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Quantitative trait loci analysis in spring wheat comparing two advanced backcross populations derived from an exotic wheat accession

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Dankbarkeit und Weizen gedeihen nur auf gutem Boden.

(Deutsches Sprichwort)

Abstract

The objective of the present study was to identify and localise favourable, exotic QTL alleles for the improvement of 16 quantitative agronomic traits, quality parameters and disease resistances in elite wheat cultivars. Therefore, two advanced backcross populations, T84 and D84, in generation BC_2F_4 were derived from crosses of two German spring wheat cultivars (Triso and Devon) and one synthetic hexaploid wheat accession (Syn-84). The revealing populations, counting 223 (T84) and 176 (D84) BC_2F_4 lines, were phenotyped in field plots at four different locations in Germany under two different nitrogen supplies (high and low) in seasons 2004 and 2005. In addition, the populations were genotyped with 94 (T84) and 106 (D84) SSR markers, respectively. Phenotype and genotype data were merged to different QTL mapping methods with a significance threshold of $P = 0.01$ including marker as fixed effect, the environment, line nested in marker genotype, marker×environment and marker×nitrogen interaction effects as random effects. Multi-environmental QTL detections were considered in three-way (high N-level) and four-way (high and low N-levels) models determined through ANOVA and REML methods in SAS programme (SAS Institute 2003). In high N-level, 105 (T84) and 78 (D84) QTLs were detected as marker main effects and marker×environment interaction effects using ANOVA method. Through REML method 10 (T84) and 4 (D84) QTLs as marker main effects were identified. In high and low N-levels, 11 (T84) and 13 (D84) N-responsive QTLs and each 48 (T84 and D84) QTLs as marker main effects were ascertained using ANOVA method. Five (T84) and 4 (D84) QTLs as marker main effects were detected using REML method.

A comparison between QTL mapping methods revealed that REML methods validated QTLs with highest F-value computed by ANOVA methods. Moreover, no significant interaction effects were permitted using REML methods. It might be postulated that non validated QTLs, which have been detected only by the ANOVA analysis, were either false positive or small QTLs that were not robust enough through the stringent REML methods. The stringent REML methods computed with three-way and four-way models revealed six (T84) and one (D84) QTLs associated with exotic alleles improving traits of interest in regard to breeding efforts. Exotic alleles reduced, for example, sensitivity to powdery mildew by 34.7% at QTL *QPm.T84-7D*, on chromosome arm 7DL in population T84. So far, this locus associated with resistance to powdery mildew was not published in QTL studies. *QPm.T84-7D* may be associated with a new resistance to powdery mildew conducted by *Aegilops tauschii*. The second population D84 validated the new QTL *QPm.T84-7D* where identical exotic alleles reduced sensitivity to powdery mildew by 27.5% ($P = 0.037$). In population T84, BC_2F_4 lines were selected, which carried favourable exotic QTL alleles in least one introgression. For days until heading, plant height and thousand grain weight eight, one and four BC_2F_4 lines were selected, which significantly improved the trait performance compared to the recurrent parent. The results of the current study prove that exotic alleles derived from synthetic hexaploid wheat can improve quantitative traits, as agronomic traits and disease resistances, in elite wheat varieties across multi-environments and two different genetic backgrounds.

Abstract (in German)

Das Ziel der vorliegenden Arbeit ist die Bestimmung und Lokalisierung von exotischen QTL-Allelen zur Verbesserung von insgesamt 16 quantitativen agronomischen Merkmalen, Qualitätsparametern und Krankheitsresistenzen in Kulturweizen. Dafür wurden zwei Rückkreuzungspopulationen, T84 und D84, in der BC_2F_4-Generation aus zwei deutschen Sommerweizensorten (Triso und Devon) mit einer synthetischen, hexaploiden Weizenakzession (Syn-84) erzeugt. Die daraus resultierenden Populationen, bestehend aus 223 (T84) und 176 (D84) BC_2F_4-Linien, wurden in den Jahren 2004 und 2005 in Feldversuchen an vier verschiedenen Standorten in zwei unterschiedlichen Stickstoffdüngungsstufen (hoch und niedrig) phänotypisch bestimmt. Zeitgleich wurden die Populationen mit 94 (T84) und 106 (D84) SSR-Markern genotypisiert. Anschließend wurden mit den phänotypischen und genotyischen Daten verschiedene QTL-Analysen bei einer Irrtumswahrscheinlichkeit von 1% durchgeführt. Die QTL-Analysen wurden in drei-faktorielle (hohe Stickstoffdüngungsstufe) und vier-faktorielle (hohe und niedrige Stickstoffdüngungsstufe) Modelle unterteilt und jeweils mit der ANOVA und der REML Schätzmethode in SAS (SAS Institute 2003) berechnet.

Für die hohe Stickstoffdüngungsstufe wurden insgesamt 105 (T84) und 78 (D84) QTLs als Markerhaupteffekte und Marker×Umwelt Interaktionseffekte mit ANOVA ermittelt. Die REML Schätzmethode ergab 10 (T84) und 4 (D84) QTLs als Markerhaupteffekte. Für die hohe und niedrige Stickstoffstufe wurden 11 (T84) und 13 (D84) stickstoffabhängige QTLs und je 48 (T84 und D84) QTLs als Markerhaupteffekte mit ANOVA ermittelt. Die REML Schätzmethode ergab 5 (T84) und 4 (D84) QTLs als Markerhaupteffekte. Ein Vergleich der Schätzmethoden ergab, dass die REML Schätzungen die QTLs der ANOVA bestätigten, aber zu robusten Ergebnissen führte, indem QTLs mit dem höchsten F-Wert in der ANOVA Methode identifiziert wurden. Zudem wurden keine signifikanten Interaktionseffekte in der REML Schätzung zugelassen. Vermutlich sind die nicht bestätigten QTLs, welche nur mit der ANOVA Methode bestimmt wurden, entweder falsch-positiv oder kleine QTL Effekte, nicht robust genug für die stringentere REML Methode. Die robusten Ergebnisse der drei- und vier-faktoriellen Modelle resultierten in 6 (T84) und 1 (D84) QTLs, an denen exotische Allele eine Verbesserung der Merkmale den Zuchtzielen entsprechend bewirkten. Das exotische Allel reduzierte z.B. die Mehltauanfälligkeit um 34,7% an einem QTL, *QPm.T84-7D*, auf dem Chromosomarm 7DL in der Population T84. Bisher wurde dieser Genort für Resistenz gegen Mehltau nicht in der Literatur beschrieben. Möglicherweise ist *QPm.T84-7D* mit einer neuen Resistenz gegen Mehltau aus *Aegilops tauschii* verbunden. Das neue QTL, *QPm.T84-7D*, wurde in der zweiten Population D84 mit einer Reduktion der Mehltauanfälligkeit um 27,5% ($P = 0{,}037$) bestätigt.

Aus der Population T84 wurden BC_2F_4-Linien selektiert, die vorteilhafte, exotische QTL-Allele an mindestens einer Introgression tragen. Für die Merkmale Blühzeitpunkt (8), Pflanzenhöhe (1) und Tausendkorngewicht (4) wurden BC_2F_4-Linien ermittelt, deren Leistung signifikant über der Leistung des Elters Triso lag. Die Ergebnisse der Arbeit zeigen, dass exotische Allele der synthetischen Weizenakzession quantitative Merkmale in Kulturweizen verbessern können.

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1 Review of literature

Wheat is the most widely grown cereal crop in the world, with an ever increasing demand. It plays a fundamental role in food security. A major challenge is to meet the requirements with new cultivars and improved cropping technologies (FAO 2002). Of the cultivated wheat area, half is located in less developed countries where there have been steady increases in productivity since the green revolution, associated with genetic improvements in yield potential, resistance to diseases, adaptation to abiotic stresses and better agronomic practices (Reynolds and Borlaug 2006a). Nonetheless, challenges to wheat production are still considerable, especially in the developing world, not only because of increased demand but also because of the increased scarcity of water resources (Shiklomanov 2000) ever more unpredictable climates (Parry et al. 2004), increased urbanisation and loss of good quality land away from agriculture (Hobbs et al. 2008) and decreased public sector investment in agriculture and rural affairs (Falcon and Naylor 2005). To meet demand in a sustainable way, more resources are required to breed a new generation of genetically improved cultivars as well as implement resource conserving agronomic management practices (Reynolds et al. 2008). In order to meet growing human needs, wheat grain production must increase at an annual rate of 2%, without any, land to become available for this crop (Gill et al. 2004). Further, new levels of understanding of the structure and function of the wheat genome is required (Gupta et al. 2008). Gupta et al. (2008) have more recently been the focus of intensive breeding efforts, including, over the last few years, the development of molecular markers and the identification of genes responsible for various traits of agronomic interest (Paterson et al. 2005). Breeding efforts in wheat have traditionally proceeded along separate lines and have produced separate communities of breeders. The USA, Europe and Australia have strong wheat communities. The lines of research pursued by each of these communities have been influenced by the particular traits of the crop they are concerned with (Doust 2007).

