo et al. 2001) and HVM68-ABG472 (at BIN 7-8, in Harrington/Morex, Steptoe/Morex, Marquez-Cedillo et al. 2001). The favorable QTL effect, which was detected at Bmag337-Bmag357$_{[5H]}$ at BIN 6, was verified by a QTL which was located at MWG635d-ABC302a$_{[5H]}$ in BIN 6 in classical QTL analysis by Marquez-Cedillo et al. (2001).

Harvest index (HI)

QTL analysis was only performed for HI in T101 where two putative QTLs were detected. Two QTLs with crossover interaction effect were associated with GBM1002$_{[1H]}$ and MGB318$_{[5H]}$. Up to now, no QTL was associated with HI in classical QTL studies in barley.

Lodging at harvest (LOH)

Twenty-two putative QTLs were detected for LOH in both populations. Among these QTLs, only one favorable QTL effect of *Hsp* alleles were detected at GMS116-HVM60$_{[3H]}$. In addition, three crossover interaction effects were located at GMS046$_{[7H]}$, BMS64-Bmag0120$_{[7H]}$ (in C101) and HvKNOX3–HvPAZXG$_{[4H]}$ (in T101). Fourteen QTLs were detected by classical barley QTL studies up to now in different crosses (Hayes et al. 1993b; Backes et al. 1995; Tinker et al. 1996). By comparing the BIN groups, four putative QTLs detected in AB-QTL analyses were verified in classical barley QTL studies. In C101, three QTL effects for LOH which were associated with EBmac0906-GMS089$_{[4H]}$ in BIN 7, GMS006-HvPAF93$_{[6H]}$ within BIN 6-7 and GBM1022-GBM1005$_{[6H]}$ in BIN 9 were verified by three classical QTLs which were located at dMlg-ABG472$_{[4H]}$ in BIN 6-8 in Harrington/TR306 (Tinker et al. 1996), MWG820c-MWG820b$_{[6H]}$ BIN 6-8 in Igri/Danilo (Backes et al. 1995) and ksuD17-Nar7$_{[6H]}$ in BIN 7-9 in Steptoe/Morex (Hayes et al. 1993b). However, the QTL effects of *Hsp* alleles were associated with an increase of plant height in C101. A crossover interaction QTL effect of the *Hsp* allele was detected for LOH at HvKNOX3-HvPAZXG$_{[4H]}$ in BIN 7 in T101. A QTL was located at dMlg-ABG472$_{[4H]}$ within BIN 6-8 in Harrington/TR306 (Tinker et al. 1996).

Thousand-grain weight (TGW)

In our AB-QTL analysis, 15 putative QTLs were detected for TGW in both populations and only one favorable QTL effect of *Hsp* allele was detected at Bmag0013[3H] in C101. In classical barley QTL analyses, 17 putative QTLs were reported for TGW (Thomas et al. 1995; Kjaer and

Jensen 1996; Bezant et al. 1997 and Powell et al. 1997). Only one putative QTL which was associated with GBM1008-GBM1022$_{[6H]}$ in BIN 9 in C101 was matched with the classical QTL detected at WG282 in BIN 9 in Blenheim/E224/3 (Thomas et al. 1995).

Yield (YLD)

Altogether, 24 putative QTLs were detected for YLD in both populations. At four QTLs, which were located at HvLEU$_{[5H]}$, HvPAF93$_{[6H]}$, GBM1008-GBM1005$_{[6H]}$ (in C101) and GBM1048$_{[4H]}$ (in T101), a crossover interaction effect of *Hsp* alleles was detected. More than 40 putative QTLs were detected for YLD in classical barley QTL studies (Hayes et al. 1993b, 1996; Backes et al. 1995; Thomas et al. 1995; Kjaer and Jensen 1996; Tinker et al. 1996; Bezant et al. 1997; Powell et al. 1997; Yin et al. 1999 and Marquez-Cedillo et al. 2001). By comparing the BIN groups, five putative QTLs which were associated with EBmac0906-GMS089$_{[4H]}$, GBM1048$_{[4H]}$, GMS006-HVM14$_{[6H]}$, GBM1008-GBM1005$_{[6H]}$ (in C101) and GBM1048$_{[4H]}$ (in T101) were verified in classical barley QTL analyses. In marker interval EBmac0906-GMS089$_{[4H]}$ in BIN 6, the unfavorable QTL effect of the *Hsp* allele was detected for YLD in C101, while Marquez-Cedillo et al. (2001) and Kjaer and Jensen (1996) located a QTL for YLD at ABG003a-MWG058$_{[4H]}$ in BIN 5-6 in Harrington/Morex and WG464-MWG058$_{[4H]}$ in BIN 6, respectively. The unfavorable QTL effect of the *Hsp* allele for YLD was associated with GBM1048$_{[4H]}$ in BIN 10-13 in C101 and T101. This QTL matched the classical QTL which was located at ABG472-ABG397$_{[4H]}$ within BIN 8-11 in Steptoe/Morex by Hayes et al. (1993b). At GMS006-HVM14$_{[6H]}$ in BIN 9, an unfavorable QTL effect of the *Hsp* allele was detected for YLD in C101. This QTL matched the classical QTL effect which was located at ABG458-ksuA3D in BIN 6-8 in Steptoe/Morex by Hayes et al. (1993b). A favorable QTL effect of the *Hsp* allele was detected for YLD in marker interval GBM1008-GBM1005$_{[6H]}$ in BIN 9 at C101, while Bezant et al. (1997) located a QTL for YLD at Amy1 in BIN 9 in Blenheim×Kym.

4.2.2 Comparison of the AB-QTL analysis in C101 and T101 with classical QTL and linkage analyses for disease resistances and non-parasitic browning

QTL analysis for disease resistance is very important because the vertical resistance, which is controlled by single genes, is only a temporary resistance. Historically, this has been explained by the gene-for-gene hypothesis (Flor 1942). However, horizontal resistance is a permanent resistance since this resistance is associated with polygenes or QTLs. Disease can affect the profitability of barley cultivation by reducing total yield and by lowering grain quality, both of which result in a lower financial return to the grower (Williams 2003). Genetic mapping of major genes and QTLs for many major diseases is revealing a heterogeneous distribution of resistance loci on

chromosomes, where more than half of the mapped loci are located in clusters. Relatively few resistance genes have been identified in cultivated barley germplasm. Studies have shown that wild *Hordeum* species contain resistance genes for major diseases, although their allelic relationship to previously mapped genes is unknown (Williams 2003). In this study, QTL analysis was performed for four diseases and one syndrome of winter barley by means of the advanced backcross strategy.

Leaf rust (LR)

Barley leaf rust, caused by the fungal pathogen *Puccinia hordei*, represents an important foliar disease occurring in temperate regions throughout the world (Ivandic et al. 1998). The use of resistant barley varieties has proved an efficient way to control the disease and to prevent yield losses which may reach 32% in susceptible cultivars (Griffey et al. 1994). Resistance in *Hv* was shown to be very limited and mainly restricted to the genes *Rph3* and *Rph7* (Jin et al. 1995). However, a large variability was found to exist in the wild progenitor *Hsp* from Israel confirming that the Near East represents a major centre for the evolution of resistance to *P. hordei* (Manisterski et al. 1986; Moseman et al. 1990). Up to now, about 16 race-specific resistance genes for leaf rust, which were designated as *Rph* loci, have been reported (Franckowiak et al. 1997). Four of these genes have been identified in *Hsp*. Feuerstein et al. (1990) detected two resistance genes, *Rph10* and *Rph11*, on chromosomes 3HL and 6HL, and Ivandic et al. (1998) mapped *Rph16* at the centromeric region of 2H. Jin et al. (1996) identified *Rph15* on chromosome 2H distal to *Rph16*. Park and Karakousis (2002) mapped a major resistance gene *Rph19* on 7HL. In classical barley QTL studies, 15 QTLs which are associated with LR resistance were reported in different studies (Thomas et al. 1995; Qi et al. 1998a, 1999 and Spaner et al. 1998). The LR resistance genes *Rph9* and *Rph12* were mapped on chromosome 5H by Borovkova et al. (1998).

In this study, eleven putative QTLs were detected for LR in both populations. Two favorable effects of the *Hsp* allele with marker main effects were found for LR at GBMS002$_{[2H]}$ and HVM33-GMS116$_{[3H]}$ in C101. However, no QTL detected in AB-QTL analyses matched the QTLs detected in classical barley QTL studies and none of the major disease resistance genes, previously identified in wild barley, mapped close to the QTLs detected in this study. Thus, the two favorable exotic QTL alleles with marker main effects, which were detected in this study, may be new QTL alleles for LR resistance.

Net blotch (NB)

Net blotch of barley, which is caused by the fungal phytopathogen *Pyrenophora teres* (previously called Drechslera teres Smedeg.), constitutes one of the most serious constraints on barley production world-wide (Shipton et al. 1973). It may lead to grain yield losses of up to 40 %

under severe infections (Steffenson 1997). Several barley lines with major gene resistance to NB have been identified. The classical genetic analysises indicated that resistance was controlled by 1-3 loci, depending on the barley accession and the NB isolate used for testing (Wilcoxson et al. 1992; Douiyssi et al. 1996; Ho et al. 1996). Three independently segregating resistance genes *Rpt1*, *Rpt2* and *Rpt3*, have been localized by trisomic analysis on chromosomes 3H, 1H and 2H in C19819, C17584 and cv. Tifang, respectively (Bockelman et al. 1977). A major resistance gene for NB was mapped on chromosome 6H using DNA markers in Rolfi×C19819 by Manninen et al (2000). QTL analysises for NB have also been reported (Arabi et al. 1990; Steffenson and Webster 1992; Steffenson et al. 1996; Spaner et al. 1998; Manninen et al. 2000).

In our AB-QTL analysis, 21 putative QTLs were located for NB on all chromosomes in both populations. Two favorable QTL effects of *Hsp* alleles were detected on chromosome 6H in C101. By comparing the BIN groups, the QTL at EBmac0906-GMS089$_{[4H]}$ with a crossover interaction effect on NB resistance, which was located in BIN 6-7 in C101, corresponds to a classical QTL which was mapped at ABG3-ABG484$_{[4H]}$ in BIN 6 in Steptoe/Morex by Steffenson et al. (1996). Simultaneously, *QnbC101-5Ha* was detected at GBM1041$_{[5H]}$ which was mapped 4 cM north of MWG522 by Thiel (2004), while a classical QTL for NB was located at MWG914$_{[5H]}$ 3 cM south of MWG522$_{[5H]}$ by Spaner et al. (1998). On chromosome 6H, two putative QTLs (*QnbC101-6Hc* and *QnbT101-6Hb*) which shared markers GMS006 and HVM14, were detected for NB in C101 and T101, respectively. These QTLs matches the major resistance gene for NB detected by Manninen et al. (2000) because they share a common marker HVM14.

Non-parasitic browning (NPB)

NPB is a relatively recent type of plant damage, appearing in cereals but primarily in barley. These spots were initially observed on barley plants in Southern Bavaria more than 10 years ago but are now detected in other German regions and European countries. NPB can result in yield losses of up to 22 % in spring barley and up to 40 % in winter barley trials (Baumer et al. 2001). Up to now, neither biotic pathogens like viruses, bacteria or fungi nor animals nor inappropriate pesticide applications have been determined to be responsible for NPB (Obst and Huber 1996). NPBs are small, often round spots that appear just after heading date and begin in the areas of the leaves that are directly exposed to solar radiation. On leaves that are in the shadow, overlapped or turned, no or only small spots have been observed (Behn et al. 2004). NPBs start on older leaves (F-2) and then continue up to the flag leaf. Later, they also appear on the leaf sheath, the culm, the ear and the awn (Baumer et al. 2001). NPBs can be distinguished from other physiological leaf spots such as cultivar-specific spots or spots caused by nutrient deficiency or by the *mlo* resistance gene (Obst

and Gehring 2002). The damage depends on the intensity of the solar radiation and the developmental stage of the plants and leaves (Behn et al. 2004).

In our AB-QTL analysis, 27 putative QTLs were detected for NPB in both populations. Four favorable QTL effects of *Hsp* alleles were located on chromosomes 2H, 5H and 7H in C101. The strongest effect was measured at EBmac0755$_{[6H]}$ where the exotic allele could reduce the NPB symptoms by 17.2 %. In classical barley QTL studies, three putative QTLs were detected for NPB in Barke×IPZ24727 by Behn et al. (2004) and the strongest effect was mapped at EBmac0635$_{[4H]}$ near the *mlo* locus. This QTL matches the *QnpbC101-4H* which was found at EBmac0679$_{[4H]}$ in C101 because EBmac0679 was mapped 1 cM south of EBmac0635 by Ramsay et al. (2000). However, the exotic allele at *QnpbC101-4H* caused an increase of NPB symptoms by 36.9 % in C101. For other QTLs which were found by Behn et al. (2004), the comparison can not be performed due to lack of sharing markers or anchor markers.

Powdery mildew (PM)

Powdery mildew caused by *Blumeria graminis* f.sp. *hordei* is economically the most important foliar disease for barley (*Hordeum vulgare*) in the temperate climate zone, as this disease can reduce the kernel yield of the affected plants dramatically (Griffey et al. 1994; Conry and Dunne 2001). Genetic resistance is the most economic and sustainable way to control this disease in barley. However, the restricted availability of new resistance genes in the gene pool of cultivated barley and a rapid development of the pathogen toward new virulence (Hovmøller et al. 2001) forces the breeders to look for effective resistance genes in the wild relatives of this crop. In the past, wild barley (*Hsp*), the ancestor of the cultivated barley, has shown its ability to provide barley breeders with numerous effective resistance genes (Jahoor and Fischbeck 1993; Schönfeld et al. 1996; Ivandic et al. 1998; Zeller 1998; Garvin et al. 2000). In barley, at least two genetically separate pathways control resistance to powdery mildew (Jørgensen 1994; Peterhänsel et al. 1997). In the first pathway, resistance is associated with recessive alleles at the *Mlo* locus (*mlo* resistance alleles). This resistance is effective against all tested powdery mildew isolates and requires for its function at least two further host genes, designated *Ror1* and *Ror2* (Freialdenhoven et al. 1996; Büschges et al. 1997). The resistance reaction is tightly linked with a rapid cellwall remodelling in host epidermal cells in response to an attempted fungal penetration (Freialdenhoven et al. 1996). The second resistance pathway can be triggered by a number of race-specific resistance genes (*R* genes; e.g. *Mla*, *Mlg*, *Mlk*, Jørgensen 1994), and is almost invariably associated with the activation of rapid host cell death at attempted infection sites (Freialdenhoven et al. 1994).

In this study, twelve putative QTLs were located for PM on all chromosomes except 4H in both populations. Four favorable exotic QTL alleles were detected for PM in C101, while no

favorable effect of the *Hsp* allele was detected in T101. The strongest favorable effect was measured at GBM1016-GBM1047$_{[2H]}$ where the exotic allele could reduce the PM symptoms by 17.8 %. By comparing the BIN groups, only one putative QTL *QpmC101-7H* which was located at AF022725A-GBMS035$_{[7H]}$ with a favorable effect on PM resistance is verified by a classical QTL which was detected at CDO36$_{[7H]}$ in BIN 5 by Heun et al. (1992). The *mlo* locus and the semi-dominantly acting *Mlg* resistance locus were mapped on chromosome 4H by Simons et al. (1997) and Kürth et al. (2001), respectively. In this study, however, no QTL was detected for PM on chromosome 4H. At GMS021-GBM1007$_{[1H]}$ where the *Mla* locus (*Mla1* and *Mla12*) was mapped by Schwarz et al. (1999), a putative QTL *QpmC101-1H* was detected for PM. However, at *QpmC101-1H,* the exotic allele with marker main effect increased the PM symptoms by 14.5 %. The PM resistance gene *Ror1* was mapped at BIN 7 on chromosome 1H by Collins et al. (2001), but in the vicinity of the *Ror1* region no QTL was detected for PM in this study. In other words, no favorable exotic QTL allele corresponds to major resistance genes against PM in this study. The favorable exotic alleles may be newly detected quantitative resistance alleles for PM.

Scald (RH)

Scald, a foliar disease caused by *Rhynchosporium secalis*, is a major disease of barley and occurs in all major barley growing regions of the world. The pathogen is characterized by an extensive genetic variability and frequent changes of the population (Tekauz 1991). Conventional resistance breeding based on field-testing is difficult because of considerable environmental variation, even when testing in carefully controlled environments (Grønnerød et al. 2002). To date, at least 14 different genes or loci, most of them based on seedling resistance, have been described (Søgaard and von Wettstein-Knowles 1987; Barua et al. 1993; Abbott et al. 1995; Graner and Tekauz 1996; Garvin et al. 2000). By means of molecular markers, RH resistance genes have been mapped on barley chromosomes 1H, 3H, 4H, 6H and 7H (Abbott et al. 1992; Barua et al. 1993; Schweizer et al. 1995; Graner and Tekauz 1996; Garvin et al. 1997, 2000). QTL analysis has also been used to study resistance to RH in barley (Backes et al. 1995; Thomas et al. 1995 and Spaner et al. 1998).