A popular hypothesis is that an extended period of plant breeding and intensive selection have further reduced genetic diversity among cultivars, narrowing the germplasm base available for future breeding advances (Tanksley and McCouch 1997). Since only a few accessions of tetraploid wheat and *Aegilops tauschii* (*Ae. tauschii*) genotypes were involved in the evolutionary origin of common wheat (*Triticum aestivum*, *T. aestivum*), the genetic diversity of common wheat is largely decreased in comparison with that of its donor species (Zhang et al. 2008b). Numerous genetic variations in the ancestral tetraploid wheat and *Ae. tauschii* are not represented at the hexaploid level due to the evolution bottleneck (Reif et al. 2005). The number of independent crosses between the progenitors of *T. aestivum* is considered limited (Dvorák et al. 1998), resulting presumably in a loss of diversity (Warburton et al. 2006, Reif et al. 2005). Plant breeders increasingly look to donor genes from wild relatives for use in the introduction of novel traits or development of durable pest and disease resistance (Henry 2005a).

1.1 Production and utilisation of wheat

Wheat is grown on 217 million hectares throughout the world with a production of approximately 607 million tons of grain during the season 2007 (FAO 2008a). In Europe, wheat is grown on 57 million hectares and is harvested with 190 million tons grain. In Germany, wheat is the leading crop grown on 3 million hectares and with 21 million tons grain harvested in 2007 (FAO 2008a). The highest average yields are obtained in Western Europe, with more than 8 tons per hectare, in contrast to less than 1 ton per hectare in several countries in Central/West Asia and North Africa. World demand for wheat by 2020 is estimated at 840 to 1,000 million tons. Yield increases are essential to meet this demand, as expanding the wheat area is not feasible (Rajaram and Braun 2008). Wheat is now extensively grown across the temperate, Mediterranean and subtropical parts of both hemispheres of the world, from 67°north in Norway, Finland and Russia, to 45°south in Argentina (Nevo et al. 2002). Conventionally, bread wheat is classified into two types, winter and spring, based on its growth habit. Winter wheat is sown in fall. The plant needs a certain period of cold temperature or vernalisation, for the plant to flowering. Spring wheat is generally sown in the spring or in the fall without experiencing cold temperature during winter. Consequently, wheat can be grown in various climates all over the world and more of the world's farmland is devoted to wheat production than to any other food crop (Briggle and Curtis 1987). Furthermore, wheat is the staple food in ancient and modern world for billions of people, but also for animal feed, occupying 17% of crop acreage worldwide. About 40% of the world population used wheat as feed and provided 20% of total food calories and protein in human nutrition. Wheat is used to produce starch, paste, malt, dextrose, gluten, alcohol and other products (Gupta et al. 2008, Nevo et al. 2002).

Wheat can also be classified into two types (hard and soft bread wheat) based on their grain texture and protein content (Giroux and Morris 1998). Roughly 95% of the wheat crop is hexaploid common wheat, used for making bread, cookies and pastries, whereas the remaining 5% is tetraploid durum wheat, used for making pasta and other semolina products. Einkorn wheat and other hulled wheat, namely emmer and spelt, are today relic crops of minor economic importance (Dubcovsky and Dvorák 2007).

1.2 Taxonomy and morphology of wheat

Wheat is a member of the Gramineae (Poaceae) family of the angiosperms. Poaceae is an attractive group for comparative genomics because they include many important crops with diverse native distributions and at least 35-fold variation in genome size (Paterson et al. 2005). Wheat consists of two genera, *Triticum* and *Aegilops* (van Slageren 1994 cited in GRIN 2008). Wheat can be divided into three groups based on ploidy level, diploid (2n = 2x = 14 chromosomes), tetraploid (2n = 4x = 28) and hexaploid (2n = 6x = 42), with the diploid and tetraploid groups including wild species. The wild wheat species *T. monococcum* ssp. *aegilopoides* (wild einkorn, diploid) and *T. turgidum* ssp. *dicoccoides* (wild emmer, tetraploid) are involved in domestication.

The cultivated diploid is *T. monococcumm* ssp. *monococcum* (einkorn). Cultivated tetraploids are divided into two species, *T. timopheevii* and *T. turgidum*. Only the subspecies *timopheevii* within *T. timopheevii* is cultivated. Seven subspecies within *T. turgidum* are cultivated: ssp. *dicoccum* (emmer), ssp. *paleocolchicum* (Georgian), ssp. *durum* (macaroni), ssp. *turgidum* (rivet or cone), ssp. *polonicum* (Polish), ssp. *turanicum* (Khorassan) and ssp. *carthlicum* (Persian). There are two cultivated hexaploids, *T. zhukovskyii* and *T. aestivum* (known as common, bread or dinkel wheat). According to Dubcovsky and Dvorák (2007), Simons et al. (2006) and Nevo et al. (2002) five subspecies within *T. aestivum* are cultivated: ssp. *aestivum* (common or bread wheat), ssp. *spelta* (dinkel or large spelt), ssp. *macha*, ssp. *compactum* (club) and ssp. *sphaerococcum* (shot).
Hexaploid bread wheat is the most prominent member of the tribe and is a highly variable group (Huang et al. 2002). The shift from wild diploid and tetraploid genotypes to cultivated genotypes of hexaploid wheat includes changes in morphological characters related to seed dispersal. These changes have revealed spike dimensions, spike rachis fragility, spikelet disarticulation, awn development, pubescence, grain size, glume tenacity and threshability.
Genotypes with soft glumes that require limited mechanical action during the de-hulling process are considered free-threshing (Jantasuiyarat et al. 2004). Bread wheat, with the exception of *T. spelta* and *T. macha*, has tough inflorescence stems that do not shatter when harvested and the seeds are easily threshed after gathering (Simons et al. 2006, Hancock 2004). Spike morphology (shape, length and density) in hexaploid wheat is known to be influenced by three major genes *q*, *C* and *s-1* on chromosomes 5AL, 2DL and 3DL (reviewed in Jantasuiyarat et al. 2004, Sourdille et al. 2000a). Square-headed wheat carrying *q* (spelt factor) combine a good threshability with a good grain size and shape. Speltoid wheat has long, lax, fragile, awned or awnless ears with tightly invested grains. That wheat is characterised by short dense-awned or awnless ears and small near-hemispherical grains. The dominant compact-ear-producing *C* allele (club spike shape) gives free-threshing cultivated wheat with short uniformly dense, oblong- or oval-awned or awnless ears (belonging to the *T. compactum* group). According to Jantasuiyarat et al. (2004) and Sourdille et al. (2000a) the characteristics of *T. sphaerococcum* are attributable to a recessive *s-1* allele with round glumes and spherical grains (*sphaerococcum* factor). The allelic variations at the *q*, *C* and *s-1* loci allowing the distinction of subspecies, namely *T. aestivum* (*QQ cc S-1S-1*), *T. compactum* (*QQ CC S-1S-1*), *T. spelta* (*qq cc S-1S-1*) and *T. sphaerococcum* (*QQ CC s-1s-1*), are probably due to major differences, while the variations within subspecies are less potent or non-existent (Sourdille et al. 2000a). Detailed morphological description of *Triticum* is listed by Clayton et al. (2006).
The genetic changes responsible for the suite of traits that differentiate domesticated plants from their wild ancestors are referred to as the domestication syndrome (reviewed in Dubcovsky and Dvorák 2007). In wheat, as in other cereals, a primary component of this syndrome was the loss of spike shattering, preventing the grains from scattering by wind and facilitating harvesting. Further, chromosome locations of the genes controlling shattering in einkorn are unknown, but in emmer wheat shattering is determined by the *Br* (brittle rachis) loci on chromosomes 3A and 3B (Nalam et al. 2006).

Another important trait for wheat domestication was the loss of tough glumes, converting hulled wheat into free-threshing wheat. The primary genetic determinants of the free-threshing habit are recessive mutations at the *Tg* loci (tenacious glumes), accompanied by modifying effects of the dominant mutation at the *Q* locus and mutations at several other loci (Jantasuiyarat et al. 2004).
The *Q* gene influences many other domestication related traits like glume shape and tenacity, rachis fragility, plant height, spike length and ear emergence time. The mutation that gave rise to the *Q* allele is the same in tetraploid and hexaploid free-threshing wheat (Simons et al. 2006). Other traits shared by all domesticated wheat are increased seed size, reduced number of tillers, more erect growth and reduced seed dormancy. The gene *Gpc-B1* affects seed size and is an early regulator of senescence with pleiotropic effects on grain nutrient content. In some genotypes and environments, the accelerated grain maturity conferred by the functional *Gpc-B1* allele is associated with smaller seeds (Uauy et al. 2006).