In this study, 16 putative QTLs were detected for RH in both populations. Only one favorable exotic QTL allele was detected at Bmag0369$_{[7H]}$ on chromosomes 7H. At this QTL, the exotic allele could reduce the RH severity by 4.9 %. By comparing the BIN groups, no QTL detected for RH in this study corresponds to previous QTLs detected in classical barley QTL studies. At *QrhC101-6Ha* which was located at GBM1021$_{[6H]}$, however, the exotic QTL allele with a crossover interaction effect on RH resistance corresponds to the RH resistance gene *Rrs13* (Abbott et al. 1995). On chromosome 7HS, a favorable exotic QTL allele was detected at Bmag0369$_{[7H]}$ with a marker main

effect in this study, while Schweizer et al. (1995) mapped the RH resistance gene *Rh2* on chromosome 7HS. The RH resistance gene *Rrs14* was positioned to barley chromosome 1H between the seed storage protein (hordein) loci Hor1 and Hor2, approximately 1.8 cM from the latter locus (Garvin et al. 2000). A dominate gene conferring resistance to RH was mapped on chromosome 3H close to the centromere (Graner and Tekauz 1996). In this study, however, no favorable exotic allele was detected for RH resistance on chromosomes 1H and 3H.

4.3 Environment-dependent QTL

M×E interaction is an essential issue in the assessment of mechanisms of inheritance as well as the prediction of performance in breeding programs because genotypic values must be inferred from phenotypic responses (Stuber et al. 1992). As we know, most traits of agronomic importance, including yield, nutritional quality and stress tolerance, are quantitatively inherited. One of the main characteristics of quantitative traits is that they are easily influenced by environmental factors. The relative rankings of genotypes may well differ between environments and the relationship may be quite complex (Allard and Bradshaw 1964). Actually, every crop variety has its own adapted environment according to the breeding goal. It suggests that the genes of crops, which are beneficial to human beings, are expressed only under special environmental factors. For this reason, the study of environment-dependent QTLs (significant M×E interaction) is very important in order to understand the inheritance of quantitative traits in crops and to use the environment-dependent QTLs in practical breeding.

Classical studies on quantitative traits have measured M×E interaction averaged across the entire genome rather than for individual QTLs (Stuber et al. 1992). Recently, the interval mapping has focused on mapping QTLs in a fixed environment (Lander and Botstein 1989; Knott and Haley 1992; Zeng 1994). Stuber et al. (1992) discerned the degree of M×E interaction at individual QTLs by first comparing QTL maps generated in six diverse environments. Following Stuber et al. (1992) and Pillen et al. (2003), we have attempted to map the QTLs with marker main effects and with M×E interactions in two BC_2DH winter barley populations.

In this study, 175 (65.3 %) out of 268 putative QTLs for C101 and T101 were detected as environment-dependent QTLs for all of 16 evaluated traits, mainly for BS, COD, LOH, NB and NPB (Table 20 and Table 22). Especially, no QTL with marker main effect was detected for NB in both populations. The rate of environment-dependent QTLs among total putative QTLs is very close in both populations (65.0 % in C101 and 65.9 % in T101, Table 31). However, the rate of environment-dependent QTLs in C101 and T101 is much higher than in two spring barley populations A101 and H101 (Pillen et al. 2003, 2004) and the marker main effects were much less in C101 and T101 than A101 and H101. In this study, the high ratio of environment-dependent

QTLs may be caused by the following two reasons: (i) though COD and N (neighbouring plots of the seriously cold-damaged plots in 2002/03) were used as co-variables in QTL analysis if these effects of seriously cold damage and N were significant in ANOVA for effects of lines, these factors may still play a major role in variation of phenotypes; (ii) for pathogen resistances, the race of diseases may be different between test locations so that the same line exhibited different resistance for the same disease.

Table 31: Comparison of QTL effect in C101 and T101 with A101 and H101

	C101		T101		A101		H101	
Effect of QTLs	**No. of QTLs**	**Per. of QTLs (%)**	**No. of QTLs**	**Per. of QTLs (%)**	**No. of QTLs**	**Per. of QTLs (%)**	**No. of QTLs**	**Per. of QTLs (%)**
M	46	25.2	15	17.6	59	68.6	67	62.0
M+M*E	18	9.8	14	16.5	5	5.8	4	3.7
M*E	119	65.0	56	65.9	22	25.6	37	34.3
Total	183	100.0	85	100.0	86	100.0	108	100.0

4.4 Conclusion of AB-QTL analysis

The AB-QTL strategy was developed by Tanksley and Nelson (1996) in order to detect and to introgress favorable genes from an unadapted donor into elite cultivars. By means of the AB-QTL strategy, favorable exotic QTL alleles for important agronomic traits have been identified for tomato (Tanksley *et al*. 1996; Fulton *et al.*1997), rice (Xiao et al. 1996, 1998), maize (Ho *et al*. 2002), wheat (Huang et al. 2003) and barley (Pillen et al. 2003, 2004). Gur and Zamir (2004) proposed a new paradigm for plant breeding: the use of the natural variation which can lift yield barriers in plant breeding. They explained that for crops that rely on a rather narrow genetic basis and have rich resources in biodiversity, the construction and screening of introgression lines (ILs) will lead to dramatic improvements in yield and other quality traits because the wild species, the relatives of modern crop plants, can be viewed as naturally mutagenized resources where every gene and regulatory element has been refined and defined by evolution. However, the potential use of the wild germplasm for the improvement of agronomic traits is different between crop species. For instance, favorable exotic alleles could lead to an increased yield of 50 % in tomato (Gur and Mazir 2004). In rice yield could be improved through introgression of the favorable exotic allele by 18 % (Xiao et al. 1998), while the effects of the favorable exotic allele led to yield increases of only up to 6 % in wheat (Huang et al. 2003). In barley, Pillen et al. (2003, 2004) reported that the strongest favorable effect of the *Hsp* allele, which was located on chromosome 4H, result in a yield increase of 7.7 %. In our study, a crossover interaction effect of the *Hsp* allele on yield, which was located on chromosome 6H, resulted in a yield increase of only 2.9 %. Pillen et al. (2003) explained

that the lower favorable effect of the exotic allele on yield compared with *Hsp* alleles from tomato and rice could be the different breeding system.

The structure of populations for AB-QTL analysis may be another factor of influencing the strength of favorable exotic allele. In tomato and rice, the AB-QTL analysises were conducted in BC_2 populations. The stronger effects on yield detected in tomato and rice might be due to heterosis effects occurring in hybrids between elite and exotic germplasm (Pillen et al. 2003). In barley, two BC_2F_2 populations were used for AB-QTL analysis (Pillen et al. 2003, 2004). Though the BC_2F_2 population is less variable than a BC_2 population, it is still a segregating population. If the dominant effect plays a role, the favorable QTL effect detected in BC_2F_2 may be not the true QTL effect. Thus, a DH population is an ideal population for AB-QTL analysis because the same genotypes could be tested in different environments and in subsequent years.

The genetic background plays a very important role in QTL detection. Four advanced backcross barley populations (C101 and T101 are BC_2DH winter barley, A101 and H101 are BC_2F_2 spring barley populations) shared the donor IRS101-23. The portion of the reproducible putative QTL effects ranged from 3 % to 26 % with an average of 12.9 %, when the comparisons were performed by shared markers between population-pairs. When the four populations were compared based on shared markers simultaneously, no QTL effect was reproducible in all four populations, 20.5 % QTL effects could be transfer between three populations and 34.7 % QTL effects were reproducible between two populations. The low reproduction of QTL effects between different genetic backgrounds may be due to the high degree of epistatic genetic interaction between the detected QTLs and genetic background. The utilization of exotic germplasm faces the challenge of the low reproduction of favorable QTL effects between different genetic backgrounds.

The population size used for AB-QTL analyses may be a crucial factor for the number of QTLs detected. For instance, Huang et al. (2003) detected 40 putative QTLs using only 72 BC_2F_1 wheat lines. Eighty-six and 108 putative QTLs were detected by Pillen et al. (2003, 2004) in 136 and 164 BC_2F_2 spring barley lines, respectively. The proportion of introgressions is decreased with advanced backcrossing, while Fulton et al. (1997) predicted that the introgression size would be reduced to an average of 34 cM in BC_2 population. The reduced proportion and size of introgressions may also reduce the statistic power to detect minor QTLs in advanced population since fewer lines share the exotic allele. If the population size is big enough, the different exotic alleles may have a high opportunity to express itself and the performance of the lines with different exotic alleles can be evaluated better in field. Thus, the favorable exotic QTL alleles with minor effects have a high probability to be detected. In our study, two BC_2DH winter barley populations, which shared same donor and consisted of very different number of lines, were employed for AB-QTL analysis. Much more putative QTLs and favorable exotic QTL alleles were detected in big

population C101 than small population T101, while the QTLs with strong effects could often be detected in both populations. In addition, the density of the marker map and the phenotype data can also affect the result of QTL detection.

The selection of the statistical method exerts a major impact on the results of a QTL experiment (Pillen et al. 2003). Up to now, different statistical methods and programs were used for QTL analysis, such as single marker analysis (Sax 1923; Edwards et al. 1987; Soller and Brody 1976), simple interval mapping (SIM, Lander and Botstein 1989; Haley and Knott 1992), composite interval mapping (CIM, Jansen and Stam 1994; Zeng 1994) and simplified CIM (sCIM, Tinker and Mather 1995). Among the programs, only QGENE (Nelson 1997) was designed for AB-QTL analysis with unbalanced populations, while other programs, such as MAPMARKER/QTL (Lander and Botstein 1989), QTL-CARTOGRAPHER (Basten et al. 1994), were used for classical QTL studies with balanced populations. However, every method has its own limitations. For instance, single marker analysis does not define the likely position of the QTL. Especially, it cannot distinguish between tight linkage to a QTL with a small effect and loose linkage to a QTL with a large effect (Lander and Botstein 1989). For Simple interval mapping (SIM), one of the major problems is the influence of closely linked QTLs. When there are two or more QTLs located on a chromosome, the mapping of QTLs can be seriously biased, and QTLs can be mapped to wrong positions (Knott and Haley 1992; Martinez and Curnow 1992). Simulation results indicated that a "ghost QTL" might appear between two real linked QTLs in interval mapping because the two real QTLs are hidden by the "ghost QTL" (Moreno-Gonzalez 1992). The composite interval mapping (CIM) can only estimate the genetic effects in a single environment. QGENE operates with single marker regression as well as simple interval mapping for QTL detection and cannot handle multiple environments (Pillen et al. 2003).

For interval mapping, the major weakness is that QTLs are detected in a single environment because the quantitative traits are easily influenced by environmental factors and the relative ranking of genotypes may well differ between environments (Allard and Bradshaw 1964). Recently, the interval mapping was intensively used for QTL analyses (Fulton et al, 1997, 2000; Manninen et al. 2000; Huang et al. 2003; Francia et al. 2004). However, if the phenotype data were collected for QTL mapping only from single environments, the detected QTLs might be false QTLs. For instance, in our study, the *Hsp* allele was associated with an increased yield of 13.8 % at HvPLASC1B$_{[7H]}$ in test location Gudow in 2002/03, but the effect of the *Hsp* allele in the vicinity of HvPLASC1B$_{[7H]}$ on yield was not significant across all environments. Thus, the reliability of the detected QTLs will be reduced due to the analysis focusing on a single environment.

Stuber et al. (1992) discerned individual QTLs into marker main effect QTLs and environment-dependent QTLs (M×E interaction) using the data from multiple environments (Pillen

et al. 2003, 2004). Even if the experiment was carried out in multiple environments and the QTL effects were analyzed by means of LSMeans across all environments, there is still the problem that the LSMeans cover the variation of the quantitative traits between environments so that a false favorable QTLs may be calculated. In our study, the relative performance of the lines with the *Hsp* alleles were significantly better than the lines with the *Hv* alleles at 56 QTLs (20.9 %) with crossover interaction effect according to the LSMeans across all environments. However, these QTLs exhibited no real favorable QTL effects, because their effects varied between environments. For instance, a crossover interaction QTL effect on COD was detected at EBmac0906-GMS089$_{[4H]}$ in T101 (Appendix 7). At this locus, the *Hsp* allele resulted in a COD reduction of 19.4 % based on the LSMeans across all environments, but the variation of the effect of the *Hsp* allele at this locus on COD ranged from 8.5 % (increased COD, at Estrées in 2002/03) to -45.8 % (decreased COD, at Dikopshof in 2002/03). If only based on the overall LSMeans or overall relative performance, this QTL effect would be defined as a favorable QTL effect. Actually, this QTL had a crossover interaction effect on COD. Therefore, in this study, the environment-dependent QTLs were distinguished into QTL effects with stable ranking across environments and the crossover interaction effects with reverse ranking between environments.

The selection of statistic models may be affecting the extraction of QTLs. For QTL analysis, different statistic models such as one-way ANOVA (simple t-test), simple linear regression, multiple linear regressions, nonlinear regression, log-linear regression, likelihood functions, mixed linear models, and Bayesian approach (Weller 1986; Lander and Botstein 1989; Haley and Knott 1992; Jansen 1992; Zeng 1994; Wang et al. 1999) were used different studies.

Though the generation of appropriate populations and phenotyping in field trials are very time consuming and expensive for the utilization of exotic germplasm, the wild relatives of the modern crops undoubtedly play an important role for improvement of the cultivars. This conclusion can be draw from multiple AB-QTL studies. Our study can also confirm this conclusion. In this study, a total 48 (17.9 %) favorable *Hsp* alleles were identified among 268 localized QTLs in both populations. These favorable *Hsp* alleles were detected for eleven out of the 16 investigated traits. Altogether, 65 (24.3 %) QTL effects among 268 putative QTLs localized in both populations and 21 (43.8 %) favorable QTL effects among 48 favorable QTL effects identified in both populations were verified in other barley QTL and linkage analyses (Appendix 5). About 56 % favorable exotic QTL alleles identified in this study were so far not detected in other barley QTL studies. These favorable *Hsp* alleles may be new alleles.

5. Summary

Barley is one of most important crops in the world. It is a diploid, largely self-fertilizing species with a large genome of 5.3×10^9 bp/1 C (Bennett and Smith, 1976). The genetic advantages of working with a self-compatible true diploid, together with the availability of a large number of genetic stocks and its considerable economic importance, have resulted in barley being proposed as a model for the entire Triticeae (Linde-Laursen *et al.* 1997). In this study, the focus of the work is directed thereby on detection of favorable QTL alleles from wild barley accession (*Hordeum vulgare* ssp *spontaneum, Hsp*) in order to broaden the genetic base of barley.

Two BC_2DH populations (C101 and T101) were developed from the crosses between the two winter barley varieties Carola and Theresa (*Hordeum vulgare* ssp. *vulgare, Hv)* and the wild barley ISR101-23 (*Hordeum vulgare* ssp. *spontaneum, Hsp*) from Israel. C101 and T101 consist of 282 and 104 lines, respectively.

Both populations were genotyped with 82 SSR markers for C101 and 78 SSR markers for T101. The genotyped markers were distributed over all seven chromosomes and covered 1,225 cM of the barley genome in both populations. However, the distribution of SSR markers on individual chromosomes was uneven. In C101, the distribution of markers ranged from 9 – 14 SSRs with an average of 11.7 on chromosomes 1H – 7H, but in T101 from 8 – 16 SSRs with an average of 11.1. In addition, distinct clusters of markers and gaps (> 30 cM) were observed on chromosomes. Among the BC_2DH lines, the percentage of *Hsp* genome ranged from 0 to 32.5% with an average of 13.2% in C101, but from 1.3 to 30.8% with an average of 13.7% in T101.

The field testing was divided into two parts: evaluation of agronomic traits and evaluation of pathogen resistances and non-parasitic browning. The experiments for agronomic performance were carried out at four test locations (Dikopshof, Gudow, Leutewitz and Irlbach) in the seasons 2002/03 and 2003/04. At each location, a randomized complete block design was applied, without replications. As a control, the recurrent parent was tested with 20 replications per block. Plot size was 6 – 8 m^2 and seeding rate was 280 - 320 kernels/m^2 (Table 3). The field management included N, P, and K fertilization and pest control according to the local practice at the respective field station. At each plot, the traits, HEA, HEI, BSP, LOH, SB, YLD and COD were scored. The experiments for pathogen resistance and non-parasitic browning were carried out at the following four test locations: Dikopshof, Gudow, Leutewitz and Estrées. Here, all BC_2DH lines from both populations were grown in the same block. The plot size was 1 – 2.25 m^2 or 6 rows, and the seeding rate 400 kernels / m^2 (Table 3). At each location, a randomized complete block design was applied, without replications. For each plot, the PM, NB, RH, LR and NPB were scored from 1 to 9 according to the visual rating of the severity of symptoms (Table 4).

Genetic correlation was analyzed by means of the SAS procedure (SAS Institute 1999). The strongest correlation was found between MAS and EAR (r = 0.78 in C101 and r = 0.79 in T101). A strong negative correlation was observed between COD and YLD in C101 (r = -0.64), while a moderate negative correlation was obtained in T101 (r = -0.40). A moderate negative correlation was revealed between P[*Hsp*] and YLD in C101. The correlations between other traits were moderate or weak (Table 6 and Table 7).

The QTL analysis was conducted using the BC$_2$DH genetic data and the field data from multiple environments by means of the procedure GLM (General Linear Model) from the SAS software (SAS Institute 1999). A single-point analysis by means of multi-factorial ANOVA (split plot mixed model) was used for QTLs analysis because data from multiple environments should be integrated. In order to reduce the effect of **COD** and **N** (neighbouring plots of the seriously cold-damaged plots) on other traits, **COD** or **N** was used as co-variables for QTL detection if the effect of **COD** or **N** was significant in the ANOVA for line effects. The models used to detect QTLs included the marker effect (**M**), the environment effect (**E**), the line effect nested in the marker genotype [**L(M)**] and the interaction between marker and environment (**M*E**). Under the assumption of a mixed model, **M** was chosen as a fixed effect, **L**(M), **E** and **M**×**E** as random effects and **N** and **C** as co-variables without classes.

The QTL detection was based on the following criteria: (i) the presence of a stable QTL in the vicinity of a marker locus was accepted, if the marker main effect was significant with $P < 0.01$, (ii) the presence of an environment-dependent QTL was accepted, if the M×E interaction was significant with $P < 0.01$, (iii) adjacent markers (≤ 20 cM) which showed the same effect were considered as a single QTL.

In total, 268 putative QTLs for eleven agronomic traits, four pathogen resistances and one syndrome were detected among 2,478 marker×trait combinations in both BC$_2$DH populations (Table 17, Table 19 and Fig. 4). At 93 putative QTLs, the marker main effect and at 207 putative QTLs, the M×E interactions were significant at $P < 0.01$. In 32 cases, both effects were significant. Among these putative QTLs, 48 (17.9 %) exotic favorable QTL alleles were identified, 35 favorable QTL alleles for agronomic traits and 13 favorable exotic alleles for pathogen resistances and non-parasitic browning. Much more putative QTLs were detected in C101 (183) than in T101 (85). Likewise, more favorable exotic QTL alleles were detected in C101 (35) than in T101 (13). Thirty-nine putative QTLs, which were detected in C101, were verified by 40 QTLs detected in T101 (Table 23 and Table 24). Most verified putative QTLs gathered on chromosome 1H (11 QTLs in C101 and 12 QTLs in T101), while little putative QTLs were verified on chromosomes 2H (2) and 7H (2). This result indicated that most of the QTL alleles on chromosome 1H from Carola and

Theresa exhibit similar effects and that these effects are significantly different from their ISR101-23 counterpart. The majority of verified QTLs were found for HEI (10), HEA (5), LOH (4) and YLD (4) in both populations and no putative QTL were verified for EAR, MAS and LR. This finding indicated that a lot of the QTL alleles for HEI, HEA, LOH and YLD from Carola and Theresa exhibit similar effects and that these effects are significantly different from their donor ISR101-23.

Altogether, 65 (24.3 %) QTL effects among 268 putative QTLs localized in both populations and 21 (43.8 %) favorable QTL effects among 48 favorable QTL effects identified in both populations were verified in other barley QTL and linkage analyses (Appendix 5). About 64 % favorable exotic QTL alleles identified in this study were so far not detected in other barley QTL studies. These favorable *Hsp* alleles may be new alleles.

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7. Appendix

Appendix 1: Analysis of variance for all traits in C101 in 2002/03 and 2003/04

Trait[1)]	Source[2)]	DF	SS	MS	F	P[3)]
BS	Line	282	968.13	3.43	1.69	< 0.001
	Error	789.55	1606.38	2.03		
	E	4	2631.57	657.89	401.72	< 0.001
	Error	730.80	1196.83	1.64		
	N	1	0.61	0.61	0.65	ns
	COD	1	0.33	0.33	0.34	ns
	Line*E	769	1590.75	2.07	2.19	< 0.001
	Error: MS(Error)	84	79.19	0.94		
BSP	Line	282	922.02	3.27	1.79	< 0.001
	Error	809.56	1477.07	1.82		
	E	4	2291.52	572.88	401.26	< 0.001
	Error	814.69	1163.14	1.43		
	N	1	1.67	1.67	2.39	ns
	COD	1	0.30	0.30	0.43	ns
	Line*E	793	1472.85	1.86	2.66	< 0.001
	Error: MS(Error)	86	60.06	0.70		
COD	Line	287	3382.22	11.78	6.19	< 0.001
	Error	1159.14	2205.59	1.90		
	E	4	4798.45	1199.61	639.94	< 0.001
	Error	1176.99	2206.34	1.87		
	Line*E	1133	2205.09	1.95	3.00	< 0.001
	Error: MS(Error)	717	465.84	0.65		
EAR	Line	282	5551549.42	19686.35	0.96	ns
	N	1	1509.12	1509.12	0.07	ns
	COD	1	579.87	579.87	0.03	ns
	Error: MS(Error)	319	6523194.00	20448.88		
HEA	Line	282	6861.27	24.33	11.13	< 0.001
	Error	1399.43	3059.48	2.19		
	E	5	80204.71	16040.94	8831.84	< 0.001
	Error	1316.00	2390.21	1.82		
	N	1	0.00	0.00	0.00	ns
	COD	1	0.18	0.18	0.18	ns
	Line*E	1390	3051.48	2.20	2.20	< 0.001
	Error: MS(Error)	112	111.55	1.00		
HEI	Line	282	55714.49	197.57	6.97	< 0.001
	Error	1352.05	38310.53	28.34		
	E	5	404089.27	80817.85	3181.16	< 0.001
	Error	1052.32	26734.42	25.41		
	N	1	108.87	108.87	5.72	< 0.05
	COD	1	9.71	9.71	0.51	ns
	Line*E	1335	37950.32	28.43	1.49	< 0.01
	Error: MS(Error)	112	2131.84	19.03		

Appendix 1 (continued)

Trait[1)]	Source[2)]	DF	SS	MS	F	P[3)]
LOH	Line	282	2916.67	10.34	3.08	< 0.001
	Error	1330.53	4468.60	3.36		
	E	5	5702.19	1140.44	426.30	< 0.001
	Error	1376.10	3681.32	2.68		
	N	1	0.02	0.02	0.02	ns
	COD	1	1.97	1.97	1.76	ns
	Line*E	1321	4469.38	3.38	3.01	< 0.001
	Error: MS(Error)	111	124.58	1.12		
LR	Line	285	792.14	2.78	2.12	< 0.001
	Error	284.23	372.06	1.31		
	E	1	45.89	45.89	25.05	< 0.001
	N	1	0.03	0.03	0.01	ns
	COD	1	12.90	12.90	6.93	< 0.05
	Line*E	284	371.71	1.31	0.70	ns
	Error: MS(Error)	56	104.22	1.86		
	Error	60.43	110.72	1.83		
MAS	Line	282	165988.33	588.61	0.74	ns
	N	1	775.46	775.46	0.98	ns
	COD	1	168.62	168.62	0.21	ns
	Error: MS(Error)	317	251151.20	792.28		
NB	Line	286	459.44	1.61	1.60	< 0.001
	Error	1402.25	1406.82	1.00		
	E	5	4511.72	902.34	1418.61	< 0.001
	Error	1511.50	961.43	0.64		
	N	1	0.00	0.00	0.00	ns
	COD	1	0.00	0.00	0.00	ns
	Line*E	1407	1391.39	0.99	9.56	< 0.001
	Error: MS(Error)	105	10.87	0.10		
NPB	Line	286	590.64	2.07	1.46	< 0.001
	Error	1104.55	1566.21	1.42		
	E	4	73.79	18.45	14.52	< 0.001
	Error	407.684	517.91	1.27		
	N	1	1.03	1.03	0.92	ns
	COD	1	0.53	0.53	0.48	ns
	Line*E	1125	1591.52	1.41	1.26	ns
	Error: MS(Error)	85	95.06	1.12		

Appendix 1 (continued)

Trait[1)]	Source[2)]	DF	SS	MS	F	P[3)]
PM	Line	286	552.04	1.93	1.38	< 0.001
	Error	847.82	1186.14	1.40		
	E	3	632.74	210.91	236.61	< 0.001
	Error	469.05	418.12	0.89		
	N	1	0.00	0.00	0.01	ns
	COD	1	0.49	0.49	0.87	ns
	Line*E	845	1185.21	1.40	2.52	< 0.001
	Error: MS(Error)	85	47.29	0.56		
RH	Line	286	665.46	2.33	1.70	< 0.001
	Error	1109.59	1514.53	1.36		
	E	4	1621.94	405.48	395.14	< 0.001
	Error	617.96	634.14	1.03		
	N	1	4.64	4.64	3.97	< 0.05
	COD	1	0.00	0.00	0.00	ns
	Line*E	1125	1525.42	1.36	2.00	< 0.001
	Error: MS(Error)	86	58.42	0.68		
TGW	Line	282	9582.16	33.98	3.13	< 0.001
	Error	1094.72	11866.34	10.84		
	E	4	19379.91	4844.98	637.81	< 0.001
	Error	1169.43	8883.31	7.60		
	N	1	0.60	0.60	0.28	ns
	COD	1	4.30	4.30	1.98	ns
	Line*E	1091	11907.79	10.91	5.02	< 0.001
	Error: MS(Error)	93	202.07	2.17		
YLD	Line	282	6138254.52	21766.86	3.49	< 0.001
	Error	1084.98	6758151.36	6228.85		
	E	4	16538682.44	4134670.61	874.37	< 0.001
	Error	1035.91	4898596.98	4728.77		
	N	1	5896.39	5896.39	2.67	ns
	COD	1	6419.36	6419.36	2.91	ns
	Line*E	1078	6755178.26	6266.40	2.84	< 0.001
	Error: MS(Error)	93	205458.86	2209.24		

[1)] Abbreviations: BS, Breaking of stem; BSP, Bending of spike; COD, Cold damage; EAR, Number of spikes; HEA, Days until heading; HEI, Plant Height; HI, Harvest index; LOH, Lodging at harvest; LR, Leaf rust; MAS, Biomass; NB, net blotch; NPB, Non-parasitic browning; PM, Powdery mildew; RH, leaf scald; TGW, Thousand-grain weight; YLD, Yield. [2)] E: Environment; N: neighbour plot; COD: cold damage. [3)] ns: not significant.

Appendix 2: Analysis of variance for all traits in seasons T101 in 2002/03 and 2003/04

Trait[1)]	Source[2)]	DF	SS	MS	F	P[3)]
BS	Line	103	147.19	1.43	1.39	< 0.05
	Error	243.30	249.70	1.03		
	E	4	476.79	119.20	141.93	< 0.001
	Error	251.96	211.61	0.84		
	N	1	1.04	1.04	2.13	ns
	COD	1	0.47	0.47	0.97	ns
	Line*E	232	245.29	1.06	2.17	< 0.01
	Error: MS(Error)	36	17.50	0.49		
BSP	Line	104	198.04	1.90	1.88	< 0.001
	Error	251.65	254.41	1.01		
	E	4	595.34	148.84	205.75	< 0.001
	Error	278.02	201.12	0.72		
	N	1	0.19	0.19	1.29	ns
	COD	1	0.01	0.01	0.04	ns
	Line*E	248	261.97	1.06	7.01	< 0.001
	Error: MS(Error)	37	5.57	0.15		
COD	Line	104.00	1654.89	15.91	6.75	< 0.001
	Error	207.02	487.90	2.36		
	E	2.00	148.85	74.43	33.41	< 0.001
	Error	211.66	471.56	2.23		
	Line*E	207.00	487.99	2.36	6.24	< 0.001
	Error: MS(Error)	368.00	139.10	0.38		
EAR	Line	104	2550275.76	24521.88	1.13	ns
	Error: MS(Line*E)	104	2251841.59	21652.32		
	E	1	90143.92	90143.92	2.63	ns
	Error	277.40	9495150.24	34228.50		
	N	1	13613.66	13613.66	0.38	ns
	COD	1	40456.47	40456.47	1.12	ns
	Line*E	104	2251841.59	21652.32	0.60	ns
	Error: MS(Error)	239	8613865.47	36041.28		
HEA	Line	104	1965.65	18.90	6.39	< 0.001
	Error	518.87	1535.70	2.96		
	E	5	20313.22	4062.64	1749.50	< 0.001
	Error	541.05	1256.41	2.32		
	N	1	1.15	1.15	1.22	ns
	COD	1	0.00	0.00	0.00	ns
	Line*E	514	1537.14	2.99	3.16	< 0.001
	Error: MS(Error)	46	43.60	0.95		
HEI	Line	104	21830.73	209.91	8.40	< 0.001
	Error	525.66	13138.58	24.99		
	E	5	154503.67	30900.73	1422.04	< 0.001
	Error	445.76	9686.39	21.73		
	N	1	5.69	5.69	0.39	ns
	COD	1	3.49	3.49	0.24	ns
	Line*E	517	13001.79	25.15	1.71	< 0.05
	Error: MS(Error)	46	677.26	14.72		

Appendix 2 (continued)

Trait[1)]	Source[2)]	DF	SS	MS	F	P[3)]
HI	Line	104	0.44	0.00	1.83	< 0.01
	Error: MS(Line*E)	104	0.24	0.00		
	E	1	0.01	0.01	23.51	< 0.001
	Error	239	0.07	0.00		
	N	1	0.00	0.00	1.20	ns
	COD	1	0.01	0.01	2.14	ns
	Line*E	104	0.24	0.00	0.90	ns
	Error: MS(Error)	239	0.60	0.00		
LOH	Line	104	1224.52	11.77	4.14	< 0.001
	Error	512.22	1458.39	2.85		
	E	5	1513.50	302.70	134.97	< 0.001
	Error	535.18	1200.28	2.24		
	N	1	0.22	0.22	0.24	ns
	COD	1	1.41	1.41	1.53	ns
	Line*E	507	1459.66	2.88	3.12	< 0.001
	Error: MS(Error)	46	42.40	0.92		
LR	Line	108	328.98	3.05	0.90	ns
	Error	101.39	342.52	3.38		
	E	1	26.22	26.22	10.30	< 0.01
	Error	60.57	154.16	2.54		
	N	1	0.17	0.17	0.07	ns
	COD	1	13.93	13.93	5.64	< 0.05
	Line*E	107	358.08	3.35	1.36	ns
	Error: MS(Error)	48	118.54	2.47		
MAS	Line	104	83954.84	807.26	0.86	ns
	Error: MS(Line*E)	104	97911.44	941.46		
	E	1	14232.52	14232.52	11.18	< 0.001
	Error	283.75	361258.63	1273.18		
	N	1	1716.68	1716.68	1.30	ns
	COD	1	1020.66	1020.66	0.77	ns
	Line*E	104	97911.44	941.46	0.71	ns
	Error: MS(Error)	239	315717.68	1320.99		
NB	Line	108	102.40	0.95	1.23	< 0.05
	Error	412.55	317.64	0.77		
	E	4	97.27	24.32	35.31	< 0.001
	Error	498.21	343.12	0.69		
	N	1	0.00	0.00	0.00	ns
	COD	1	0.05	0.05	0.08	ns
	Line*E	420	322.48	0.77	1.32	< 0.05
	Error: MS(Error)	127	74.14	0.58		

Appendix 2 (continued)

Trait[1)]	Source[2)]	DF	SS	MS	F	P[3)]
NPB	Line	108	380.68	3.52	2.17	< 0.001
	Error	309.06	501.12	1.62		
	E	3	249.93	83.31	60.80	< 0.001
	Error	358.01	490.54	1.37		
	N	1	0.01	0.01	0.01	ns
	COD	1	0.20	0.20	0.17	ns
	Line*E	314	507.44	1.62	1.42	< 0.05
	Error: MS(Error)	104	118.24	1.14		
PM	Line	108	371.41	3.44	2.06	< 0.001
	Error	305.07	509.17	1.67		
	E	3	804.17	268.06	181.09	< 0.001
	Error	312.63	462.76	1.48		
	N	1	0.55	0.55	0.41	ns
	COD	1	0.24	0.24	0.18	ns
	Line*E	311	517.79	1.66	1.26	ns
	Error: MS(Error)	99	130.84	1.32		
RH	Line	108	455.50	4.22	3.13	< 0.001
	Error	304.80	410.37	1.35		
	E	3	264.28	88.09	60.57	< 0.001
	Error	317.32	461.51	1.45		
	N	1	4.27	4.27	2.68	ns
	COD	1	0.69	0.69	0.43	ns
	Line*E	313	422.26	1.35	0.85	ns
	Error: MS(Error)	99	157.66	1.59		
TGW	Line	104	3748.14	36.04	3.97	< 0.001
	Error	405.04	3680.11	9.09		
	E	4	6571.38	1642.84	245.36	< 0.001
	Error	410.19	2746.54	6.70		
	N	1	5.89	5.89	2.08	ns
	COD	1	2.12	2.12	0.75	ns
	Line*E	401	3685.59	9.19	3.26	< 0.001
	Error: MS(Error)	39	110.12	2.82		
YLD	Line	104	2209719.25	21247.30	4.13	< 0.001
	Error	379.34	1951626.40	5144.86		
	E	4	3612450.59	903112.65	241.28	< 0.001
	Error	395.83	1481565.55	3742.96		
	N	1	16217.60	16217.60	11.17	< 0.01
	COD	1	1321.22	1321.22	0.91	ns
	Line*E	375	1958927.62	5223.81	3.60	< 0.001
	Error: MS(Error)	38	55152.65	1451.39		

[1)] Abbreviations: BS, Breaking of stem; BSP, Bending of spike; COD, Cold damage; EAR, Number of spikes; HEA, Days until heading; HEI, Plant Height; HI, Harvest index; LOH, Lodging at harvest; LR, Leaf rust; MAS, Biomass; NB, net blotch; NPB, Non-parasitic browning; PM, Powdery mildew; RH, leaf scald; TGW, Thousand-grain weight; YLD, Yield. [2)] E: Environment; N: neighbour plot; COD: cold damage. [3)] ns: not significant.