1.3 Origin of A, B and D genomes

Wheat is adapted to temperate regions of the world and was one of the first crops to be domesticated (Gupta et al. 2008). The domestication of wheat occured in South-Eastern Turkey near the Tigris and Euphrates rivers approximately 10,500 years before present (Dubcovsky and Dvorák 2007, Luo et al. 2007, Hancock 2004, Özkan et al. 2002).
Allopolyploidy has played a major role in the evolution of crop plants sustaining mankind (Zhang et al. 2008b). The allopolyploids arose from interspecific hybridisation events followed by spontaneous chromosome doubling (Huang et al. 2002). Amphiploids are the usually fertile products of spontaneous or induced chromosome doubling of sterile interspecific or intergeneric hybrids (Chen and Ni 2006). Wheat has undergone sufficient divergence that the duplicated chromosomes normally do not pair and the sequences of gene pairs are usually distinguishable (Paterson 2006). At the cytogenetic level, common wheat is a segmental allohexaploid having three closely related genomes A, B and D. Each genome has seven chromosomes ($n = 21$) that are organized in seven homologous groups. Each homologous group has three closely related chromosomes, one from each of the three related genomes (Gupta et al. 2008).
The expansion of agriculture lead to the dissemination of domesticated einkorn (*T. monococcum*) and domesticated emmer (*T. turgidum* ssp. *dicoccum*) across Asia, Europe and Africa. According to Luo et al. (2007) the domestication of hulled emmer was the first step that ultimately resulted in the evolution of free-threshing tetraploid durum wheat (*T. turgidum* ssp. *durum*) and hexaploid bread wheat (*T. aestivum* ssp. *aestivum*). Bread wheat (*T. aestivum*) has the genome composition AABBDD, which arose from spontaneous hybridisation, meaning two polyploidisations (McFadden and Sears 1946 and Kihara 1944 cited in Zhang et al. 2008b). Domestication of wheat resulted from mutations that gave rise to traits such as soft glumes, a nonfragile rachis and the free-threshing character (Simons et al. 2006). The first polyploidisation produced *T. turgidum* with the genome composition of AABB, in which *T. urartu* donated the A genome (Gupta et al. 2008).

The A and D genomes of allopolyploid wheat share a high degree of homology with the diploid genomes of *T. urartu* and *Ae. tauschii* (Feldman and Levy 2005). *Ae. tauschii* is the donor of D genome, this has recently been confirmed through analysis of DNA sequences of the two genes *Acc-1* (plastid acetyl-CoA carboxylase) and *Pgk-1* (plastid 3-phosphoglycerate kinase) and the *GluDy* allele variation (Giles and Brown 2006, Huang et al. 2002). *T. aestivum* was formed by the second polyploidisation after the crossing between cultivated *T. turgidum* and *Ae. tauschii* followed by chromosome doubling (Huang et al. 2002). The B genome donor is still controversial (Nevo et al. 2002) and believed to be extinct, much modified or not yet detected, but it was probably an ancestor of *Ae. speltoid*es (Zhang et al. 2008b, Huang et al. 2002).
DNA sequences of the above genes, *Acc-1* and *Pgk-1* also proved to be of no help in identifying of the progenitor of the B genome (Gupta et al. 2008). However, it is not known which AB tetraploid (*qq* or *QQ* genotype) was involved in the hybridisation with *Ae. tauschii* (D genome) that gave rise to hexaploid wheat. And, with regard to *q*, it has been a matter of speculation whether it first arose in the tetraploid progenitor of hexaploid wheat or if it arose independently in hexaploids and tetraploids (Simons et al. 2006). DNA sequences of genes other than the above two genes have also been used for the study of origin and evolution of the component genomes of bread wheat (Gupta et al. 2008). The study supports the recent evidence of independent origins of the wheat B and G genomes (Kilian et al. 2007). Nulli-tetrasomic wheat lines suggested that B genome chromosomes of hexaploid wheat were derived from chromosomes of *Ae. speltoides*. Further in this study, an analysis of the haplotypes at nuclear and chloroplast loci in *Aegilops* and *Triticum* accessions revealed that both B and G genomes of polyploid wheat are unique samples of *Ae. speltoides* haplotype diversity. However, it is likely that due to the outbreeding nature of *Ae. speltoides*, no modern *Ae. speltoides* lines have preserved the B genome donor genotype in its ancestral state (Gupta et al. 2008).

1.4 Genetic diversity and resources in wheat

Plant genetic resources for food and agriculture are an integral component of agricultural biodiversity. The genetic diversity contained in traditional varieties and modern cultivars, crop wild relatives and landraces provide a basis for food production and also act as buffer for adaptation and resilience in face of the climate change (FAO 2008b). Small initial population sizes and intense human selection for agronomic traits are thought to have decreased the available genetic diversity of most crop plants (Tanksley and McCouch 1997). Domestication can be seen as a population bottleneck in most crop species (Buckler et al. 2001). Cultivation, domestication and breeding have resulted in today's elite, cultivated crop gene pools that contain only a fraction of the available diversity in the species (Feuillet et al. 2008). Plant breeders have long recognised the existence of useful genetic variation in the wild ancestors of our domesticated crop species (Kovach and McCouch 2008). Populations including wild accessions are an important source of genetic resources for economically important plants (Henry 2005b).

The wild gene pool of domesticated crop species could possess substantial levels of novel genetic variability for characters of commercial significance that may be introgressed into bread wheat (Gororo et al. 2002, Tanksley and Nelson 1996a). Wheat landraces and wild relatives of wheat as new sources of genetic diversity are a potent resource for addressing biotic and abiotic stress constraints that limit wheat productivity (Skovmand et al. 2001). These are distributed in the three gene pools of the Triticeae (Rizwan et al. 2007). The wild wheat group is not highly polymorphic, with only 212 polymorphic sites among the 21,720 bp sequenced and, during domestication, diversity was further reduced in cultivated forms, by 69% in bread wheat and 84% in durum wheat, with considerable differences between loci (Haudry et al. 2007). Close evolutionary relationship and extensive genetic diversity for favourable traits have made tetraploid wheat and *Ae. tauschii* especially interesting for common wheat improvement (Nevo 2001).

Polyploid wheat has been able to compensate for diversity bottlenecks caused by domestication and polyploidy by capturing a relatively large proportion of the variability of its tetraploid wild progenitor (Dubcovsky and Dvorák 2007). The wild relatives of cultivated wheat are rich in genetic resources and are one of the best sources for wheat improvement. Wild emmer wheat represents best source for enriching the genetically impoverished cultivars and advancing cereal improvement. Wild emmer wheat comprises wide range of genotypes, especially in regard to abiotic (waterlogging, drought, cold, heat, soil micronutrient imbalances and salt tolerances) and biotic stresses (viral, bacterial, fungal), high-quantity and high-quality storage proteins (glutenins and gliadins), amylase, lodging resistance, early maturity, photosynthetic performance and herbicide resistance (Trethowan and Mujeeb-Kazi 2008, Farooq and Azam 2001, Valkoun 2001, Nevo 2001). Besides, numerous studies mentioned that *Ae. tauschii* should be considered a primary genetic resource for trait improvement of the adapted gene pool (Tyrka and Chelkowski 2004, Gororo et al. 2002, Tanksley and Nelson 1996a). It has a greater genetic variability for endosperm proteins, gliadins and glutenins, compared to *T. aestivum* (Pflüger et al. 2001) and is accepted as a major contributor of disease resistance (Oliver et al. 2005, Assefa and Fehrmann 2004, del Blanco et al. 2000).

The genetic diversity may be introgressed into common wheat by the 'bridge' of synthetic hexaploid or amphidiploids derived from the artificial synthesis of hexaploid wheat (tetraploid wheat×*Ae. tauschii*), which is analogous to the evolution of hexaploid wheat (Zhang et al. 2008b). The hexaploid wheat has no direct wild relatives (Devos and Gale 2000), therefore synthetic hexaploid wheat is a promising source to improve quantitative traits in wheat (McFadden and Sears 1944 cited in Feldman and Levy 2005). These quantitative traits vary continuously in a population. Hybrids between synthetic and natural hexaploid wheat exhibit complete chromosome pairing at meiosis and are usually fully fertile (Kihara and Lilienfeld 1949 cited in Feldman and Levy 2005). Many synthetic hexaploid wheat have been obtained (Warburton et al. 2006, Lage et al. 2003, Mujeeb-Kazi et al. 1996, Lange and Jochemsen 1992a), which resembled certain natural hexaploid wheat.

Breeding programmes, such as those at the international wheat improvement programme of the Centro Internacional de Mejoramiento de Maiz y Trigo (CIMMYT), have produced over 1,100 synthetic wheat lines since the early 1990s and the new genetic diversity represented in this material is being incorporated increasingly into wheat breeding programmes worldwide (Kishii et al. 2008, CIMMYT 2004). Further groups in the United States of America (Wheat Genetic and Genomic Resources Center (WGGRC) and in Australia (Department of Primary Industries, Victoria) have developed such synthetic hexaploid wheat and are using them in prebreeding programmes (van Ginkel and Ogbonnaya 2006).

Using cytological techniques bread wheat can be artificially recreated by intercrossing modern tetraploid wheat with present-day derivatives of diploid *Ae. tauschii* (Lage et al. 2003). The successful strategy consisted of the production of allotriploid interspecific hybrids, followed by doubling the number of chromosomes using colchicine. The majority of studies used synthetics derived from crosses of *T. turgidum* ssp. *durum*×*Ae. tauschii* (Börner et al. 2002, Mujeeb-Kazi et al. 1996, Nelson et al. 1995b) and *T. turgidum* ssp. *dicoccoides*×*Ae. tauschii* (Lange and Jochemsen 1992a, 1992b).

Despite some technical difficulties in intercrossing synthetic and modern bread wheat, many synthetic derivatives have been developed. A number of them have shown great promise in improving yield and yield components (Calderini and Reynolds 2000, Villareal et al. 1996, Villareal et al. 1994), resistance to most major wheat disease and biotic resistances (Hartel et al. 2004, Berzonsky et al. 2004, Lage et al. 2004, Mujeeb-Kazi et al. 2001b, 2001a, Loughman et al. 2001, Arraiano et al. 2001, Assefa and Fehrmann 2000, Ma et al. 1995a, Kema et al. 1995, Lutz et al. 1995, Innes and Kerber 1994, Gill et al. 1985) and tolerance to abiotic stresses such as drought, heat, salinity and waterlogging (Trethowan and Mujeeb-Kazi 2008, Reynolds et al. 2005, Villareal et al. 2001).