Appendix 3: List of significant marker main effects and M×E interaction in C101

Trait [1]	Marker [2]	Chr [3]	Pos [4] (in cM)	Factor [5]	Sign [6]	LSM [*Hsp*] [7]	R^2_G [9] or R^2_{GI} [9] (%)	RP[*Hsp*] [10] (in %)
BS	GBM1042	1H	39	M*E	**	3.74	3.51	9.81
	Bmag0211	1H	68	M*E	**	3.98	2.90	18.03
	GBM1004	1H	75	M	**	4.01	5.48	19.57
	BMS32	1H	105	M*E	***	3.71	3.95	7.55
	GMS114	1H	115	M*E	**	3.87	2.96	13.69
	EBmac0684	2H	80	M*E	**	3.37	3.82	-3.48
	GBM1047	2H	150	M*E	**	3.92	3.32	14.22
	GBM1048	4H	162	M*E	***	4.13	6.19	19.45
	GBM1015	4H	170	M*E	***	4.20	5.80	21.67
	HvJASIP	4H	180	M*E	***	4.24	4.64	23.81
	HVM67	4H	180	M*E	***	4.16	5.16	21.41
	HDAMYB	4H	190	M*E	***	4.14	4.44	21.07
	HvBAMY	4H	190	M*E	***	4.14	4.52	21.37
	Bmac0163	5H	24	M*E	**	3.71	3.57	9.59
	GBM1026	5H	30	M*E	***	3.81	4.58	14.28
	HvHEMH1	5H	35	M*E	***	3.79	4.69	12.69
	Bmag0337	5H	43	M*E	**	3.78	3.53	12.46
	Bmag0357	5H	48	M*E	**	3.82	3.51	14.64
	GBM1041	5H	75	M*E	***	3.79	5.90	12.65
	Bmag0613	6H	112	M*E	**	3.34	3.35	-5.16
	GBM1008	6H	135	M*E	**	2.90	2.88	-18.47
	AF022725A	7H	59	M*E	***	3.49	4.12	0.48
	HvSS1	7H	62	M*E	***	3.45	7.39	-1.51
	GBMS035	7H	77	M*E	**	3.53	3.52	0.99
	Bmac0167	7H	93	M*E	***	3.62	3.99	6.03
	Bmag0321	7H	100	M*E	***	3.61	4.24	5.66
	Bmag0369	7H	100	M*E	***	3.60	4.49	5.25
	EBmac0755	7H	166	M*E	***	3.25	7.51	-8.12
	HVM49	7H	178	M*E	***	3.57	5.01	2.19
BSP	GBM1032	1H	50	M*E	***	4.50	5.51	1.21
	HvALAAT	1H	63	M*E	***	4.57	3.69	2.23
	Bmag0211	1H	68	M*E	***	4.49	4.83	0.75
	GBM1004	1H	75	M*E	***	4.52	5.65	0.55
	GMS114	1H	115	M*E	**	4.30	3.01	-4.11
	GBM1041	5H	75	M*E	***	4.51	6.14	1.69
	HvLOXC	5H	114	M	**	5.05	1.68	14.77
	GMS006	6H	96	M*E	**	4.63	3.32	4.47
	HVM14	6H	103	M*E	**	4.61	3.22	3.49
COD	BMS32	1H	105	M + M*E	***	4.90	10.05	28.26
	GMS114	1H	115	M	**	4.68	5.10	20.81
	Bmag0579	1H	175	M*E	**	3.86	0.93	-4.45
	HVM36	2H	17	M + M*E	**	5.04	4.43	27.93
	GBM1035	2H	27	M + M*E	**	5.09	4.45	28.63
	EBmac0684	2H	80	M	**	2.81	4.22	-31.33
	GBM1016	2H	139	M*E	**	3.72	0.86	-8.90
	EBmac0415	2H	146	M*E	**	3.67	0.93	-9.54
	HvLTPPB	3H	25	M + M*E	**	5.27	6.96	34.44
	EBmac0705	3H	30	M + M*E	**	5.37	7.61	36.90
	HDAMYB	4H	190	M*E	**	4.68	0.76	18.73
	HvLEU	5H	53	M*E	**	3.71	0.83	-8.51

Appendix 3 (continued)

Trait [1]	Marker[2]	Chr[3]	Pos [4] (in cM)	Factor[5]	Sign [6]	LSM [*Hsp*] [7]	$R^{29)}_{G}$ or $R^{29)}_{GI}$ (%)	RP[*Hsp*] [10] (in %)
COD	GBM1041	5H	75	M + M*E	**	5.26	35.37	49.49
	HvLOXC	5H	114	M + M*E	**	6.26	22.00	63.36
	Bmac0316	6H	6	M + M*E	***	5.14	9.51	32.70
	GBM1008	6H	135	M*E	**	3.57	0.82	-12.23
	Bmac0167	7H	93	M*E	***	4.38	1.78	14.35
	Bmag0321	7H	100	M*E	***	4.40	1.79	15.11
	Bmag0369	7H	100	M*E	***	4.34	1.70	13.62
	GMS046	7H	120	M*E	***	4.37	1.56	12.75
	BMS64	7H	146	M*E	**	4.36	0.93	11.72
	EBmac0755	7H	166	M*E	***	3.72	1.18	-8.09
HEA	BMS32	1H	105	M + M*E	**	57.04	6.86	-2.35
	GBMS012	1H	144	M + M*E	**	57.18	4.55	-1.99
	Bmag0579	1H	175	M + M*E	***	56.88	7.80	-2.68
	HVM36	2H	17	M*E	***	57.18	1.08	-1.83
	GBM1035	2H	27	M*E	***	57.08	1.17	-2.08
	GBMS002	2H	50	M*E	***	57.55	0.90	-1.10
	GBM1016	2H	139	M*E	***	57.98	1.04	-0.45
	HVM54	2H	143	M*E	***	57.65	1.09	-1.06
	EBmac0415	2H	146	M*E	***	57.82	1.14	-0.71
	GBM1047	2H	150	M*E	**	57.44	0.55	-1.45
	HvLTPPB	3H	25	M*E	**	58.79	0.64	1.13
	EBmac0705	3H	30	M*E	**	58.71	0.67	0.99
	GBM1031	3H	47	M*E	***	54.92	0.77	-5.62
	Bmac0209	3H	63	M*E	***	54.92	0.77	-5.66
	Bmag0603	3H	70	M*E	***	54.92	0.77	-5.64
	HvPEPD1PR	3H	80	M*E	***	54.92	0.76	-5.61
	EBmac0679	4H	132	M	**	54.50	3.58	-6.38
	GBM1048	4H	162	M + M*E	**	56.73	4.31	-2.70
	HvLEU	5H	53	M + M*E	**	57.24	3.05	-1.88
	GBM1041	5H	75	M*E	***	57.88	2.55	-0.71
	HvLOXC	5H	114	M*E	***	57.54	2.20	-1.20
	Bmac0316	6H	6	M*E	**	58.21	0.59	0.06
	GMS006	6H	96	M*E	***	58.57	0.75	0.66
	HVM14	6H	103	M*E	***	58.53	0.79	0.69
	AF022725A	7H	59	M*E	**	57.98	0.65	-0.43
	Bmag0321	7H	100	M*E	**	58.17	0.57	-0.02
	BMS64	7H	146	M*E	**	58.35	0.54	0.39
	HVM49	7H	178	M	**	56.44	2.96	-3.08
HEI	BMS32	1H	105	M	**	105.76	3.81	-2.99
	GBMS012	1H	144	M*E	**	106.64	0.77	-2.22
	Bmag0579	1H	175	M*E	***	107.19	1.22	-1.48
	HVM36	2H	17	M	**	104.55	3.12	-3.97
	GBM1035	2H	27	M	**	104.72	2.85	-3.92
	GBMS002	2H	50	M	**	104.11	3.36	-4.43
	GBM1016	2H	139	M*E	**	109.58	1.03	1.11
	EBmac0415	2H	146	M*E	**	109.18	0.79	0.62
	HvLTPPB	3H	25	M	**	105.04	2.66	-3.53
	EBmac0705	3H	30	M	**	105.00	2.59	-3.55
	HVM33	3H	94	M	***	113.65	6.84	5.04
	GMS116	3H	100	M	***	113.00	6.10	4.42
	Bmag0013	3H	155	M	***	114.18	11.59	5.82
	GBM1059	3H	161	M	**	110.49	2.21	2.07

Appendix 3 (continued)

Trait [1)]	Marker[2)]	Chr[3)]	Pos [4)] (in cM)	Factor[5)]	Sign [6)]	LSM [*Hsp*] [7)]	$R^{29)}_{G}$ or $R^{29)}_{GI}$ (%)	RP[*Hsp*] [10)] (in %)
HEI	HVM62	3H	165	M	***	111.62	5.14	3.29
	EBmac0708	3H	169	M	**	111.62	3.95	3.08
	Bmac0029	3H	190	M	***	114.23	11.81	5.79
	HvPAZXG	4H	44	M*E	**	107.76	0.91	-0.65
	EBmac0679	4H	132	M	**	108.15	3.24	-0.82
	GBM1048	4H	162	M	**	104.64	3.36	-3.89
	GBM1015	4H	170	M + M*E	**	103.36	6.62	-5.13
	HvJASIP	4H	180	M + M*E	**	103.79	5.83	-4.77
	HVM67	4H	180	M + M*E	**	103.86	6.46	-4.74
	HDAMYB	4H	190	M + M*E	**	104.22	5.88	-4.46
	HvBAMY	4H	190	M + M*E	**	104.22	5.79	-4.42
	Bmag0337	5H	43	M*E	**	109.26	0.80	0.81
	Bmag0357	5H	48	M*E	***	108.94	1.13	0.47
	HvLEU	5H	53	M*E	***	106.53	1.10	-2.27
	GBM1041	5H	75	M*E	***	108.62	1.36	0.23
	GMS006	6H	96	M*E	***	107.55	1.38	-1.21
	HVM14	6H	103	M*E	***	107.32	1.35	-1.34
	Bmag0206	7H	19	M	**	112.01	3.57	3.39
	HVM49	7H	178	M	***	102.48	3.26	-5.73
LOH	GBM1042	1H	39	M*E	***	4.34	3.59	14.63
	GBM1032	1H	50	M*E	***	4.58	2.72	21.97
	HvALAAT	1H	63	M*E	***	4.41	2.41	18.09
	Bmag0211	1H	68	M*E	***	4.53	2.82	21.12
	GBM1004	1H	75	M*E	***	4.53	3.18	23.82
	BMS32	1H	105	M*E	***	4.75	4.72	28.05
	GMS114	1H	115	M*E	***	4.58	2.39	22.46
	GBMS012	1H	144	M*E	***	4.77	2.80	27.16
	Bmag0579	1H	175	M*E	***	4.17	2.55	8.71
	GMS116	3H	100	M*E	***	3.43	2.37	-12.63
	HVM60	3H	110	M*E	**	3.12	2.13	-20.47
	EBmac0906	4H	37	M*E	***	5.22	3.30	36.51
	HvRCABG	4H	42	M*E	***	5.46	3.57	43.04
	HvPAZXG	4H	44	M*E	***	5.42	3.77	41.87
	HVM13	4H	55	M*E	***	5.50	3.78	44.45
	GMS089	4H	57	M*E	***	5.28	3.11	38.05
	EBmac0679	4H	132	M*E	***	5.40	2.67	39.20
	GBM1048	4H	162	M*E	**	4.00	2.17	2.94
	Bmac0163	5H	24	M*E	***	4.42	4.66	21.15
	GBM1026	5H	30	M*E	***	4.50	4.30	23.72
	HvHEMH1	5H	35	M*E	***	4.50	4.82	23.01
	Bmag0337	5H	43	M*E	***	4.51	3.90	23.50
	Bmag0357	5H	48	M*E	***	4.40	3.63	20.60
	HvLEU	5H	53	M*E	**	4.24	1.99	10.41
	GBM1041	5H	75	M*E	**	4.32	2.30	15.23
	GBM1021	6H	40	M*E	***	4.49	2.48	17.93
	GMS006	6H	96	M*E	***	4.37	6.42	14.21
	HVM14	6H	103	M*E	***	4.46	7.29	16.98
	HvPAF93	6H	108	M*E	***	4.08	2.96	5.64
	GBM1022	6H	145	M*E	***	4.82	2.60	26.73
	GBM1005	6H	155	M*E	**	4.26	1.99	10.20
	GMS046	7H	120	M*E	***	3.74	2.81	-5.96

Appendix 3 (continued)

Trait [1)]	Marker[2)]	Chr[3)]	Pos [4)] (in cM)	Factor[5)]	Sign [6)]	LSM [*Hsp*] [7)]	$R^{29)}_{G}$ or $R^{29)}_{GI}$ (%)	RP[*Hsp*] [10)] (in %)
LOH	BMS64	7H	146	M*E	***	3.67	2.80	-7.68
	Bmag0120	7H	152	M*E	**	3.69	1.80	-6.98
	HVM49	7H	178	M*E	**	4.25	2.17	9.96
LR	GBM1007	1H	28	M	**	2.48	2.48	21.73
	Bmag0211	1H	68	M*E	**	2.25	2.25	9.28
	GBM1004	1H	75	M*E	**	2.19	2.19	9.27
	BMS32	1H	105	M*E	**	2.36	2.36	15.65
	GMS114	1H	115	M*E	**	2.43	2.43	19.04
	Bmag0579	1H	175	M	**	2.49	2.49	23.94
	GBMS002	2H	50	M	**	1.59	1.59	-25.32
	EBmac0415	2H	146	M	**	2.44	2.44	19.26
	HVM33	3H	94	M	***	1.59	1.59	-26.15
	GMS116	3H	100	M	**	1.63	1.63	-23.95
	EBmac0906	4H	37	M	**	2.96	3.00	45.67
	HvRCABG	4H	42	M	**	3.12	2.96	52.75
	GMS089	4H	57	M	***	3.00	3.12	47.68
	Bmag0613	6H	112	M	***	2.62	2.62	30.28
	GBM1005	6H	155	M	***	2.98	2.98	48.35
NB	GMS021	1H	14	M*E	**	2.74	2.86	-10.95
	GBM1007	1H	28	M*E	***	2.70	5.36	-12.40
	GBM1042	1H	39	M*E	***	2.76	5.01	-10.33
	GBM1032	1H	50	M*E	***	3.04	5.09	-0.02
	HvALAAT	1H	63	M*E	**	3.02	3.13	-0.61
	Bmag0211	1H	68	M*E	***	3.01	4.66	-0.52
	GBM1004	1H	75	M*E	***	2.98	5.29	-2.92
	BMS32	1H	105	M*E	***	2.88	6.56	-6.30
	GMS114	1H	115	M*E	***	2.95	3.57	-3.51
	Bmag0579	1H	175	M*E	**	3.06	3.16	0.80
	GBM1016	2H	139	M*E	**	2.91	2.96	-5.29
	HVM60	3H	110	M*E	***	3.16	3.70	4.41
	EBmac0906	4H	37	M*E	***	2.63	3.49	-13.96
	HvRCABG	4H	42	M*E	***	2.64	3.56	-14.00
	HvPAZXG	4H	44	M*E	***	2.57	4.14	-16.05
	HVM13	4H	55	M*E	**	2.62	3.18	-14.29
	GMS089	4H	57	M*E	**	2.67	2.67	-12.86
	GBM1044	4H	95	M*E	**	3.86	3.00	26.98
	GBM1041	5H	75	M*E	***	3.01	7.19	-1.13
	MGB318	5H	150	M*E	**	3.24	3.34	7.02
	Bmag0222	5H	162	M*E	***	3.25	3.64	7.64
	GMS001	5H	187	M*E	**	3.39	3.41	12.07
	Bmac0316	6H	6	M*E	***	3.30	4.30	9.91
	GBM1021	6H	40	M*E	***	2.61	6.05	-15.92
	GMS006	6H	96	M*E	***	2.23	24.46	-29.37
	HVM14	6H	103	M*E	***	2.22	23.25	-29.39
	HvPAF93	6H	108	M*E	***	2.30	14.85	-26.88
	Bmag0613	6H	112	M*E	***	2.60	7.42	-16.51
	GBM1008	6H	135	M*E	***	2.47	10.21	-20.43
	GBM1022	6H	145	M*E	***	2.45	10.31	-20.77
	GBM1005	6H	155	M*E	***	2.50	6.27	-18.99
	AF022725A	7H	59	M*E	***	3.02	5.07	-0.54
	HvSS1	7H	62	M*E	***	2.97	3.68	-3.95

Appendix 3 (continued)

Trait [1)]	Marker[2)]	Chr[3)]	Pos [4)] (in cM)	Factor[5)]	Sign [6)]	LSM [*Hsp*] [7)]	$R^{29)}_{G}$ or $R^{29)}_{GI}$ (%)	RP[*Hsp*] [10)] (in %)
NB	GBMS035	7H	77	M*E	***	3.04	4.58	-0.00
	EBmac0755	7H	166	M*E	***	2.74	4.34	-10.66
NPB	GBM1007	1H	28	M*E	**	3.52	1.52	-0.53
	GBMS012	1H	144	M + M*E	**	3.64	1.51	3.30
	HVM36	2H	17	M*E	***	4.49	3.73	29.19
	GBM1035	2H	27	M*E	***	4.48	3.32	29.56
	GBMS002	2H	50	M	**	4.47	5.88	27.51
	GBM1047	2H	150	M	**	3.10	3.68	-14.47
	HvLTPPB	3H	25	M*E	***	4.73	6.40	37.11
	EBmac0705	3H	30	M*E	***	4.69	5.99	35.92
	GBM1059	3H	161	M + M*E	***	4.13	10.66	22.16
	HVM62	3H	165	M + M*E	**	4.14	9.29	21.23
	EBmac0708	3H	169	M + M*E	**	4.10	7.23	19.96
	Bmac0029	3H	190	M + M*E	**	4.09	5.23	18.55
	EBmac0679	4H	132	M*E	**	4.83	1.68	36.94
	Bmac0163	5H	24	M*E	***	3.20	3.20	-13.35
	GBM1026	5H	30	M*E	***	3.16	3.15	-14.49
	HvHEMH1	5H	35	M + M*E	**	3.13	7.11	-14.86
	Bmag0337	5H	43	M*E	***	3.15	3.82	-15.14
	HvLEU	5H	53	M*E	***	3.54	2.30	-0.03
	MGB318	5H	150	M*E	**	3.70	1.74	4.58
	Bmag0222	5H	162	M*E	***	3.70	2.12	4.98
	Bmac0316	6H	6	M*E	***	4.23	5.10	22.50
	GMS006	6H	96	M	**	2.95	6.02	-18.58
	HVM14	6H	103	M	***	2.91	6.59	-19.85
	HvPAF93	6H	108	M	**	2.93	5.70	-19.24
	Bmag0613	6H	112	M*E	***	3.28	3.03	-8.62
	GBM1008	6H	135	M*E	***	3.22	2.94	-10.01
	GBM1022	6H	145	M*E	***	3.28	2.34	-7.91
	GBM1005	6H	155	M*E	**	3.55	1.78	0.21
	HvSS1	7H	62	M	**	3.30	2.76	-9.67
	GBMS035	7H	77	M*E	**	3.28	1.67	-9.01
	GMS046	7H	120	M*E	**	3.46	1.52	-3.49
	BMS64	7H	146	M*E	***	3.56	2.22	0.57
	EBmac0755	7H	166	M	**	2.97	3.35	-17.24
PM	GMS021	1H	14	M	***	4.93	5.97	14.50
	GBM1007	1H	28	M	**	4.89	5.05	13.28
	GBM1016	2H	139	M*E	***	4.09	2.54	-7.78
	HVM54	2H	143	M*E	***	3.90	3.80	-12.78
	EBmac0415	2H	146	M*E	***	4.15	2.82	-5.99
	GBM1047	2H	150	M*E	***	3.69	3.13	-17.81
	HVM33	3H	94	M*E	***	4.08	2.63	-7.76
	GMS116	3H	100	M*E	***	3.98	2.46	-10.62
	HVM60	3H	110	M*E	**	3.96	2.09	-10.16
	Bmac0163	5H	24	M	**	4.13	4.08	-8.33
	GBM1026	5H	30	M	**	4.11	4.02	-8.53
	Bmag0337	5H	43	M	**	4.13	3.46	-8.08
	Bmag0357	5H	48	M	**	4.14	7.17	-7.58
	HvLEU	5H	53	M	***	5.01	4.33	16.49
	GBM1041	5H	75	M*E	***	4.21	3.18	-5.89
	HvLOXC	5H	114	M*E	***	4.47	3.63	1.93

Appendix 3 (continued)

Trait [1]	Marker[2]	Chr[3]	Pos [4] (in cM)	Factor[5]	Sign [6]	LSM [*Hsp*] [7]	$R^{29)}_G$ or $R^{29)}_{GI}$ (%)	RP[*Hsp*] [10] (in %)
PM	GBM1021	6H	40	M*E	**	4.91	2.03	13.72
	GMS006	6H	96	M	***	4.89	5.80	14.52
	HVM14	6H	103	M	**	4.96	5.84	14.76
	HvPAF93	6H	108	M	***	5.06	7.85	17.95
	Bmag0613	6H	112	M	***	5.15	11.98	20.60
	GBM1008	6H	135	M	***	5.49	18.43	28.67
	GBM1022	6H	145	M	***	5.47	15.02	27.60
	GBM1005	6H	155	M	***	5.58	17.75	30.69
	AF022725A	7H	59	M*E	***	3.90	2.93	-13.25
	GBMS035	7H	77	M	**	3.91	5.83	-13.22
RH	GBM1004	1H	75	M	**	4.12	2.79	8.44
	BMS32	1H	105	M	**	4.25	4.52	11.21
	GMS114	1H	115	M	**	4.29	4.64	11.79
	HVM36	2H	17	M*E	**	3.81	2.15	-2.46
	GBM1035	2H	27	M*E	**	3.79	2.08	-3.25
	GBMS002	2H	50	M*E	**	3.77	1.91	-3.37
	GBM1047	2H	150	M	**	4.32	4.66	12.97
	GBM1048	4H	162	M	**	4.52	5.55	17.53
	GBM1015	4H	170	M	**	4.39	3.63	13.80
	HvJASIP	4H	180	M	**	4.31	2.59	11.43
	HDAMYB	4H	190	M	***	4.35	3.79	13.22
	HvBAMY	4H	190	M	***	4.35	3.62	12.86
	Bmac0163	5H	24	M	**	4.10	3.00	7.56
	GBM1026	5H	30	M	***	4.11	3.47	8.42
	HvHEMH1	5H	35	M	***	4.13	3.71	8.73
	Bmag0337	5H	43	M	***	4.10	2.77	7.45
	Bmag0357	5H	48	M	***	4.08	2.86	7.30
	GBM1041	5H	75	M	**	4.25	7.46	13.37
	GBM1021	6H	40	M*E	**	3.81	2.20	-2.72
	Bmag0613	6H	112	M*E	**	3.85	2.12	-1.34
	GBM1008	6H	135	M*E	**	3.90	2.23	-0.04
	Bmag0369	7H	100	M	**	3.77	1.41	-4.90
	EBmac0755	7H	166	M	**	4.36	3.10	13.01
	HVM49	7H	178	M	***	4.75	5.04	22.93
TGW	GBM1007	1H	28	M*E	**	40.39	2.00	-0.65
	GBM1042	1H	39	M*E	***	39.23	2.08	-4.25
	GBM1032	1H	50	M + M*E	**	38.91	10.58	-5.34
	HvALAAT	1H	63	M + M*E	**	39.03	9.35	-5.20
	Bmag0211	1H	68	M + M*E	**	38.84	11.34	-5.46
	GBM1004	1H	75	M + M*E	**	38.74	12.84	-5.78
	BMS32	1H	105	M*E	***	39.27	4.21	-4.10
	GMS114	1H	115	M*E	***	39.03	2.25	-4.72
	Bmag0013	3H	155	M	**	41.70	2.28	3.05
	GBM1015	4H	170	M	**	38.80	4.14	-4.87
	HvJASIP	4H	180	M	**	38.95	3.70	-4.52
	HVM67	4H	180	M	**	38.99	3.98	-4.45
	HDAMYB	4H	190	M	**	39.06	3.90	-4.38
	HvBAMY	4H	190	M	**	39.06	3.73	-4.29
	GBM1041	5H	75	M*E	***	40.58	2.95	-0.16
	MGB318	5H	150	M*E	***	39.41	3.08	-3.28
	Bmag0222	5H	162	M*E	***	39.51	2.85	-3.09

Appendix 3 (continued)

Trait [1]	Marker[2]	Chr[3]	Pos [4] (in cM)	Factor[5]	Sign [6]	LSM [*Hsp*] [7]	$R^{29)}_G$ or $R^{29)}_{GI}$ (%)	RP[*Hsp*] [10] (in %)
TGW	GMS001	5H	187	M*E	***	39.37	4.62	-3.31
	GBM1021	6H	40	M*E	***	39.16	2.34	-4.22
	GMS006	6H	96	M*E	***	39.33	3.54	-3.58
	HVM14	6H	103	M*E	***	39.23	3.25	-3.91
	GBM1008	6H	135	M*E	***	39.59	2.42	-2.84
	GBM1022	6H	145	M*E	**	39.97	2.06	-1.78
YLD	GBM1032	1H	50	M	**	703.89	9.62	-7.02
	HvALAAT	1H	63	M	**	716.25	5.00	-5.25
	Bmag0211	1H	68	M	**	708.18	8.04	-6.34
	GBM1004	1H	75	M	***	708.23	9.21	-6.72
	BMS32	1H	105	M	***	687.95	17.18	-9.62
	GMS114	1H	115	M	***	694.26	12.25	-8.51
	GBMS012	1H	144	M	***	704.89	7.62	-6.66
	HvLTPPB	3H	25	M*E	***	699.33	2.21	-6.85
	EBmac0705	3H	30	M*E	***	697.58	2.31	-7.08
	EBmac0906	4H	37	M*E	**	729.46	1.71	-2.48
	HvRCABG	4H	42	M*E	***	721.79	2.34	-3.64
	HvPAZXG	4H	44	M*E	***	707.32	2.90	-5.62
	HVM13	4H	55	M*E	***	715.72	2.47	-4.44
	GMS089	4H	57	M*E	***	728.13	2.23	-2.59
	GBM1048	4H	162	M	**	708.47	2.80	-5.61
	Bmac0163	5H	24	M*E	***	724.01	3.07	-4.49
	GBM1026	5H	30	M*E	***	713.27	3.21	-6.27
	HvHEMH1	5H	35	M*E	***	713.01	3.64	-6.28
	Bmag0337	5H	43	M*E	***	711.87	4.24	-6.34
	Bmag0357	5H	48	M*E	***	715.58	4.68	-6.18
	HvLEU	5H	53	M*E	***	752.59	2.44	0.75
	GBM1041	5H	75	M*E	***	700.04	5.88	-8.57
	HvLOXC	5H	114	M*E	***	706.73	4.63	-5.95
	Bmac0316	6H	6	M*E	***	704.41	2.49	-6.40
	GMS006	6H	96	M*E	**	741.59	1.77	-0.69
	HVM14	6H	103	M*E	**	741.55	1.65	-0.84
	HvPAF93	6H	108	M*E	**	763.19	1.68	2.48
	GBM1008	6H	135	M*E	***	763.38	2.43	2.40
	GBM1022	6H	145	M*E	***	756.70	2.84	1.38
	GBM1005	6H	155	M*E	***	766.76	4.17	2.88
	AF022725A	7H	59	M	**	715.62	4.80	-5.20
	HvSS1	7H	62	M	**	725.23	3.45	-3.91
	HVM49	7H	178	M	**	676.76	4.52	-9.78

[1] Trait abbreviations: BS, Breaking of stem; BSP, Bending of spike; COD, Cold damage; EAR, Number of spikes; HEA, Days until heading; HEI, Plant Height; HI, Harvest index; LOH, Lodging at harvest; LR, Leaf rust; MAS, Biomass; NB, net blotch; NPB, Non-parasitic browning; PM, Powdery mildew; RH, leaf scald; TGW, Thousand-grain weight; YLD, Yield. [2] Name of **QTLs** contains the prefix 'Q' (QTL), abbreviation of trait, abbreviation of population, chromosomal location and the ordinal number of QTLs on chromosome. [3] Chromosomal assignment of SSR. [4] [4] Marker exhibited significant effect. [5] Position of marker in cM derived from von Koff et al. (2004). [6] Factor M or M*E significant in QTL analysis. [7] Level of significance of the marker main effect or the MxE interaction, with **: $P < 0.01$, ***: $P < 0.001$; if there were more than one significant marker effect in the QTL interval, then the highest level of significance was taken. [8] The least square mean across all tested environments for homozygous *Hsp* genotypes at the given marker locus. [9] The difference of LSM: [aa] - [AA]. [10] The portion of genetic variance which is explained by marker main effect (R_G) or by M×E interaction (R_{GI}). [11] Relative performance of *Hsp* genotype: RP[*Hsp*] = ([*Hsp*]-[*Hv*]) x 100 / [*Hv*], where [*Hsp*] and [*Hv*] are the least square means of the homozygous *Hsp* and *Hv* genotypes, respectively, calculated across all environments tested; if there were more than one significant marker effect in the QTL interval, then the highest RP[*Hsp*] was taken.

Appendix 4: List of significant marker main effects and M×E interaction in T101

Trait [1]	Marker[2]	Chr[3]	Pos [4] (in cM)	Factor[5]	Sign [6]	LSM [*Hsp*] [7]	$R^{29)}_G$ or $R^{29)}_{GI}$ (%)	RP[*Hsp*] [10] (in %)
BS	HVM40	4H	14	M*E	**	2.84	11.36	0.97
	HvRCABG	4H	42	M*E	**	2.37	9.70	-20.74
	HvPAZXG	4H	44	M*E	**	2.32	11.64	-22.96
	GMS089	4H	57	M*E	**	2.31	9.57	-22.41
	HDAMYB	4H	190	M*E	***	3.78	14.01	37.68
	Bmag0337	5H	43	M*E	**	3.49	11.55	27.83
	GBM1021	6H	40	M*E	***	3.50	12.85	28.71
	GMS006	6H	96	M*E	**	3.33	9.22	24.14
BSP	GBM1002	1H	80	M*E	***	3.51	11.99	3.44
	HVM40	4H	14	M*E	**	3.58	7.65	5.41
	HvKNOX3	4H	31	M	***	2.86	8.79	-19.34
	GBM1048	4H	162	M*E	**	3.44	9.38	1.33
	HVM14	6H	103	M*E	**	3.33	8.33	-4.65
COD	GBM1042	1H	39	M*E	**	3.47	2.32	6.30
	HvALAAT	1H	63	M*E	***	3.47	2.84	5.23
	Bmag0211	1H	68	M*E	***	3.43	2.98	3.90
	GBM1004	1H	75	M*E	***	3.51	3.59	10.82
	GBM1002	1H	80	M*E	***	4.35	6.71	46.21
	BMS32	1H	105	M*E	**	3.44	2.13	6.80
	GBMS012	1H	144	M*E	***	3.98	4.47	33.79
	GBM1035	2H	27	M*E	**	4.40	2.01	40.70
	HVM33	3H	94	M*E	**	3.93	2.01	21.10
	HVM60	3H	110	M*E	***	5.33	4.09	64.28
	EBmac0906	4h	37	M*E	**	2.88	2.39	-11.90
	HvRCABG	4h	42	M*E	**	2.86	2.88	-15.69
	HVM13	4H	55	M*E	**	2.81	2.19	-15.47
	GMS089	4H	57	M*E	***	2.77	2.41	-19.42
	GBM1041	5H	75	M	**	4.80	37.31	72.28
	GBM1041	5H	75	M*E	***	4.80	8.03	72.28
	GBM1021	6H	40	M*E	**	3.81	2.08	20.68
EAR	Bmac0163	5H	24	M*E	**	655.20	8.02	-0.81
HEA	GBM1042	1H	39	M	**	60.69	7.74	2.87
	HvALAAT	1H	63	M	**	60.20	10.18	2.39
	Bmag0211	1H	68	M	**	60.26	9.36	2.30
	GBM1004	1H	75	M	***	60.34	11.90	2.64
	GBM1002	1H	80	M + M*E	**	57.44	28.00	-3.76
	GBMS012	1H	144	M + M*E	**	57.62	14.68	-3.05
	Bmag0579	1H	175	M	***	56.57	15.36	-4.68
	GBM1041	5H	75	M*E	***	58.78	7.37	-0.82
	HvPLASC1B	7H	8	M	**	56.39	7.25	-4.82
	AF022725A	7H	59	M*E	***	59.25	4.10	0.17
	GBMS035	7H	77	M*E	***	59.17	3.36	0.08
	BMS64	7H	146	M*E	***	58.21	4.44	-1.85
HEI	GBM1042	1H	39	M	**	112.29	8.13	5.37
	HvALAAT	1H	63	M + M*E	***	113.28	29.67	7.55
	Bmag0211	1H	68	M + M*E	***	113.31	29.34	7.52
	GBM1004	1H	75	M + M*E	***	113.28	26.65	7.25