A cross between synthetic wheat and an improved variety has almost as much genetic diversity as its crossing parents. The current challenge is to make the best use of this new diversity (CIMMYT 2004). Potential exists for identifying the loci encoding quantitatively inherited yield traits using quantitative trait locus (QTL) analysis in mapping of delayed backcross generations (Tanksley and Nelson 1996a). Several studies published about synthetic hexaploid wheat as a valuable source of germplasm for increasing grain nutrient concentration for iron, manganese, potassium, phosphor and zinc (Calderini and Ortiz-Monasterio 2003, Cakmak et al. 1999), resistance against fungal diseases (Naz et al. 2008) and baking quality traits, which might be useful for breeding improved wheat varieties (Kunert et al. 2007, Narasimhamoorthy et al. 2006, Pflüger et al. 2001).

Very large number of wheat genotypes, wild relatives, landraces and synthetic accessions, are held in germplasm collections. There are more than 800,000 accessions of wheat held in genebanks around the world (FAO 1996). The Systemwide Information Network for Genetic Resources (SINGER) is the germplasm information exchange network of the Consultative Group on International Agricultural Research (CGIAR) and its partners.

The largest collections including 77,466 *Triticum* accessions are held at the CIMMYT genebank, followed by the genebank of the International Center for Agricultural Research in the Dry Areas (ICARDA) with 36,793 *Triticum* and 3,922 *Aegilops* accessions and 34,936 *Triticum* and 2,255 *Aegilops* accessions at the Vavilov Institute (SINGER 2008, VIR 2008). The European Wheat Database (EWDB) holds about 220,000 accessions of the genus *Triticum* and the set of characterisation and evaluation descriptors consists of 21 basic descriptors (EWDB 2008).

1.5 Wheat breeding

Worldwide wheat breeding in the last 50 years had many priorities, of which yield increase, maintenance of biotic resistance and increased abiotic tolerance, especially manipulation of traits for drought and heat, have been given a lot of attention. In the last 40 years, many researchers have investigated yield increases in wheat. There have been constant increases in yield potential in many geographic regions of the world, both developed and developing countries (Rajaram and Braun 2008).

In favourable environments, breeding for increased yield potential and biotic stress tolerance/resistance has been the norm for the last 100 years since Mendelian genetics were redetected. According to Koebner and Summers (2003), increases in wheat yield potential have resulted mostly from manipulation of few major genes, such as *Rht* (determinat of semi-dwarf habit), *Ppd* (adaption to photoperiod) and *Vrn* (vernalisation requirement). One of the most important breakthroughs was the incorporation of the dwarfing genes *Rht1* and *Rht2*. This led to the Green Revolution, especially in the Indian subcontinent. The genetic gains as a result of international wheat breeding efforts have been spectacular (Rajaram and Braun 2008).

Breeders have introgressed genes for disease resistance into high yielding and popular cultivars. There has not been a parallel phenomenon in relation to combining yield potential and tolerance to drought, heat and other abiotic environmental stresses. Breeders developing cultivars for abiotic stress environments have mostly ignored yield potential and focused on stress tolerance. However, there is a need for stress tolerant cultivars with high yield potential in years with high rainfall. In such years, tall cultivars lodge and yields are further reduced due to disease susceptibility (Rajaram and Braun 2008).

The development of molecular markers in wheat and their application in breeding and related research programmes, poses several significant challenges compared with some other crop plants (Marshall et al. 2001, Gupta et al. 1999). Features of wheat add greatly to the complexity of breeding and selection, the wide range of end uses, each with different but specific quality requirements, the complexity of the polyploid wheat genome and the low level of polymorphism in bread wheat, leading to a larger number of markers that need to be screened. The complexity of the genome reveals two problems: the size of the wheat genome and the presence of three related genomes. The success of wheat breeding has largely come from the application of new technologies to breeding and selection.

Particularly important were the introgression of chromosome regions from wild relatives and the development of new selection strategies. Biotechnology offers two new means for improving wheat, firstly through genetic engineering and secondly through the development and application of molecular markers (Langridge et al. 2001). Molecular marker systems for crop plants were developed to create high-resolution genetic maps and exploit genetic linkage between markers and important crop traits (Edwards et al. 1987). Further, molecular markers were used in several breeding methods, such as backcrossing, gene pyramiding, pedigree breeding and recurrent selection. The introgression of one or a few genes into a current elite cultivar via backcrossing is a common plant breeding practice. Results from mapping studies provide greatly improved estimates for the number of loci, allelic effects and gene action controlling traits of interest. Genomic segments can be readily identified that show statistically significant associations with quantitative traits (Moose and Mumm 2008). The majority of quantitative traits tend to be controlled by a few quantitative trait loci (QTLs) with major effects plus minor QTLs of lesser effects (Tanksley 1993). A QTL is a statistical construct that identifies a particular region of the genome as containing one or more genes associated with a quantitative trait. It is represented as an interval in a genetic linkage group within which the probability of association is plotted for each marker used in a mapping experiment (Jaiswal et al. 2006). QTLs of major effects should be most amenable to manipulation as discrete units of simple Mendelian inheritance via marker-assisted selection (Bernacchi et al. 1998b). A large number of marker×trait associations facilitated the use of molecular markers for marker-assisted selection (MAS) in bread wheat, which is gaining momentum in several countries (Gupta et al. 2008). MAS has been utilised for transfer of as many as 27 different insect and pest resistance genes and 20 alleles with beneficial effects on bread making and pasta quality into approximately 180 lines adapted to the primary United States of America production regions (Sorrells 2007). The wheat breeding programme in Australia involved improvement of 20 different traits, including resistance to some abiotic stresses and has already led to releases of some improved cultivars (Eagles et al. 2001). In addition, MAS has been incorporated in backcross breeding in order to introgress quantitative trait loci for improvement of transpiration efficiency and for negative selection for unfavourable traits such as yellow flour colour (Landjeva et al. 2007).

At CIMMYT markers associated with 25 different genes governing insect pest resistance, protein quality, homologous pairing and other agronomic characters are currently being utilised in wheat breeding programmes in order to develop improved wheat cultivars (Rajaram and Braun 2008, William et al. 2007). Further, at CIMMYT shuttle breeding at three contrasting locations in Mexico, wide adaptation, selection for resistance against *Fusarium*, *Septoria*, *Helminthosporium* and drought tolerance, international multi-site testing and the appropriate use of genetic variation to enhance yield gains of subsequently produced lines are carried out (Ortiz et al. 2007). The CIMMYT efforts to breed common wheat cultivars for resource poor farmers in the developing world has met with notable success in terms of improved yield, yield stability and quality traits (grain hardness and glutenins), tolerance to drought situation, increased disease resistance and utilisation efficiency of agricultural inputs (Kishii et al. 2008, Warburton et al. 2006).

1.6 Nitrogen use efficiency

The increase in crop yields during the past century is attributed to the selection of genotypes with a higher yield potential and to the parallel increase in the application of fertilisers, particularly nitrogen (Borlaug 2007). In the last 50 years the nitrogen (N) fertilisation of crop plants has increased more than 20-fold worldwide. The use of this fertiliser is generally inefficient with only about 50% being recovered in the harvested crop (Miflin and Habash 2002). The sharp increase in energy cost has also made N-fertiliser more expensive. Leaching of nitrogen into surface and sea water also causes environmental problems, including algal blooms. Increasing the efficiency with which crops utilise nitrogen represents an urgent priority for ensuring cost-effective and sustainable agriculture for the future (Collins et al. 2008). The improvement of nitrogen use efficiency, particularly in cereals, is a major goal of crop improvement. Such improved crops would make better use of the N-fertiliser supplied, they would also produce higher yields with better protein content (Miflin and Habash 2002).

In wheat, studies published that such wheat varieties grown with low N-input levels can sustain profit margins even if yields are lower. Wheat varieties that are specifically N-stress tolerant still need to be developed and genetic variation for adaptation traits to N-deficiency is required. These varieties will have to maintain yield and grain protein content under moderate N-deficiency as well as in the event of the intense N-stress which occasionally occurs under low input cropping systems (Laperche et al. 2007). Hence, direct selection for yield under a low N-supply would be more efficient than indirect selection conducted under high N-levels (Brancourt-Hulmel et al. 2005). Studies published genetic variability for N-uptake efficiency and N-utilisation efficiency and concluded that the selection for N-efficiency and particularly N-uptake efficiency was possible (Le Gouis et al. 2000, Dhugga and Waines 1989). A recent QTL meta-analysis and factorial regression were deployed to investigate QTL×nitrogen interaction effects, revealing fluences of the three major phenological trait loci, *Ppd-D1*, *Rht-B1* and *B1*, on N-related QTLs (Laperche et al. 2007). In addition, QTL clusters for glutamine synthetase (GS) activity coincided with the location of *GS* and *GSr* genes. Although QTL alleles for higher GS activity were associated with higher grain nitrogen, they showed minor or no effects on grain yield components (Habash et al. 2007). However, Laperche et al. (2008) commended that future studies should focus on low nitrogen breeding schemes.