Appendix 4 (continued)

Trait [1]	Marker[2]	Chr[3]	Pos [4] (in cM)	Factor[5]	Sign [6]	LSM [*Hsp*] [7]	$R^{29)}_{G}$ or $R^{29)}_{GI}$ (%)	RP[*Hsp*] [10] (in %)
	GBM1002	1H	80	M + M*E	**	101.14	1.97	-7.26
	BMS32	1H	105	M + M*E	***	111.77	3.59	6.09
	GMS114	1H	115	M + M*E	***	111.91	3.60	6.50
	GBMS012	1H	144	M + M*E	**	101.46	22.36	-6.27
	Bmag0579	1H	175	M	**	100.35	26.72	-6.75
	HVM36	2H	17	M*E	***	113.08	25.71	6.12
	GBM1035	2H	27	M*E	***	113.08	12.15	6.04
	HVM33	3H	94	M + M*E	**	115.77	10.50	8.51
	GMS116	3H	100	M + M*E	**	115.77	8.36	8.44
	HVM60	3H	110	M*E	***	116.75	6.61	9.47
	Bmag0013	3H	155	M + M*E	**	114.69	3.80	8.08
	GBM1059	3H	161	M*E	***	111.37	3.77	4.58
	HVM62	3H	165	M*E	**	108.94	4.16	2.25
	Bmac0029	3H	190	M*E	**	110.11	5.95	3.35
	HVM40	4H	14	M*E	***	105.84	7.22	-1.54
	HvJASIP	4H	180	M*E	**	102.19	11.36	-4.85
	HVM67	4H	180	M*E	**	101.97	13.43	-5.04
	HvBAMY	4H	190	M*E	**	101.07	18.24	-5.97
	Bmac0163	5H	24	M*E	***	104.15	17.77	-3.41
	GBM1026	5H	30	M*E	***	103.83	12.96	-3.85
	HvHEMH1	5H	35	M*E	**	103.83	13.06	-3.87
	Bmag0337	5H	43	M*E	**	103.74	8.06	-3.86
	Bmag0357	5H	48	M + M*E	**	103.53	7.54	-4.34
	HvLEU	5H	53	M*E	**	104.63	5.75	-3.07
	GBM1021	6H	40	M + M*E	**	102.15	6.65	-5.67
	GMS006	6H	96	M	**	103.85	1.97	-4.07
	Bmag0613	6H	112	M*E	**	102.04	3.59	-5.17
HI	GBM1002	1H	80	M*E	**	0.55	3.60	3.32
	MGB318	5H	150	M*E	**	0.51	22.36	-4.48
LOH	HvALAAT	1H	63	M	***	6.01	26.72	38.95
	Bmag0211	1H	68	M	***	6.16	25.71	42.76
	GBM1004	1H	75	M	***	6.15	12.15	42.65
	BMS32	1H	105	M	**	5.46	10.50	25.46
	GMS114	1H	115	M	**	5.39	8.36	23.14
	HVM60	3H	110	M	**	7.43	6.61	62.31
	GBM1059	3H	161	M	**	5.64	3.80	24.10
	HvKNOX3	4H	31	M*E	**	4.11	3.77	-14.73
	HvPAZXG	4H	44	M*E	**	4.38	4.16	-7.76
	HDAMYB	4H	190	M*E	**	4.74	5.95	3.34
LR	HVM67	4H	180	M*E	**	4.4	7.22	25.53
	HvBAMY	4H	190	M*E	**	4.5	11.36	28.95
NB	GBM1002	1H	80	M*E	**	1.51	13.43	-10.05
	HvLOXC	5H	114	M*E	**	2.20	18.24	36.38
	GBM1021	6H	40	M*E	***	1.51	17.77	-9.75
	GMS006	6H	96	M*E	***	1.52	12.96	-9.64
	HVM14	6H	103	M*E	**	1.53	13.06	-7.04
	HVM49	7H	178	M*E	**	1.91	8.06	17.97
MAS	HVM60	3H	110	M*E	**	131.84	7.54	5.81
	HVM62	3H	165	M*E	**	121.95	5.75	-2.42
NPB	GBM1002	1H	80	M*E	**	3.57	6.65	11.23
	BMS32	1H	105	M*E	***	3.41	1.97	4.64

Appendix 4 (continued)

Trait 1)	Marker 2)	Chr 3)	Pos 4) (in cM)	Factor 5)	Sign 6)	LSM [*Hsp*] 7)	$R^{29)}_{G}$ or $R^{29)}_{GI}$ (%)	RP[*Hsp*] 10) (in %)
NPB	GMS114	1H	115	M*E	**	3.31	4.64	0.45
	Bmag0579	1H	175	M*E	**	3.32	5.06	0.58
	HVM33	3H	94	M*E	**	3.15	4.63	-4.77
	GMS116	3H	100	M*E	**	3.15	4.74	-4.58
	GBM1059	3H	161	M*E	**	3.37	5.49	2.19
	HVM62	3H	165	M*E	**	3.41	5.61	4.08
	Bmac0029	3H	190	M*E	***	3.54	6.97	8.86
	GBM1021	6H	40	M*E	**	3.38	4.89	2.86
	GMS006	6H	96	M*E	**	3.10	4.84	-7.77
PM	GMS116	3H	100	M*E	**	3.97	5.71	9.11
RH	Bmag0579	1H	175	M*E	**	3.44	3.06	18.88
	HVM67	4H	180	M*E	**	4.03	3.78	40.28
	HvBAMY	4H	190	M*E	**	3.97	3.13	38.38
	GBM1026	5H	30	M	**	3.38	4.05	20.04
	HvHEMH1	5H	35	M	**	3.39	4.10	20.45
	Bmag0337	5h	43	M	**	3.40	4.00	20.50
TGW	GBM1042	1H	39	M	**	39.79	7.00	-5.43
	HvALAAT	1H	63	M*E	***	39.90	10.79	-6.10
	Bmag0211	1H	68	M*E	***	39.75	8.52	-6.14
	GBM1004	1H	75	M*E	***	39.68	7.38	-6.39
	GBM1002	1H	80	M*E	**	41.82	4.45	-0.15
	HvKNOX3	4H	31	M*E	**	39.90	4.89	-5.50
	HvRCABG	4h	42	M*E	**	40.10	4.37	-4.80
	HVM13	4H	55	M*E	**	39.88	4.42	-5.43
	GBM1048	4H	162	M*E	**	39.12	4.28	-7.28
	GMS006	6H	96	M*E	***	40.05	7.92	-5.60
	Bmag0613	6H	112	M	**	39.17	10.66	-7.01
YLD	HvALAAT	1H	63	M*E	***	733.13	8.03	-7.77
	Bmag0211	1H	68	M*E	***	738.58	7.39	-6.73
	GBM1004	1H	75	M*E	***	740.67	7.41	-6.57
	GBM1002	1H	80	M	**	746.24	9.75	-5.88
	GMS114	1H	115	M	**	752.81	9.36	-5.28
	HVM54	2H	143	M*E	**	752.85	3.19	-5.22
	EBmac0415	2H	146	M*E	**	756.37	3.38	-4.70
	HVM40	4H	14	M	**	736.12	13.80	-7.24
	HvKNOX3	4H	31	M*E	**	724.97	3.91	-8.35
	GBM1048	4H	162	M*E	**	784.14	3.26	0.30
	HvLOXC	5H	114	M*E	***	739.87	5.17	-5.60
	GMS006	6H	96	M*E	***	742.60	4.19	-6.59

1) Trait abbreviations: BS, Breaking of stem; BSP, Bending of spike; COD, Cold damage; EAR, Number of spikes; HEA, Days until heading; HEI, Plant Height; HI, Harvest index; LOH, Lodging at harvest; LR, Leaf rust; MAS, Biomass; NB, net blotch; NPB, Non-parasitic browning; PM, Powdery mildew; RH, leaf scald; TGW, Thousand-grain weight; YLD, Yield. 2) Name of **QTLs** contains the prefix 'Q' (QTL), abbreviation of trait, abbreviation of population, chromosomal location and the ordinal number of QTLs on chromosome. 3) Chromosomal assignment of SSR. 4) 4) Marker exhibited significant effect. 5) Position of marker in cM derived from von Koff et al. (2004). 6) Factor M or M*E significant in QTL analysis. 7) Level of significance of the marker main effect or the MxE interaction, with **: $P < 0.01$, ***: $P < 0.001$; if there were more than one significant marker effect in the QTL interval, then the highest level of significance was taken. 8) The least square mean across all tested environments for homozygous *Hsp* genotypes at the given marker locus. 9) The difference of LSM: [aa] - [AA]. 10) The portion of genetic variance which is explained by marker main effect (R_G) or by M×E interaction (R_{GI}). 11) Relative performance of *Hsp* genotype: RP[*Hsp*] = ([*Hsp*]-[*Hv*]) x 100 / [*Hv*], where [*Hsp*] and [*Hv*] are the least square means of the homozygous *Hsp* and *Hv* genotypes, respectively, calculated across all environments tested; if there were more than one significant marker effect in the QTL interval, then the highest RP[*Hsp*] was taken.

Appendix 5: Alignment of common QTL between C101, T101 and other QTL and linkage analyses in barley based on marker BIN groups

Trait[1)]	Chr[2)]	Range[3)]	Marker interval[4)]	QTL[5)]	P/N[6)]	$BIN_{[M]}$[7)]	QTL/Cand Gene[8)]	$BIN_{[R]}$[9)]	Reference
BS	4H	24-57	HvRCABG-GMS089	QbsT101-4Hb	°	7	MWG820c-MWG820b	4-8	Backes et al. 1995
COD	5H	75	GBM1041	QcodC101-5Hb	-		***HvCBF4***		Francia et al. 2004
	5H	114	HvLOXC	QcodC101-5Hc	-		***Vrn-H1***		Francia et al. 2004
	6H	145	GBM1022	QcodT101-1Hc	+	9	***Dhn***	9	Choi et al. 1999
HEA	1H	39	GBM1042	QheaT101-1Ha	-	5-7	Hord-ABG452	4-7	Pan et al. 1994
	1H	63-75	HvALAAT-GBM1004	QheaT101-1Hb	-	5-7	Hord-ABG452	4-7	Pan et al. 1994
							HVALAAT		Pillen et al. 2003
							Bmag0211		Pillen et al. 2004
	1H	80	GBM1002	QheaT101-1Hc	+	12	ipdg-BCD265c	12	Pan et al. 1994
							Vrn-H3	12	Cattivelli et al. 2002
	1H	144	GBMS012	QheaC101-1Hb	+	13-14	***Ppd-H2***	14	Laurie et al. 1995
							ABG195c-MWG912	13-14	Marquez-Cedillo et al. 2001
	1H	144	GBMS012	QheaT101-1Hd	+	13-14	***Ppd-H2***	14	Laurie et al. 1995
							ABG195c-MWG912	13-14	Marquez-Cedillo et al. 2001
	2H	17-27	HVM36-GBM1035	QheaC101-2Ha	+	3-4	HVM36		Pillen et al. 2003
							Rbcs-ABG2	3-4	Hayes et al. 1993
							Ppd-H1	3-4	Laurie et al. 1995
							MWG557-MWG769	3-4	Backes et al. 1995
	2H	50	GBMS002	QheaC101-2Hb	°	4	***Ppd-H1***	3-4	Laurie et al. 1995
							Rbcs-ABG2	3-4	Hayes et al. 1993
							MWG557-MWG769	3-9	Backes et al. 1995
	2H	139-150	GBM1016-GBM1047	QheaC101-2Hc	+	11-15	HVM54		Pillen et al. 2003
							HVM54		Pillen et al. 2004
							ABG14-Cgr3a	9-12	Hayes et al. 1993
	2H	139-150	EBmac0415	QheaC101-2Hc	+	13	EBmac0415		Pillen et al. 2003
	3H	47-80	GBM1031-HVPEPD1PR	QheaC101-3Hb	+	6	ABG396-ABG703A	6	Hayes et al. 1993
	3H	63	Bmac0209	QheaC101-3Hb	+		Bmac0209		Pillen et al. 2003
	4H	132	EBmac0679	QheaC101-4Ha	+		EBmac0679		Pillen et al. 2003
	5H	75	GBM1041	QheaC101-5Hb	°	9-10	ABC168-ABC717	9-10	de la Pena et al. 1999
	5H	114	HvLOXC	QheaC101-5Hc	°		HvLOXC		Pillen et al. 2003
	6H	96	GMS006	QheaC101-6Hb	-		GMS006		Pillen et al. 2003

Appendix 5 (continued)

Trait[1)]	Chr[2)]	Range[3)]	Marker interval[4)]	QTL[5)]	P/N[6)]	$BIN_{[M]}$[7)]	QTL/Cand Gene[8)]	$BIN_{[R]}$[9)]	Reference
HEA	7H	62	HvSS1	QheaT101-7Hb	-	1	HvSS1		Pillen et al. 2003
							eps7S	1	Laurie et al. 1995
	7H	146	BMS64	QheaC101-7Hc	+		BMS64		Pillen et al. 2004
	7H	178	HVM49	QheaC101-7Hd	+	12	MWG539-MWG929	11-12	Backes et al. 1995
HEI	1H	63-75	HvALAAT-GBM1004	QheiT101-1Hb	-	5-7	ABG452	7-8	Marquez-Cedillo et al. 2001
							HVALAAT		Pillen et al. 2004
							Bmag0211		Pillen et al. 2004
	1H	144	GBMS012	QheiC101-1Hb	+	13-14	MWG844c	12-14	Zhu et al. 1999
							MWG911-MWG514	13-14	Backes et al. 1995
	1H	144	GBMS012	QheiT101-1Hc	+	13-14	MWG844c	12-14	Zhu et al. 1999
							MWG911-MWG514	13-14	Backes et al. 1995
	2H	17-27	HVM36-GBM1035	QheiC101-2Ha	+	3-4	Rbcs-ABG2	3-4	Hayes et al. 1993
	2H	17-27	HVM36-GBM1035	QheiT101-2H	+	3-5	Rbcs-ABG2	3-4	Hayes et al. 1994
	2H	50	GBMS002	QheiC101-2Hb	+	4	Rbcs-ABG2	3-4	Hayes et al. 1993
	3H	30	EBmac0705	QheiC101-3Ha	+		EBmac0705		Pillen et al. 2003
	3H	94-100	HVM33-GMS116	QheiC101-3Hb	-	7-8	E45M55-274-E40M32-397	7-8	Qi et al. 1998
	3H	94-110	HVM33-HVM60	QheiT101-3Ha	-	7-8	E45M55-274-E40M32-397	7-8	Qi et al. 1998
	3H	155-190	Bmag0013-Bmac0029	QheiC101-3Hc	-	13-15	***denso***	13-14	Laurie et al. 1995
	3H	155-165	Bmag0013-HVM62	QheiT101-3Hb	-	13-15	***denso***	13-14	Laurie et al. 1995
	4H	14	HVM40	QheiT101-4Ha	°	2-3	int-c-Phy2	2-4	Marquez-Cedillo et al. 2001
	4H	44	HvPAZXG	QheiC101-4Ha	°	7-8	HVM68-ABG472	6-8	Marquez-Cedillo et al. 2001
	4H	162-190	GBM1048-HvBAMY	QheiC101-4Hc	+	10-13	Bmy1	12-13	Hackett et al. 1992
							HvBAMY		Pillen et al. 2003
							HvBAMY		Pillen et al. 2004
	4H	180-190	HvJASIP-HvBAMY	QheiT101-4Hb	+	13	Bmy1	12-13	Hackett et al. 1992
							HvBAMY		Pillen et al. 2003
							HvBAMY		Pillen et al. 2004
	5H	24-53	Bmag0337-Bmag0357	QheiT101-5H	+	6	MWG635d-ABC302a	4-8	Marquez-Cedillo et al. 2001
							MWG2227b-ABC302	4-8	de la Pena et al. 1999
	6H	96	GMS006	QheiC101-6H	+		GMS006		Pillen et al. 2003

Appendix 5 (continued)

Trait[1)]	Chr[2)]	Range[3)]	Marker interval[4)]	QTL[5)]	P/N[6)]	$BIN_{[M]}$[7)]	QTL/Cand Gene[8)]	$BIN_{[R]}$[9)]	Reference
LOH	1H	63-75	HvALAAT-GBM1004	QlohT101-1Ha	-	5-7	HVALAAT Bmag0211		Pillen et al. 2004 Pillen et al. 2004
	4H	37-57	EBmac0906-GMS089	QlohC101-4Ha	-	6-7	dMlg-ABG472	6-8	Tinker et al. 1996
	4H	31-44	HvKNOX3-HvPAZXG	QlohT101-4Ha	°	7	dMlg-ABG472	6-8	Tinker et al. 1996
	6H	96-108	GMS006-HvPAF93	QlohC101-6Hb	-	6-7	MWG820c-MWG820b	6-8	Backes et al. 1995
	6H	145-155	GBM1022-GBM1005	QlohC101-6Hc	-	9	ksuD17-Nar7	7-9	Hayes et al. 1993
NB	4H	37-57	EBmac0906-GMS089	QnbC101-4Ha	°	6-7	ABG3-MWG484		Steffenson et al. 1996.
	5H	75	GBM1041	QnbC101-5Ha	°	8-10	MWG914	10	Spaner et al. 1998
	6H	96-112	GMS006-Bmag0613	QnbC101-6Hc	°	6-7	***R***	6-7	Manninen et al. 2000
	6H	96-103	GMS006-HVM14	QnbT101-6Hb	°	6-7	***R***	6-7	Manninen et al. 2000
NPB	4H	132	EBmac0679	QnpbC101-4H	-		EBmac0635		Behn et al. 2004
PM	1H	14-28	GMS021-GBM1007	QpmC101-1H	-	5-7	***Mla***	5-7	Schwarz et al. 1999
	7H	59-77	AF022725A-GBMS035	QpmC101-7H	+	5	CDO36	5	Heun et al. 1992.
RH	6H	14	GBM1021	QrhC101-6Ha	°	5-7	***Rrs13***	3-6	Abbott et al 1995
TGW	1H	63	HvALAAT	QtgwC101-1Ha	-	7	HVALAAT		Pillen et al. 2003
	1H	63	HvALAAT	QtgwT101-1Hb	-	7	HVALAAT		Pillen et al. 2003
	3H	155	Bmag0013	QtgwC101-3Hc	+	13-15	Bmag0013		Pillen et al. 2003
	6H	135-145	GBM1008-GBM1022	QtgwC101-6Hc	-	9	WG282	9	Thomas et al. 1995.
YLD	2H	143-146	HVM54	QyldT101-2H	-	13	HVM54 EBmac0415		Pillen et al. 2004 Pillen et al. 2004
	4H	37-57	EBmac0906-GMS089	QyldC101-4Ha	-	6	ABG003a-MWG058 WG464-MWG058	5-6 6	Marquez-Cedillo et al. 2001 Kjaer and Jensen 1996
	4H	162	GBM1048	QyldC101-4Hb	-	10-13	ABG472-ABG397	8-11	Hayes et al. 1993
	4H	162	GBM1048	QyldT101-4Hb	°	10-13	ABG472-ABG397	8-11	Hayes et al. 1993
	5H	114	HvLOXC	QyldC101-5Hd	-		HvLOXC		Pillen et al. 2003
	5H	114	HvLOXC	QyldT101-5H	-		HvLOXC		Pillen et al. 2003
	6H	96-103	GMS006-HVM14	QyldC101-6Hb	-	6-7	ABG458-ksuA3D	6-8	Hayes et al. 1993
	6H	135-155	GBM1008-GBM1005	QyldC101-6Hd	°	9	Amy1	9	Bezant et al. 1997

[1)] Trait abbreviations: BS, Breaking of stem; COD, Cold damage; HEA, Days until heading; HEI, Plant Height; LOH, Lodging at harvest; NB, net blotch; NPB, Non-parasitic browning; PM, Powdery mildew; RH, leaf scald; TGW, Thousand-grain weight; YLD, Yield. [2)] Chromosomal assignment of SSR. [3)] Position of marker in cM derived from von Koff et al. (2004). [4)] Marker exhibiting significant QTL effects. [5)] Name of **QTLs** contains the prefix 'Q' (QTL), abbreviation of trait, abbreviation of population, chromosomal location and the ordinal number of QTLs on chromosome. [6)] Effects of QTLs; see Table 17. [7)] $BIN_{[M]}$: The assignment of SSR markers to BIN groups is based on mapping results of Dr. A. Kleinhofs in Steptoe×Morex. [8)] Marker or marker interval where the QTL was detected in other QTL studies or candidate gene. [9)] $BIN_{[R]}$: The BINgroup of a refference marker or marker interval which is identical or, at least overlapping with $BIN_{[M]}$.

Appendix 6: QTL effects detected as significant crossover interaction in different environments in C101

Trait[1)]	QTL[2)]	Repr. Marker[3)]	Chr[4)]	Range[5)] (in cM)	RP[*Hsp*][6)] (in %)						
					D03l	D03k	G03l	G03k	I03l	L03l	E03k
COD	QcodC101-1Hb	Bmag0579	1H	175	-24.14	-20.59	-7.68	-1.05	0.68	3.25	4.91
	QcodC101-2Hc	EBmac0415	2H	139-146	-29.70	-22.72	-15.42	-11.87	-6.61	0.18	6.36
	QcodC101-5Ha	HVLEU	5H	53	-13.99	-34.75	-16.50	1.15	-9.34	0.82	-2.62
	QcodC101-7Ha	Bmag0321	7H	93-120	44.74	38.33	20.20	11.08	12.77	4.64	-1.51
	QcodC101-7Hc	EBmac0755	7H	166	-34.25	-32.69	-17.87	7.10	8.97	-0.72	-7.73

Trait[1)]	QTL[2)]	Repr. Marker[3)]	Chr[4)]	Range[5)] (in cM)	RP[*Hsp*][6)] (in %)										
					D03	D04	G03	G04a	G04b	I03	I04	L03	L04	E03	E04
BS	QbsC101-1Ha	GBM1042	1H	39	12.07	-8.98	12.71			22.48	10.73				
	QbsC101-1Hb	GBM1004	1H	68-75	18.33	-2.47	26.06			19.94	51.40				
	QbsC101-1Hc	GMS114	1H	105-115	8.29	3.77	12.46			7.06	62.08				
	QbsC101-2Ha	EBmac0684	2H	80	15.13	-40.80	-6.66			24.53	-25.51				
	QbsC101-2Hb	GBM1047	2H	150	-8.97	14.13	14.40			13.44	52.99				
	QbsC101-4H	HvJASIP	4H	162-190	-0.90	10.08	34.84			20.04	95.90				
	QbsC101-5Ha	GBM1026	5H	24-48	5.06	18.03	-7.90			10.81	46.90				
	QbsC101-5Hb	GBM1041	5H	75	1.29	17.68	-5.62			2.06	63.91				
	QbsC101-6Ha	Bmag0613	6H	112	13.83	-2.45	29.39			-16.83	-24.19				
	QbsC101-6Hb	GBM1008	6H	135	6.22	-30.48	-10.27			-20.89	-27.74				
	QbsC101-7Ha	AF022725A	7H	59	-2.85	5.84	-4.41			-11.86	32.31				
	QbsC101-7Hb	HvSS1	7H	62	5.69	16.53	-12.00			-19.58	9.63				
	QbsC101-7Hc	Bmag0321	7H	77-100	16.27	22.15	-6.36			-7.27	4.52				
	QbsC101-7Hd	EBmac0755	7H	166	-8.92	15.81	-22.40			-32.20	18.99				
	QbsC101-7He	HVM49	7H	178	-17.25	17.54	-34.95			-18.70	77.04				
BSP	QbspC101-1Ha	HvALAAT	1H	50-75	-11.49	-4.18	3.32			18.64	29.58				
	QbspC101-1Hb	GMS114	1H	115	-12.78	-9.49	-5.95			11.53	16.98				
	QbspC101-5Ha	GBM1041	5H	75	-11.56	1.65	-0.83			2.39	38.05				
	QbspC101-6H	GMS006	6H	96-103	18.27	12.40	-4.58			-2.30	-12.21				

Appendix 6 (continued)

Trait[1)]	QTL[2)]	Repr. Marker[3)]	Chr[4)]	Range[5)] (in cM)	RP[*Hsp*][6)] (in %)										
					D03	D04	G03	G04a	G04b	I03	I04	L03	L04	E03	E04
HEA	QheaC101-1Ha	BMS32	1H	105	-2.45	-3.10	-0.52			-2.01	-2.88		-3.48		
	QheaC101-1Hb	GBMS012	1H	144	-1.47	-1.25	-1.98			-3.73	-1.93		-1.64		
	QheaC101-1Hc	Bmag0579	1H	175	-2.02	-1.79	-2.31			-4.47	-3.26		-2.32		
	QheaC101-2Ha	GBM1035	2H	17-27	-0.08	-1.89	-0.51			-2.56	-4.43		-3.06		
	QheaC101-2Hb	GBMS002	2H	50	1.11	-0.43	-0.24			-1.76	-3.38		-1.76		
	QheaC101-2Hc	GBM1047	2H	139-150	-0.49	-1.13	-1.28			-3.30	-1.45		-1.16		
	QheaC101-3Ha	HvLTPPB	3H	25-30	1.81	-0.30	2.61			1.17	0.95		0.23		
	QheaC101-3Hb	Bmac0209	3H	47-80	-4.34	-5.40	-2.42			-1.85	-11.86		-7.86		
	QheaC101-4Hb	GBM1048	4H	162	-1.84	-2.24	-2.23			-5.20	-2.43		-2.54		
	QheaC101-5Ha	HvLEU	5H	53	-1.51	-0.60	-1.91			-3.01	-2.73		-1.45		
	QheaC101-5Hb	GBM1041	5H	75	-0.48	-2.99	1.07			0.11	-1.28		-1.15		
	QheaC101-5Hc	HvLOXC	5H	114	-0.95	-2.96	0.91			1.66	-3.93		-2.12		
	QheaC101-6Ha	Bmac0316	6H	6	0.78	-1.32	1.02			0.60	-0.31		-0.59		
	QheaC101-6Hb	HVM14	6H	96-103	-0.85	0.18	0.96			2.41	1.27		0.12		
	QheaC101-7Ha	AF022725A	7H	59	0.79	-0.82	-0.23			-1.95	-0.18		-0.35		
	QheaC101-7Hb	Bmag0321	7H	100	0.32	-0.13	0.64			0.39	-0.73		-0.62		
	QheaC101-7Hc	BMS64	7H	146	0.69	0.33	1.05			0.90	-0.28		-0.31		
HEI	QheiC101-1Hb	GBMS012	1H	144	-1.96	-0.34	-3.91			-5.45	-0.91		-1.96		
	QheiC101-1Hc	Bmag0579	1H	175	-2.32	0.39	-1.72			-6.00	0.06		-0.73		
	QheiC101-2Hc	GBM1016	2H	139-146	1.95	3.18	0.82			-1.02	0.36		0.15		
	QheiC101-4Ha	HvPAZXG	4H	44	-2.42	-2.00	3.54			-4.38	3.67		-1.94		
	QheiC101-4Hc	GBM1015	4H	162-190	-3.22	-2.40	-6.59			-5.86	-11.39		-3.50		
	QheiC101-5Ha	Bmag0357	5H	43-48	1.66	1.44	-0.69			1.51	1.99		-0.70		
	QheiC101-5Hb	HvLEU	5H	53	-2.16	-3.54	0.53			-7.11	-1.37		-1.12		
	QheiC101-5Hc	GBM1041	5H	75	2.01	0.75	-2.71			1.89	-0.15		-0.25		
	QheiC101-6H	HVM14	6H	96-103	-2.30	-3.69	-1.29			2.27	-0.16		-0.97		
LOH	QlohC101-1Ha	GBM1004	1H	39-75	15.39	0.41	62.44			37.77	33.31		36.34		
	QlohC101-1Hb	BMS32	1H	105-115	13.25	3.42	75.93			51.85	26.05		36.74		
	QlohC101-1Hc	GBMS012	1H	144	13.69	2.32	55.87			38.57	37.64		71.02		
	QlohC101-1Hd	Bmag0579	1H	175	-7.12	-3.55	22.48			3.62	29.71		61.90		
	QlohC101-3H	HVM60	3H	100-110	-16.07	-0.46	-61.05			-7.70	-31.88		-36.48		
	QlohC101-4Ha	HVM13	4H	37-57	6.33	3.22	78.73			114.88	64.56		93.38		
	QlohC101-4Hb	EBmac0679	4H	132	-24.20	-6.34	119.46			140.17	-31.45		90.09		

Appendix 6 (continued)

Trait[1)]	QTL[2)]	Repr. Marker[3)]	Chr[4)]	Range[5)] (in cM)	RP[*Hsp*][6)] (in %)										
					D03	D04	G03	G04a	G04b	I03	I04	L03	L04	E03	E04
	QlohC101-4Hc	GBM1048	4H	162	-16.21	-1.13	40.82			11.73	-33.51		11.28		
	QlohC101-5Ha	GBM1026	5H	24-53	33.57	6.02	56.23			-3.64	40.41		48.58		
	QlohC101-5Hb	GBM1041	5H	75	17.07	3.22	46.80			4.39	11.51		21.54		
	QlohC101-6Ha	GBM1021	6H	40	5.58	2.45	33.45			55.34	-3.48		30.26		
	QlohC101-6Hb	HVM14	6H	96-108	3.05	-2.99	25.73			100.88	-15.45		4.72		
	QlohC101-6Hc	GBM1022	6H	145-155	6.51	3.50	41.26			77.22	39.03		42.28		
	QlohC101-7Ha	GMS046	7H	120	0.30	-2.01	-28.88			-17.32	9.85		17.80		
	QlohC101-7Hb	BMS64	7H	146-152	2.80	-3.70	-26.49			-26.12	12.58		6.92		
	QlohC101-7Hc	HVM49	7H	178	-1.58	1.09	69.84			-29.64	21.63		23.87		
LR	QlrC101-1Hb	Bmag0211	1H	68-75										35.16	-4.37
	QlrC101-1Hc	GMS114	1H	105-115										50.01	2.84
NB	QnbC101-1Ha	GBM1007	1H	14-75	-1.86	-1.32	-11.25	-13.38					1.89	-5.08	
	QnbC101-1Hb	BMS32	1H	105-115	7.48	-7.68	-3.95	-2.31					-1.60	33.04	
	QnbC101-1Hc	Bmag0579	1H	175	8.99	0.36	5.61	-3.22					-1.14	31.12	
	QnbC101-2H	GBM1016	2H	139	2.48	1.59	-2.95	-10.17					-0.66	1.73	
	QnbC101-3H	HVM60	3H	110	-9.30	8.71	-4.32	-2.61					5.06	-6.07	
	QnbC101-4Ha	HvPAZXG	4H	37-57	-2.40	-2.12	-19.55	-22.34					2.64	-10.58	
	QnbC101-4Hb	GBM1044	4H	95	6.72	-2.24	10.82	15.99					48.06	-23.14	
	QnbC101-5Ha	GBM1041	5H	75	-4.19	0.89	2.49	8.48					5.27	8.03	
	QnbC101-5Hb	Bmag0222	5H	150-162	5.40	-1.43	3.31	9.91					-9.56	-8.05	
	QnbC101-5Hc	GMS001	5H	187	0.49	2.00	6.71	12.76					2.44	-10.16	
	QnbC101-6Ha	Bmac0316	6H	6	12.30	9.36	12.30	17.67					2.27	-0.62	
	QnbC101-6Hb	GBM1021	6H	40	-3.92	-14.43	-16.97	-17.25					-6.22	-9.04	
	QnbC101-6Hc	HVM14	6H	96-112	-26.64	-15.25	-34.36	-31.98					-6.68	7.39	
	QnbC101-6Hd	GBM1022	6H	135-155	-14.28	-7.26	-22.35	-26.55					-6.12	-9.51	
	QnbC101-7Ha	HvSS1	7H	59-77	3.79	-10.47	-0.76	-0.62					2.59	13.91	
	QnbC101-7Hb	EBmac0755	7H	166	-15.92	-14.87	-2.51	-10.11					4.41	12.45	
NPB	QnpbC101-1Ha	GBM1007	1H	28	-9.46		6.29	-4.93	3.01				14.91	-15.91	
	QnpbC101-1Hb	GBMS012	1H	144	20.41		7.91	1.77	-0.48				1.99	-12.23	
	QnpbC101-2Ha	GBM1035	2H	17-27	3.35		28.60	30.24	19.49				21.08	93.25	
	QnpbC101-3Ha	HvLTPPB	3H	25-30	17.78		28.74	29.70	18.42				26.04	134.25	
	QnpbC101-3Hb	GBM1059	3H	161-169	27.23		14.18	17.90	18.89				11.36	55.02	
	QnpbC101-3Hc	Bmac0029	3H	190	25.84		5.02	18.67	15.59				6.48	47.99	

Appendix 6 (continued)