1.7 SSR markers

Repetitive deoxyribonucleic acid (DNA) sequences such as variable number tandem repeat loci serve as highly informative genetic markers. Thus, it was subsequently suggested that the highly informative nature of variable number tandem repeat loci be combined with the specificity and rapidity of polymerase chain reaction (PCR) technology (reviewed in Akkaya et al. 1992). Further, it was suggested that high levels of polymorphism exist in dinucleotide tandem repeat sequences. They can be found anywhere in the genome, both in protein-coding and noncoding regions (Tautz 1989).

This type of reiterated sequence has been named simple sequence repeat (SSR, Jacob et al. 1991), short tandem repeat (Edwards et al. 1991) or microsatellite (Litt and Luty 1989). SSR markers consist of direct tandem repeats of 1-6 nucleotides in length. The number of repeat units evolves rapidly, leading to SSR markers exhibiting high polymorphism rates. SSR analysis is easy to conduct on a large scale. Polymorphisms are detected as length differences. SSR markers provide co-dominant genotype information and, once mapped, are fully transferable between populations (reviewed in Ablett and Henry 2008, McMullen 2003). Further, these markers are used for a wide range of efforts in genetic studies including genetic linkage and comparative mapping, positional cloning, genotypic profiling, marker-assisted selection and the detection of QTLs (Liu et al. 2005). SSR markers are highly amenable to automation, user-friendly, efficient in detecting polymorphism and they detect few loci (Liu et al. 2005). The usefulness of SSR markers as genetic markers in crop plants has been demonstrated for several species, including rice (Wu and Tanksley 1993), barley (Saghai Maroof et al. 1994), maize (Senior and Heun 1993) and hexaploid wheat (Plaschke et al. 1995).

In wheat, SSR markers are abundant, highly polymorphic, evenly distributed throughout the genome and require only small amounts of genomic DNA for analysis (Nicot et al. 2004, Saha et al. 2004, Yu et al. 2004, Röder et al. 1998b, Stephenson et al. 1998). Further, SSR markers were shown to be successfully usable across different wheat species, making them a powerful tool for population genetics and mapping studies in wild and cultivated wheat (Fahima et al. 2002, Pestsova et al. 2000b, Li et al. 2000). Recent studies on SSR markers published a high level of polymorphism among diploid wheat species (Hammer et al. 2000), tetraploid wild wheat accessions (Fahima et al. 2002) and hexaploid wheat varieties (Plaschke et al. 1995). According to Gupta et al. (2002) and Stephenson et al. (1998) SSR markers are mainly genome specific and detect usually single-locus in one of the three genomes (A, B and D). The isolation of SSR markers from a diploid ancestral wheat could appear as a powerful method to develop such markers for the corresponding genome at the polyploid level (Guyomarc'h et al. 2002a, 2002b).

Molecular markers in wheat are now available (http://wheat.pw.usda.gov/GG2/index.shtml) and these are underpinning genetic diversity analyses and comparative studies between wheat, barley and model genomes (Feuillet et al. 2008). The Wheat Microsatellite Consortium (WMC) primer sequences were published online (http://wheat.pw.usda.gov/ggpages/SSR/WMC/). The BARC markers were developed for the United States Wheat and Barley Scab Initiative to map and characterise genes for fusarium resistance (Song et al. 2005, Song et al. 2002). The CFA and CFD markers (http://wheat.pw.usda.gov/ggpages/SSRclub/) were provided by the Institut National de la Recherche Agronomique (INRA, France). The GWM and GDM markers were developed at the Leibniz Institute of Plant Genetics and Crop Plant Research (IPK, Germany, Pestsova et al. 2000a, Röder et al. 1998a). Other sources are public databases, which include a very large number of expressed sequenced tags (ESTs, Qi et al. 2004).

1.8 Wheat genome and genomics in wheat

Diploid and tetraploid wheat along with common wheat form a polyploidy series with genome sizes of approximately 4,000 Mb (diploid, *Ae. tauschii*), 12,500 Mb (tetraploid, *T. turgidum*) and 16,000 Mb (hexaploid, *T. aestivum*). According to Bennett and Leitch (2005) the hexaploid wheat genome is also much larger than any of the current plant model species, approximately 35 times larger than rice (490 Mb) and 108 times larger than *Arabidopsis thaliana* (157 Mb).

Wheat has emerged as a classic polyploid model. Polyploidy is a widespread evolutionary strategy in angiosperms and research on wheat has greatly contributed to the understanding of this important phenomenon (Qi et al. 2004). Molecular tools have recently been used for cytogenetic studies in wheat, so that all recent cytogenetic studies in wheat now have a molecular component, thus paving the path for wheat genomics research (Gupta et al. 2008). These studies in the area of molecular cytogenetics have been relatively difficult in bread wheat due to its three closely related genomes and a large genome (1C = > 16 billion bp) with high proportion (> 80%) of repetitive DNA (Gill et al. 2004). Modern hexaploid wheat has an even larger genome, although there are related diploid species with smaller genomes such as *T. urartu*. These large amounts of repetitive DNA may make chromosome walking extremely difficult, potential problems may be circumvented by using a small-genome relative as a model, provided that the genes in the target region are present in almost precisely the same order as those in the larger reference genome (Devos and Gale 2000). Wheat breeders have been interested in finding closely related species with smaller genome (*Brachypodium distachyon*) that may act as model for these important crops, whose genome is at present being sequenced (Paterson 2006, Huo et al. 2006).

Illegitimate recombination (between homologous chromosomes) may induce sequence rearrangements in specific loci controlling grain hardness (*Ha*) and leaf rust resistance (*Lr*) in hexaploid wheat and its diploid and tetraploid relatives (Chen and Ni 2006, Isidore et al. 2005). Therefore, recombination between homologous chromosomes with or without transposon involvement may be a general mechanism for observed inter-chromosomal exchanges in allopolyploids (Chen and Ni 2006). Even more can be present in wheat genomes, where there are three copies of *PhyC* that are all expressed (Devos et al. 2005b).

In recent years, a number of initiatives have been taken to develop new tools for wheat genomics research. These include construction of large insert libraries and development of massive EST collections, genetic and physical molecular maps and gene targeting systems (Gupta et al. 2008). The number of wheat ESTs has massively increased up to over 1,051,300 in 2008 (NCBI 2008), thus forming the largest EST collection in any crop as a resource for genome analysis. This huge amount of EST-derived sequence information is important for wheat, particularly as markers, as sources of candidate genes and as a valuable resource for systematic study of the functional portion of the wheat genome (Chao et al. 2006).

Further, ESTs are being used for a variety of activities including development of functional molecular markers, preparation of transcript maps and construction of cDNA arrays (Gupta et al. 2008). A variety of molecular markers that were developed either from ESTs or from genomic DNA also helped to discover relationships between genomes and to compare marker×trait associations in different crops (Gale and Devos 1998). EST-SSRs served as a valuable source for a variety of studies including gene mapping, marker-assisted selection and eventually positional cloning of genes (Gupta et al. 2008).

Comparative genomics, involving major crop grasses including wheat, has also been used not only to study evolutionary relationships, but also to design crop improvement programmes (Devos 2005a). Functional genomics research in wheat has recently witnessed significant progress. For instance, ribonucleic acid (RNA) interference, targeting induced local lesions in genomics (TILLING) and expression genetics leading to mapping of expression QTLs (eQTLs) have been used to identify functions of individual genes (Hansen et al. 2008, Jordan et al. 2007). To sequence gene-rich regions of the wheat genome, a multi-national collaborative programme named International Wheat Genome Sequencing Consortium (IWGSC) was launched (Moolhuijzen et al. 2007).

The Triticeae research community through the International Triticeae Mapping Initiative (ITMI, http://wheat.pw.usda.gov/ITMI/) has focused on the development of genomics tools and resources to enable a thorough understanding of genome structure and behaviour (Feuillet et al. 2008). In addition, GrainGenes (http://wheat.pw.usda.gov/) is a genome database for Triticeae and related species. Besides, Gramene (http://www.gramene.org) is a curated resource for genetic, genomic and comparative genomics data for the major crop species, including rice, maize, wheat and many other plant (mainly grass) species (Liang et al. 2008).

1.9 Molecular maps in wheat

Marker-assisted breeding has opened up exciting possibilities for the effective use of variation within crop gene pools and in searching for further useful variation in the wild relatives of crops (Tanksley and McCouch 1997). Molecular markers in bread wheat have been used for the preparation of genetic and physical maps.

Genetic maps

Mapping of molecular markers on wheat genome were initially made during the late 1980s (Chao et al. 1989), a systematic construction of molecular maps in wheat started only in 1990, with the organization of ITMI, which coordinated the construction of molecular maps of the wheat genome. Individual groups prepared maps for chromosomes belonging to each of the seven different homologous groups (Gupta et al. 2008). A detailed account on mapping of chromosomes of individual homologous groups and that of the whole wheat genome is available at GrainGenes (http://wheat.pw.usda.gov/).

Many genes controlling a variety of traits (both qualitative and quantitative) have already been tagged or mapped using a variety of molecular markers (McIntosh et al. 2008). Molecular genetic maps can be used to exploit the genetic potential of wild species for the improvement of yield and quality in modern plant cultivars (Tanksley and Nelson 1996a).

In the 1990s, molecular mapping in wheat took a leap forward with the application of DNA markers. Restriction fragment length polymorphism (RFLP) was the first DNA marker system to be used to construct the linkage maps of wheat in a recombinant inbred population from a cross of Opata and the synthetic hexaploid line W-7984, which was formed by crossing the durum cultivar Altar84 with *Ae. tauschii* (accession 219) followed by colchicine doubling (Marino et al. 1996, Nelson et al. 1995a, van Deynze et al. 1995).

The density of wheat genetic maps was improved with the development of SSR markers leading to the construction of SSR maps of wheat (Gupta et al. 2002), such as for hexaploid wheat 279 loci (Röder et al. 1998a), 1,235 loci covering 2,569 cM (Somers et al. 2004) and 1,406 loci covering 2,654 cM (Song et al. 2005) mapped in Synthetic×Opata recombinant inbred lines. More than 2,500 mapped genomic SSR markers are available in wheat, which will greatly facilitate the preparation of high-density genetic maps, so that the option consits to identify key recombination events in breeding populations and fine-map genes (Gupta et al. 2008). In addition, over 5,420 EST-SSR markers could be placed on the genetic map of the wheat genome (La Rota et al. 2005). EST-SSR markers are useful for enhancing individual species maps, but can be used as anchor probes for creating links between maps in comparative studies when designed from sets of orthologous genes (Yu et al. 2004). Chromosome bin map of ESTs is a unique resource for comparative mapping and structural and functional analysis of the wheat genome (Qi et al. 2004).

Comparative genetic maps

Comparative mapping involves the alignment of chromosomes of related species based on genetic mapping of common molecular markers. The idea behind comparative mapping is that comparing the genomes of two related species can help locate important genes that have been identified in one species but not in another and can provide clues about how both species evolved from a common ancestor. Comparative genetic maps (consensus maps, integrated maps, composite maps) where map information from multiple genomes or multiple maps were merged into a single comprehensive map, involving more than one type of molecular markers, were also prepared in wheat (Somers et al. 2004), 381 loci covering 3,636 cM mapped in Chuan35050×Shannong483 recombinant inbred lines (Li et al. 2007b) and 659 loci covering 3,685 cM mapped in Courtot×Chinese Spring doubled haploid lines (Sourdille et al. 2003).

As the value of comparative genomics became clear and relationships between an increasing number of species were unraveled, it became necessary to devise new visualisation methods that could display multiple comparisons in an adequate way (Devos 2005a). In 1995, the first ‘Crop Circle’ diagram was published (Moore et al. 1995).

The display has since been updated to more precisely delineate syntenic relationships between species of the grass family (Gale and Devos 1998). A consensus map of 12 grass genomes including wheat is available, representing chromosome segments of each genome relative to those in rice on the basis of mapping of anchor molecular markers (Gale et al. 2002). Some of the immediate applications of comparative genomics in wheat include a study of evolution, isolation and characterisation of genes using the model genome of rice (Wicker et al. 2007). The genes, which have been examined using comparative genomics method include the pairing gene *Ph1* (Huo et al. 2006), gene *Phs* controlling preharvest sprouting (Gale et al. 2002), gene *Lrk* responsible for receptor-like kinase associated with *Lr* locus (Feuillet et al. 2001), gene *Ha* for grain hardness (Chantret et al. 2004), genes *Rg* and *Bg* for red and black glume coloration (Khlestkina et al. 2006) and gene *Pm3* responsible for resistance against powdery mildew (Wicker et al. 2007).

Physical maps

Molecular markers in bread wheat have also been used for the preparation of physical maps, which were then compared with the available genetic maps involving the same markers. These maps allowed comparisons between genetic and physical distances to give information about variations in recombination frequencies and cryptic structural changes in different regions of individual chromosomes (Gupta et al. 2008). In wheat, physical mapping of genes to individual chromosomes began with the development of aneuploids, which led to mapping of genes to individual chromosomes. Later, deletion lines of wheat chromosomes were extensively used as a tool for physical mapping of molecular markers (Endo and Gill 1996). Using these deletion stocks, genes for morphological characters were also mapped to physical segments of wheat chromosomes directly in case of unique and genome specific markers or indirectly in case of duplicate or triplicate loci through the use of intergenomic polymorphism between the A, B and D genomes. In addition to physical mapping of genomic SSRs, ESTs and EST-SSRs were also subjected to physical mapping. Across the wheat genome 16,000 EST loci and 725 SSR loci were successfully mapped using 101 wheat deletion stocks (Qi et al. 2004, Sourdille et al. 2004).

1.10 QTL mapping

A plant breeder aims to develop improved cultivars, mainly through selection, whereas a geneticist aims to understand the inheritance and variation of traits. Breeding programmes obviously require genetic variation for selection to act on, but genetic variation per se is not the main interest of a breeder. Given this context, Bernardo (2008) mentioned two general goals of QTL mapping in plants to (I) increase our biological knowledge of the inheritance and genetic architecture of quantitative traits, both within a species and across related species; and (II) identify markers that can be used to select for a complex trait.

This latter goal, which focuses more on breeding than on pure genetics, can be further subdivided into two subgoals: (II-a) identify a few major QTL (with large estimated effects) that can be introgressed by standard breeding procedures into other germplasm or (II-b) identify many QTL that can serve as the basis for selection for a complex trait in elite germplasm.

QTL mapping was defined as the general class of linkage-based methods for finding QTL (Dudley 1993). These statistical methods detect associations between DNA markers and traits, QTLs can be detected in relation to a linkage map. This process had an enormous impact on the characterisation and understanding of the genetic control of quantitative traits (Collard et al. 2005b, Wu and Tanksley 1993). An ultimate goal of QTL mapping is to determine which genes are responsible for variation in the trait (Hansen et al. 2008). A key development in the field of complex trait analysis was the establishment of large collections of molecular markers, which offered the possibility of mapping QTLs depending on the level of resolution and density of the genetic maps. Recent and continuing advances in molecular genetics and statistical techniques make it possible to identify the chromosomal regions where these QTL are located (Tanksley 1993). In crop species, a wider range of structured mapping populations have been utilised for QTL analysis, including doubled haploids, F_2-progeny and backcross populations (Hansen et al. 2008).

The statistical analysis to detect QTL associations between phenotype (visual character of an individual) and genotype (part of an individuals combination of alleles) in a population include single-marker locus analysis (Liu 1998). Numerous kinds of single-marker methods, including marker-based methods, *t*-test, analysis of variances, regression analysis and maximum likelihood method and trait-based methods, are developed (Zhang 2006). Linear regression is commonly used for computing the effect of the QTL as coefficient of determination (R^2) from the marker explains the phenotypic variation arising from the QTL linked to the marker (Collard et al. 2008b).

The use of variance component models is rapidly increasing in QTL analysis. In traditional variance component methods, all effects are assumed unrelated and contribute two alleles each with effects drawn from an allelic effect distribution (Goldgar 1990). Methods using fixed effect models generally assume bi-allelic QTLs and that the founder lines are assumed to be fixed for alternative QTL alleles (Haley et al. 1994). A common feature of QTL analyses is that marker effects depend on environment. Many researchers have dealt with this problem by analysing each environment separately. This method is quite useful, if a breeder is interested in the particular test environments (Piepho 2000). Separate analyses of environments circumvent the problem of dealing with marker×environment interaction and avoid complications due to environmental heterogeneity. The results of separate analyses are difficult to interpret and they do not take advantage of the built-in replication provided by multiple environments (Tinker and Mather 1995). Test environments are just a sample from a target population and the breeder is interested in making broad inferences not restricted to the particular test environments (Melchinger et al. 1998). Therefore, a mixed-model analysis with random environments might be advantegous (Piepho 2000).

Presently QTL mapping software does not handle a full range of mixed linear model problems as experiment and environment designs, random polygenic variances. Experiment and environment design problems are typically handled by estimating progeny least square means using Statistical Analysis System software (SAS, http://www.sas.com) or other software for linear models and using the progeny means as input data for QTL mapping software (Knapp 1997). QTL or marker effects are usually handled as fixed effects in QTL mapping experiments. There are circumstances where they should be handled as random effects as QTL or marker variance component estimates are needed for implementing marker-assisted selection. Variance component methods based on restricted maximum likelihood (REML) have been used as an attractive method for estimating the QTL position (Lee and van der Werf 2006).

For the majority of agricultural experiments and surveys, the data can be regarded as realisations of a normally distributed random variable with an underlying linear model. Quite often, the linear model contains more than one random source of variation and, thus, can be treated in a mixed model. In addition, quite often, the data are unbalanced in the sense that the number of observations is not constant across factor combinations. Balanced designs may become unbalanced, when one or more observations are lost. For balanced data, simple arithmetic treatment means have optimal properties. This does not apply to unbalanced data, where adjusted means (least squares means, LS-means) are preferable. Adjusted means are obtained as a linear combination of estimated fixed effects and they guarantee an unbiased estimation of treatment means. Thus, the MIXED procedure of SAS software only computes adjusted means (LSMEANS statement). It should be noted that for balanced data, adjusted means and arithmetic means are identical, but not for unbalanced data. Thus, adjusted LS-means will always be correct, while simple means should only be used with balanced data (Spilke et al. 2005). In most applications, the variances of random effects will be unknown and need to be estimated. While for balanced data, estimates based on analysis of variance (ANOVA) mean squares have optimal properties; this is no longer true for unbalanced data. The preferable method for unbalanced data is that based on the REML method, as has been verified by simulations with data structures relevant in agricultural research (Guiard et al. 2003).