Trait[1]	QTL[2]	Repr. Marker[3]	Chr[4]	Range[5] (in cM)	RP[*Hsp*][6] (in %)										
					D03	D04	G03	G04a	G04b	I03	I04	L03	L04	E03	E04
	QnpbC101-4H	EBmac0679	4H	132	-0.59		8.14	47.00	20.78				36.52	128.09	
	QnpbC101-5Ha	HvHEMH1	5H	24-53	-1.17		-9.58	-12.67	-14.32				-13.26	-43.60	
	QnpbC101-5Hb	Bmag0222	5H	150-162	-9.74		-5.76	1.08	9.19				-0.25	44.77	
	QnpbC101-6Ha	Bmac0316	6H	6	5.62		19.42	19.41	13.28				9.73	89.51	
	QnpbC101-6Hb	HVM14	6H	96-112	-15.93		10.15	-17.43	-13.42				-2.61	-41.14	
	QnpbC101-6Hc	GBM1008	6H	135-145	-20.85		10.25	-7.51	-3.13				-0.02	-46.18	
	QnpbC101-6Hd	GBM1005	6H	155	-14.40		22.49	-1.79	5.02				8.31	-21.34	
	QnpbC101-7Hb	GMS046	7H	120	-9.23		-8.51	-2.13	-0.61				-10.38	13.80	
	QnpbC101-7Hc	BMS64	7H	146	-8.15		-5.27	-0.49	1.00				-3.18	26.49	
PM	QpmC101-2H	GBM1047	2H	139-150		-44.10	-34.45	-4.70	-7.89				-13.56		
	QpmC101-3H	GMS116	3H	94-110		-19.63	-33.72	-2.69	-3.68				-2.63		
	QpmC101-5Hc	GBM1041	5H	75		-22.15	12.05	-11.84	-6.01				-2.99		
	QpmC101-5Hd	HvLOXC	5H	114		-24.12	31.22	-6.34	-2.18				8.04		
	QpmC101-6Ha	GBM1021	6H	40		39.29	1.36	16.31	13.60				6.72		
	QpmC101-7H	AF022725A	7H	59-77		-12.05	-33.49	-5.32	-8.56				-10.91		
RH	QrhC101-2Ha	GBM1035	2H	17-27	-9.80	-12.50	16.17	0.27	-7.92				-27.30		
	QrhC101-2Hb	GBMS002	2H	50	-17.09	-20.29	15.90	-1.90	-2.20				-26.29		
	QrhC101-6Ha	GBM1021	6H	40	14.26	-6.83	-3.57	-5.78	4.46				-28.83		
	QrhC101-6Hb	Bmag0613	6H	112	9.63	-8.93	-3.78	2.22	6.14				-29.64		
	QrhC101-6Hc	GBM1008	6H	135	14.11	-24.84	3.81	-1.24	8.03				-21.09		
TGW	QtgwC101-1Ha	GBM1004	1H	28-75	-0.67		-6.23			-8.28	-6.89		-6.70		
	QtgwC101-1Hb	GMS114	1H	105-115	0.31		-4.08			-6.65	-6.34		-6.92		
	QtgwC101-5Ha	GBM1041	5H	75	3.36		1.24			0.65	-3.34		-2.71		
	QtgwC101-5Hb	MGB318	5H	150-162	0.39		-2.27			-1.69	-10.86		-1.24		
	QtgwC101-5Hc	GMS001	5H	187	-1.33		-0.51			0.72	-15.55		1.13		
	QtgwC101-6Ha	GBM1021	6H	40	-0.66		-7.07			-3.60	-1.85		-7.59		
	QtgwC101-6Hb	HVM14	6H	96-103	1.45		-7.18			-5.82	-0.87		-6.86		
	QtgwC101-6Hc	GBM1008	6H	135-145	2.81		-5.58			-5.12	-0.70		-5.36		

Appedix 6 (continued)

Trait[1)]	QTL[2)]	Repr. Marker[3)]	Chr[4)]	Range[5)] (in cM)	RP[*Hsp*][6)] (in %)										
					D03	D04	G03	G04a	G04b	I03	I04	L03	L04	E03	E04
YLD	QyldC101-3H	EBmac0705	3H	25-30	-12.97		-9.04			-10.38	-1.80		-1.53		
	QyldC101-4Ha	HvPAZXG	4H	37-57	0.52		-7.24			5.00	-9.50		-13.65		
	QyldC101-5Ha	Bmag0337	5H	24-48	-7.15		-8.88			-4.50	-0.23		-9.33		
	QyldC101-5Hb	HvLEU	5H	53	7.11		-0.59			1.42	-4.04		-1.27		
	QyldC101-5Hc	GBM1041	5H	75	-12.35		-12.09			-9.62	-1.85		-6.34		
	QyldC101-5Hd	HvLOXC	5H	114	-15.16		-4.48			-12.45	-0.33		1.96		
	QyldC101-6Ha	Bmac0316	6H	6	-10.07		-8.98			-11.67	-1.85		-0.91		
	QyldC101-6Hb	HVM14	6H	96-103	0.43		-0.51			6.34	-1.45		-6.01		
	QyldC101-6Hc	HvPAF93	6H	108	4.98		5.78			7.12	-0.83		-2.82		
	QyldC101-6Hd	GBM1005	6H	135-155	8.95		8.65			7.08	-5.23		-4.01		

[1)] Trait abbreviations: BS, Breaking of stem; BSP, Bending of spike; COD, Cold damage; HEA, Days until heading; HEI, Plant Height; LOH: Lodging at harvest; LR: Leaf rust; NB: net blotch; NPB: Non-parasitic browning; PM: Powdery mildew; RH: leaf scald; TGW: Thousand-grain weight; YLD: Yield. [2)] Name of **QTLs** contains the prefix 'Q' (QTL), abbreviation of trait, abbreviation of population, chromosomal location and the ordinal number of QTLs on chromosome. [3)] Representive marker, see Table 17. [4)] Chromosomal assignment of SSR. [5)] Position of marker in cM derived from von Koff et al. (2004). [6)] Relative performance of *Hsp* genotype in each environment: RP[*Hsp*] = ([*Hsp*]-[*Hv*]) x 100 / [*Hv*], where [*Hsp*] and [*Hv*] are the least square means of the homozygous *Hsp* and *Hv* genotypes, respectively, calculated in each environment tested. if there were more than one significant marker effect in the QTL interval, then the highest RP[*Hsp*] was taken.

Appendix 7: QTL effects detected as significant crossover interaction in different environments in T101

Trait[1)]	QTL[2)]	Marker Interval[4)]	Chr[3)]	Range[5)] (in cM)	RP[*Hsp*][8)] (in %)							
					D03	D04	G03	I03	I04	L04	E03	E04
BS	QbsT101-4Ha	HVM40	4H	14	-8,48	33,37	-8,87	-26,73	30,85			
	QbsT101-4Hb	HvPAZXG	4H	42-57	-39,22	-7,79	2,75	-35,89	-0,44			
	QbsT101-4Hc	HDAMYB	4H	190	33,03	-12,79	-3,54	101,86	51,54			
	QbsT101-5H	Bmag0337	5H	43	26,46	-6,81	-10,03	68,25	49,63			
	QbsT101-6Ha	GBM1021	6H	40	14,84	47,74	-13,08	33,57	34,96			
	QbsT101-6Hb	GMS006	6H	96	20,28	38,05	-8,78	21,81	29,13			
BSP	QbspT101-1H	GBM1002	1H	80	0,74	11,16	-12,90	-42,02	67,58			
	QbspT101-4Ha	HVM40	4H	14	3,97	-14,56	0,25	50,48	43,86			
	QbspT101-4Hc	GBM1048	4H	162	-8,78	33,32	-5,90	-12,50	-31,47			
	QbspT101-6H	HVM14	6H	103	-7,99	-16,24	16,92	23,85	-21,55			

Appendix 7 (continued)

Trait[1]	**QTL[2]**	**Marker Interval[4]**	**Chr[3]**	**Range[5] (in cM)**	**RP[*Hsp*][8] (in %)**							
					D03k	**D03l**	**G03k**	**G03l**	**I03l**	**E03k**		
COD	QcodT101-1Ha	GBM1042	1H	39	-6,00	5,28	-31,30	22,48	37,71	5,78		
	QcodT101-1Hb	GBM1002	1H	63-80	103,99	108,93	45,43	44,02	14,56	5,00		
	QcodT101-1Hc	BMS32	1H	105	0,93	5,00	-15,90	13,28	30,53	6,35		
	QcodT101-1Hd	GBMS012	1H	144	86,47	82,66	36,67	28,08	-0,02	3,66		
	QcodT101-2H	GBM1035	2H	27	69,71	66,95	-5,54	57,99	50,56	15,55		
	QcodT101-3H	HVM33	3H	94-110	44,88	61,79	-36,74	24,10	35,13	8,18		
	QcodT101-4H	GMS089	4H	37-57	-40,61	-50,89	8,51	-31,77	-10,14	3,67		
	QcodT101-6H	GBM1021	6H	40	47,37	46,80	22,64	20,21	10,53	-6,26		
					D03	**D04**	**G03**	**I03**	**I04**	**L04**	**E03**	**E04**
EAR	QearT101-5H	Bmac0163	5H	24	-13,92	10,46						
HEA	QheaT101-1Hc	GBM1002	1H	80	-6,09	-6,09	-0,96	-2,63	-3,44	-4,21		
	QheaT101-1Hd	GBMS012	1H	144	-3,94	-6,64	-1,16	-2,09	-2,14	-3,10		
	QheaT101-5H	GBM1041	5H	75	0,15	-5,34	0,60	1,10	-1,01	-0,96		
	QheaT101-7Hb	AF022725A	7H	59-77	1,20	3,24	-2,64	-1,17	1,16	0,13		
	QheaT101-7Hc	BMS64	7H	146	-1,24	-6,54	-0,45	-0,48	-1,29	-1,70		
HEI	QheiT101-1Hb	HvALAAT	1H	63-75	8,95	9,81	5,87	11,99	6,47	3,49		
	QheiT101-1Hc	GBM1002	1H	80	-11,37	-7,71	-8,84	-6,47	-3,45	-4,39		
	QheiT101-1Hd	GMS114	1H	105-115	7,68	7,78	4,29	8,31	7,25	4,27		
	QheiT101-1He	GBMS012	1H	144	-9,20	-6,85	-6,62	-6,23	-3,68	-4,28		
	QheiT101-2H	HVM36	2H	17-27	9,50	9,11	3,57	2,30	8,34	2,26		
	QheiT101-3Ha	HVM60	3H	94-110	9,55	12,25	4,49	8,22	7,98	7,54		
	QheiT101-3Hb	Bmag0013	3H	155-165	11,20	10,21	6,61	7,64	9,19	3,33		
	QheiT101-3Hc	Bmac0029	3H	190	6,22	4,53	-1,17	6,34	2,67	1,87		
	QheiT101-4Ha	HVM40	4H	14	-4,71	-2,30	-1,14	1,57	0,53	-1,13		
	QheiT101-4Hb	HvBAMY	4H	180-190	-4,19	-1,81	-10,14	-2,00	-12,84	-5,75		
	QheiT101-5H	HvHEMH1	5H	24-53	-5,69	-5,17	-4,34	-1,75	-3,77	-4,01		
	QheiT101-6Ha	GBM1021	6H	40	-7,89	-7,26	-6,23	-3,48	-3,52	-4,09		
	QheiT101-6Hb	Bmag0613	6H	96-112	-3,93	-5,80	-9,75	-0,77	-5,31	-4,27		
HI	QhiT101-1H	GBM1002	1H	80	7,15	-0,58						
	QhiT101-5H	HK03N02R	5H	150	-12,62	4,03						
LOH	QlohT101-4Ha	HvKNOX3	4H	31-44	-1,62	-19,30	12,60	-21,96	-1,67	-40,06		
	QlohT101-4HB	HDAMYB	4H	190	10,74	28,84	-22,23	2,10	-42,34	0,48		
LR	QlrT101-4H	HvBAMY	4H	180-190							77,95	-11,63

Appendix 7 (continued)

Trait[1]	**QTL**[2]	**Marker Interval**[4]	**Chr**[3]	**Range**[5] **(in cM)**	**RP[*Hsp*]**[8] **(in %)**							
					D03	**D04**	**G03**	**I03**	**I04**	**L04**	**E03**	**E04**
MAS	QmasT101-3H	HVM60	3H	110	38,89	-18,80						
	QmasT101-3H	HVM62	3H	165	12,20	-12,90						
NB	QnbT101-1H	GBM1002	1H	80	-9,72	9,06	-31,92			-1,27	-3,57	
	QnbT101-5H	HvLOXC	5H	114	-8,84	2,06	102,86			-1,00	76,79	
	QnbT101-6Ha	GBM1021	6H	40	-11,72	8,89	-41,04			-1,18	21,94	
	QnbT101-6Hb	GMS006	6H	96-103	-1,70	2,67	-39,52			-1,28	14,60	
	QnbT101-7H	HVM49	7H	178	3,56	2,15	71,05			-1,04	-14,41	
NPB	QnpbT101-1Ha	GBM1002	1H	80	44,98		-2,26			13,00	-9,25	
	QnpbT101-1Hb	BMS32	1H	105-115	-23,93		13,61			3,53	38,24	
	QnpbT101-1Hc	Bmag0579	1H	175	37,05		-31,78			7,63	2,11	
	QnpbT101-3Ha	HVM33	3H	94-100	-52,99		24,80			-11,11	23,39	
	QnpbT101-3Hb	HVM62	3H	161-165	-27,23		0,13			9,58	51,45	
	QnpbT101-3Hc	Bmac0029	3H	190	-33,85		26,73			3,67	52,43	
	QnpbT101-6Ha	GBM1021	6H	40	32,63		-15,59			2,35	2,44	
	QnpbT101-6Hb	GMS006	6H	96	8,79		-23,95			3,30	-19,15	
PM	QpmT101-3H	GMS116	3H	100		57,02	-5,02			-5,02	29,92	
RH	QrhT101-1H	Bmag0579	1H	175	11,98	4,80	36,69			-7,20		
	QrhT101-4H	HVM67	4H	180-190	106,75	13,39	12,84			45,44		
TGW	QtgwT101-1Hb	GBM1004	1H	63-80	1,07	-6,19	-11,08	-7,54	-7,76	-5,88		
	QtgwT101-4Ha	HvKNOX3	4H	31-55	-2,46	-8,44	-8,52	-2,64	-9,32	-0,35		
	QtgwT101-4Hb	GBM1048	4H	162	-9,05	-15,77	-6,30	-4,99	-7,06	-0,45		
	QtgwT101-6H	Bmag0613	6H	96-112	2,07	-6,05	-7,83	-4,46	-7,78	-9,27		
YLD	QyldT101-1Ha	HvALAAT	1H	63-80	-5,51	-5,61	-11,92	-6,12	0,49	-17,42		
	QyldT101-2H	HVM54	2H	143-146	-6,41	-2,19	-4,08	-3,59	-12,02	-3,90		
	QyldT101-4Ha	HvKNOX3	4H	14-31	-8,69	-6,16	-18,69	-6,55	-8,36	-2,27		
	QyldT101-4Hb	GBM1048	4H	162	1,97	-0,45	-5,38	-2,64	-4,80	11,48		
	QyldT101-5H	HvLOXC	5H	114	-10,10	3,16	-12,79	-7,64	-24,42	13,14		
	QyldT101-6Hb	GMS006	6H	96	-7,10	-4,77	-8,98	-8,63	1,40	-10,53		

[1] Trait abbreviations: BS, Breaking of stem; BSP, Bending of spike; COD, Cold damage; HEA, Days until heading; HEI, Plant Height; LOH, Lodging at harvest; LR, Leaf rust; NB, net blotch; NPB, Non-parasitic browning; PM, Powdery mildew; RH, leaf scald; TGW, Thousand-grain weight; YLD, Yield. [2] Name of **QTLs** contains the prefix 'Q' (QTL), abbreviation of trait, abbreviation of population, chromosomal location and the ordinal number of QTLs on chromosome. [3] Representive marker, see Table 17. [4] Chromosomal assignment of SSR. [5] Position of marker in cM derived from von Koff et al. (2004). [6] Relative performance of *Hsp* genotype in each environment: RP[*Hsp*] = ([*Hsp*]-[*Hv*]) x 100 / [*Hv*], where [*Hsp*] and [*Hv*] are the least square means of the homozygous *Hsp* and *Hv* genotypes, respectively, calculated in each environment tested.

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10.Abbreviations

Abbreviation	Explanation
AB-QTL strategy	Advanced backcross quantitative trait locus strategy
AFLP	Amplified fragment length polymorphism
BAC	Bacterial artificial chromosome
ANOVA	Analysis of variance
BC_i	i-th backcross
bp	base pairs
cDNA	Complementary DNA
CIM	Composite interval mapping
cM	CentiMorgan
DH	Doubled haploid
DNA	Desoxyribonucleic acid
EST	Expressed sequence tag
F_i	i-th filial generation
GLM	General linear mosel
Hsp	*Hordeum vulgare* ssp. *spontaneum* (exotic genotype)
Hv	*Hordeum vulgare* ssp. *vulgare* (elite genotype)
kb	Kilobase pairs
MAS	Marker assisted selection
mRNA	Messenger RNA
NIL	Near-isogenic line
OWB	Oregon Wolfe Barley
PCR	Polymerase chain reaction
QTL	Quantitative trait locus
RAPD	Random amplified polymorphic DNA
RFLP	Restriction fragment length polymorphism
RI	Recombinant inbred
RNA	Ribonucleic acid
SIM	Simple interval mapping
SNP	Single nucleotide polymorphism
SSR	Simple sequence repeats
YAC	Yeast artificial chromosome

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