Different methods of single-locus multi-environmental QTL detection are possible. The detection of QTL using SAS software can be carried out using a mixed hierarchical model in the GLM procedure or MIXED procedure following the ANOVA or the REML method (Bauer et al. 2009, von Korff et al. 2005). Further, a multi-locus multi-environmental QTL detection could be computed using a REML multi-locus analysis including a forward selection method. This REML forward selection seems to be a powerful strategy accounting for both multiple loci and marker×environment interactions. This QTL analysis is suitable, especially if the lines are cultivated in multi-environmental field trials (Bauer et al. 2009).

Other methods for QTL mapping range from simple interval mapping (Lander and Botstein 1989), composite interval mapping (Zeng 1994), simplified composite interval mapping (Tinker and Mather 1995), multiple interval mapping (Kao et al. 1999), multiple QTL mapping (Jansen and Stam 1994), marker regression (Kearsey and Hyne 1994) and Bayesian methods

(Sillanpää and Arjas 1998). The interval mapping methods use flanking markers and are based on maximum likelihood estimations or multiple linear regression methods (Haley and Knott 1992, Lander and Botstein 1989). QTL mapping methods can be computed using different software packages. Most of the packages surveyed handle backcross, doubled haploid, recombinant inbred and F_2 to F_t progeny (Knapp 1997). Software packages for QTL mapping with these populations or germplasm collections are available, QTL Cartographer (Basten et al. 2002, http://statgen.ncsu.edu/qtlcart/), Plabqtl (Utz and Melchinger 2003, https://www.uni-hohenheim.de/plantbreeding/software/), Mapmaker/QTL (Lander et al. 1987, http://www.genome.wi.mit.edu/science/software/software), Map Manager/QTX (http://www.mapmanager.org/mmQTX.html) and MapQTL (van Ooijen and Maliepaard 1996, http://www.plant.dlo.nl/default.asp?section=products&page=/products/mapping/). Further, QGene (Nelson 1997, http://coding.plantpath.ksu.edu/qgene/download.php) handle advanced backcross generations or inbred lines developed from backcross or advanced backcross generations (Knapp 1997).

1.11 QTL studies

A large number of QTL studies for various traits have been conducted in bread wheat, leading to mapping of QTLs for these traits on different chromosomes. QTL analysis allows quantitatively inherited traits to be resolved into their individual genetic components (Zanetti et al. 2001). In most of these studies, either single-marker regression method or QTL interval mapping has been utilised (Gupta et al. 2008). Most of QTL studies involved mapping of QTLs with main effects only, there are also reports of QTLs, which have no main effects but have significant digenic epistatic interactions and QTL×environment interactions (Kumar et al. 2007, Kulwal et al. 2005, 2004).

Several studies published molecular mapping of loci for agronomic traits identified using QTL analysis in wheat, such as yield and yield components, heading time, plant height and lodging (Groos et al. 2003, Gervais et al. 2003, Sourdille et al. 2000b, Keller et al. 1999b, Cadalen et al. 1998). Beyond, quality parameters, characterise many economically relevant traits by a continuous distribution, which suggests that they are influenced by several genes (Zanetti et al. 2001). Studies in hexaploid wheat have investigated QTLs for grain protein content (Kulwal et al. 2005, Groos et al. 2003, Igrejas et al. 2002), grain hardness (Arbelbide and Bernardo 2006b, Igrejas et al. 2002, Galande et al. 2001, Sourdille et al. 1996), sedimentation value (Huang et al. 2006, Tanaka et al. 2005, Rousset et al. 2001, Zanetti et al. 2001) and bread-making quality (Pshenichnikova et al. 2008, Weightman et al. 2008, McCartney et al. 2006, Nelson et al. 2006, Charmet et al. 2005, Campbell et al. 2003, Prasad et al. 2003, Perretant et al. 2000). In addition, numerous QTL analyses have focused on QTLs for pathogen resistance against leaf rust (Schnurbusch et al. 2004), powdery mildew (Muranty et al. 2008, Tucker et al. 2007, Liang et al. 2006, Bougot et al. 2006, Mingeot et al. 2002, Liu et al. 2001, Keller et al. 1999b, Sourdille et al. 1999) and *Septoria* leaf blotch (Simón et al. 2004, Eriksen et al. 2003).

Latter QTL mapping studies for tolerance to low nitrogen use were described in rice (Senthilvel et al. 2008, Cho et al. 2007, Manneh et al. 2007, Lian et al. 2005), maize (Liu et al. 2008, Ribaut et al. 2007, Agrama et al. 1999), barley (Mickelson et al. 2003) and also in wheat (Laperche et al. 2008, 2007, Habash et al. 2007, An et al. 2006).

1.12 AB-QTL studies

Advanced backcrosses are multiple-generation crosses in which the progeny from each backcross generation are mated with the same recurrent parent to produce the next generation. A modified QTL detection method termed advanced backcross QTL (AB-QTL) analysis, has been proposed for the simultaneous discovery and transfer of useful QTLs from wild species into established domesticated lines (Tanksley and Nelson 1996a). Advanced backcross populations are useful to identify QTLs associated with improved performance in rice and to clone genes underlying key QTLs of interest.

AB-QTL analysis is capable of successfully uncovering positive (favourable) alleles in wild germplasm that were not obvious based on the phenotype of the parent, offering an estimation of the breeding value of exotic germplasm. Subsequently nearly-isogenic lines (NILs) can be developed that can be used as the basis for gene isolation and also as donor parents for further crossings in a variety development programme which is based on marker-assisted selection (Collard and Mackill 2008a, Swamy and Sarla 2008). The AB-QTL analysis method represents one way in which valuable wild alleles can be unmasked and transferred into elite cultivars to effect superior performance. This process not only results in improved elite varieties, but also in a general enrichment of cultivated germplasm (Bernacchi et al. 1998a).

According to Bernardo (2008) this QTL mapping method exemplified by QTLs with favourable exotic alleles therefore relies on (I) identifying unique germplasm as sources of useful QTL alleles, (II) finding closely linked markers for a few QTL that account for a substantial portion of the genetic variance for the trait, (III) confirming the effect of the major QTL alleles in different genetic backgrounds and (IV) deploying the QTL alleles widely in a breeding programme.

The value of the AB-QTL population design quickly became apparent with the successful detection of many transgressive QTLs in the early AB-QTL studies using wild species of the *Lycopersicon* taxon crossed with cultivated tomato (Bernacchi et al. 1998a). Since the first report in tomato (Tanksley et al. 1996b), AB-QTL analysis has been successfully applied in many crops to detect and transfer valuable QTLs from unadapted germplasm into elite breeding lines, such as in rice (Tan et al. 2008, Xiao et al. 1998), in barley (von Korff et al. 2006, 2005, Wang 2005, Pillen et al. 2003, Moncada et al. 2001) and in maize (Li et al. 2007, Ho et al. 2002).

Previously AB-QTL analyses were conducted using different synthetic hexaploid wheat accessions as donor of unadapted alleles for the advanced backcrosses. Numerous synthetic wheat accessions were analysed in crosses between durum wheat×*Ae. tauschii* (Imtiaz et al. 2008, Narasimhamoorthy et al. 2006, Huang et al. 2003b), *T. timopheevii*×*Ae. tauschii* (Leonova et al. 2007), *T. carthlicum*×*Ae. tauschii* (Liu et al. 2006), emmer wheat×*Ae. tauschii*

(Huang et al. 2004) and wild emmer wheat×*Ae. tauschii* (Kunert 2007a, Mohamed 2007, Naz 2007). Significant associations for agronomic traits, including yield and yield contributed traits and plant adaption traits, were identified in the advanced backcross populations Prinz×W-7984 (Huang et al. 2003b), Flair×XX86 (Huang et al. 2004), Batis×Syn-22 and Zentos×Syn-86 (Kunert 2007a) and Karl92×TA4152-4 (Narasimhamoorthy et al. 2006). Moreover, Narasimhamoorthy et al. (2006) and Kunert et al. (2007b) detected QTLs for baking quality traits. Resistances to plant diseases were identified in three advanced backcross populations, studied by Leonova et al. (2007) and Naz et al. (2008). Further, preharvest sprouting resistance QTLs were located in Syn-37×Janz advanced backcross population (Imtiaz et al. 2008). In addition, Mohamed (2007) used two advanced backcross populations, Triso×Syn-84 and Devon×Syn-84, for mapping QTLs associated with drought tolerance.

1.13 Objectives

The present research work was aimed to use the AB-QTL strategy for the detection and localisation of favourable exotic alleles for agronomic traits, quality parameters and disease resistances in spring wheat. The specific objectives of this study were to:

I) Conduct an AB-QTL analysis in two advanced backcross populations derived from two crosses of two German spring wheat cultivars (Triso and Devon) with one hexaploid synthetic wheat accession (Syn-84). This AB-QTL analysis is carried out to detect quantitative trait loci for agronomic traits, quality parameter and disease resistances in BC_2F_4 lines.

II) Assess the potential of exotic alleles from the synthetic hexaploid wheat donor to improve agronomic traits, quality parameter and disease resistances in two different genetic backgrounds (favourable QTLs).

III) Dissect the stability of favourable exotic QTL alleles across eight environments in two different genetic backgrounds by quantification of marker×environment interaction effects.

IV) Compare the QTLs between the two advanced backcross populations.

V) Assess the stability of the effect of exotic alleles across multiple environments and two different N-treatments in two different genetic backgrounds by a quantification of marker×nitrogen interaction effects (N-responsive QTLs).

VI) Compare the QTLs between two different QTL mapping methods (ANOVA and REML).

2 Materials and methods

The present study describes the application of the advanced backcross QTL strategy to detect QTLs for agronomic traits, quality parameters and disease resistances in two advanced backcross populations derived from crosses between two German spring wheat cultivars and single synthetic wheat. The following chapters specify parents and generation of advanced backcross populations, investigation of genotypic and phenotypic data and computation of statistical analyses.

2.1 Plant material

Both advanced backcross populations were developed according to the advanced backcross strategy of Tanksley and Nelson (1996a). The synthetic wheat was used as the donor of exotic alleles for backcrosses revealing an increased allelic diversity in advanced backcross populations. These introgressed synthetic wheat alleles can be eventually improving the trait performance.

Exotic genotype

The synthetic wheat Syn-84 is a non-adapted exotic hexaploid wheat germplasm. This synthetic wheat was developed and obtained by the Centre for Genetic Resources (CPRO, Wageningen, The Netherlands). According to Lange and Jochemsen (1992a, 1992b) the synthetic wheat was hybridised from *T. turgidum* ssp. *dicoccoides* (wild emmer wheat including the A and B genomes with 2n = 28, accession G4M-1M from the Volcani Centre, Bet Dagan, Israel) and *Ae. tauschii* (*Ae. squarrosa*, goat grass including the D genome with 2n = 14, accession Gat-473 from the Genbank, Gatersleben, Germany).

Elite genotypes

Two spring wheat cultivars Triso and Devon were selected as recurrent parents from the list Beschreibende Sortenliste Getreide, Mais, Ölfrüchte, Leguminosen, Hackfrüchte 1997 (Bundessortenamt 1997). Both cultivars are bread wheat (*T. aestivum* ssp. *aestivum*, allohexaploid with 2n = 42) and contain the A, B and D genomes. Cultivar Triso (*Eliteweizen*, > 14% protein, both winter and spring wheat) was developed and obtained by the breeder Deutsche Saatveredlung Lippstadt – Bremen GmbH (Lippstadt, Deutschland). The second cultivar Devon (*Qualitätsweizen*, > 12% protein, solely spring wheat) was developed by the breeder Züchter Hege (Waldenburg, Germany) and obtained by the breeder Monsanto Agrar Deutschland GmbH (Düsseldorf, Germany).

Generation of the advanced backcross populations

The initial cross between spring wheat cultivars and the exotic wheat accession was carried out in 1997. Triso and Devon, the recurrent parents (female) and Syn-84 as the donor of the male parent were used to generate the F_1 generation, as depicted in Figure 1.

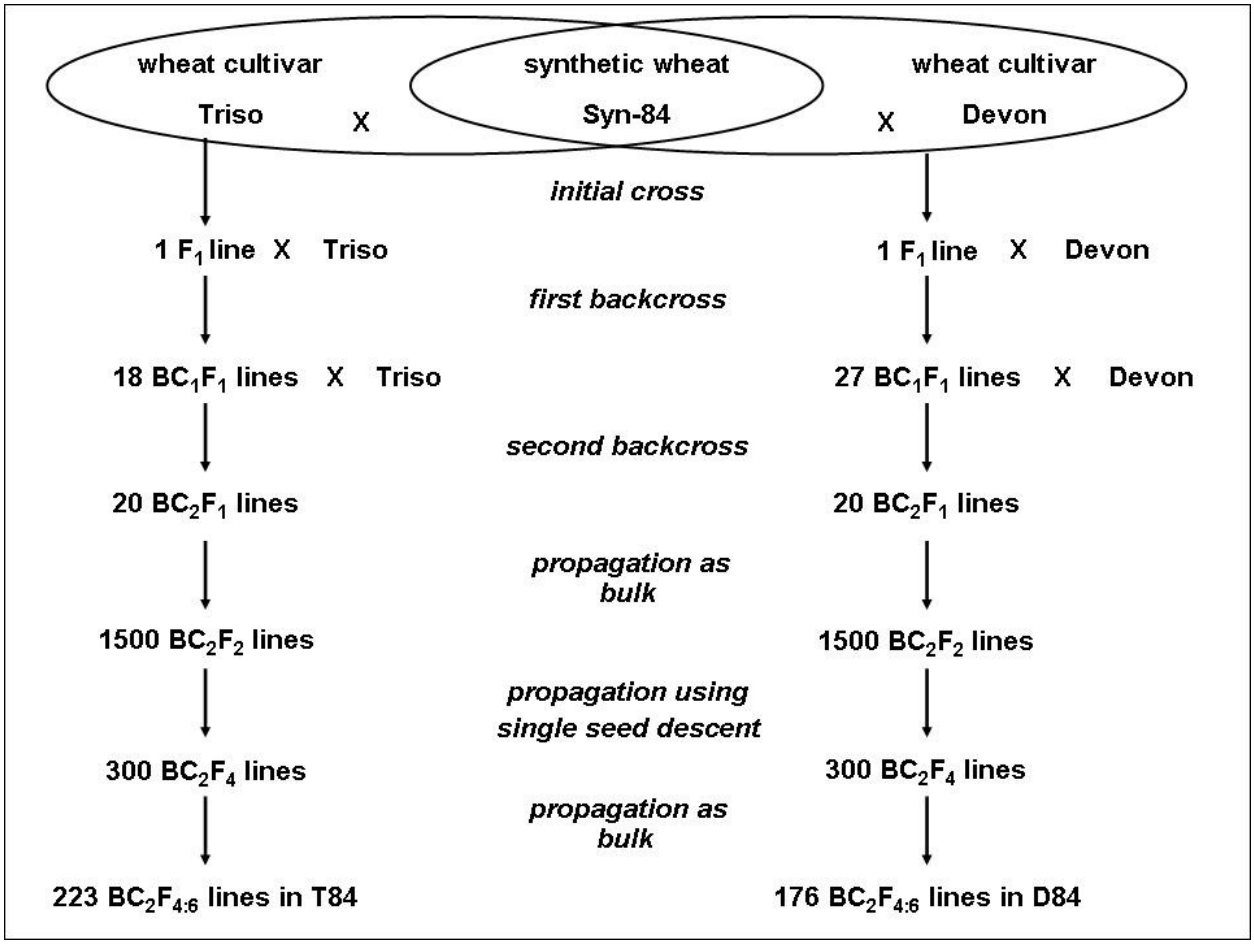

Figure 1: Development of advanced backcross lines by introgressing chromosome segments from the synthetic wheat Syn-84 into two sping wheat cultivars, Triso and Devon. Numbers indicated population sizes.

In each case a single F_1 plant (maternal) was backcrossed with the recurrent parent (paternal). From each initial cross 18 Triso and 27 Devon BC_1F_1 plants were once again backcrossed with the respective cultivar (Appendix 1, Appendix 2). The backcrosses were developed in green houses. The following steps were exemplary described for one backcross. Twenty BC_2F_1 plants were pooled following the bulk method. Fifteen kernels per BC_2F_1 plant were randomly selected for selfing in the season 2000. Resulting 1500 BC_2F_2 lines were propagated using single seed descent up to BC_2F_4 generation. Then, 300 BC_2F_4 lines were propagated as bulk to $BC_2F_{4:5}$ generation in field plots in the season 2003. In the following two years the $BC_2F_{4:6}$ generation and the $BC_2F_{4:7}$ generation were grown in field plots for measuring phenotypic data. For convenience the two BC_2F_4 populations are labelled as T84 (Triso×Syn-84) and D84 (Devon×Syn-84). Resulting 223 BC_2F_4 lines in T84 and 176 BC_2F_4 lines in D84 were pre-selected on threshability, seed size and phenotypic homogeneity.

2.2 DNA isolation

The isolation of genomic wheat DNA from Triso, Devon and BC_2F_4 lines was carried out according to Saghai Maroof et al. (1984). Ten seedlings per BC_2F_4 line germinated in petri

dishes were harvested and directly transferred into 96-deep well plates. The frozen leaf material was homogenised with tungsten carbid beads (Qiagen, Hilden, Germany) using the Tissue Lyser (Qiagen, Hilden, Germany) at 20 Hz (1 min.). Afterwards, a short centrifugation step (2 min., 3,000 rpm, Heraeus Labofuge 400, Germany) moved the leaf material on the bottom of the wells. To each sample 200 µl microprep buffer (100 µl microprep buffer consisted of 42 µl sorbitol buffer [350 mM sorbitol, 100 mM Tris-HCl (pH 7.5), 5 mM EDTA] + 0.8 mg sodium bisulfite, 42 µl lysis buffer [200 mM Tris-HCl (pH 7.5), 50 mM EDTA, 2 M NaCl, 2% CTAB] and 16 µl 5% lauryl sarcosine) were added. After incubation at 60°C (60 min.) the plates cooled down at 4°C (15 min.). The suspensions were extracted with 200 µl chloroform:isoamyl alcohol (24:1). Before centrifugation (30 min., see above) the volume of the aqueous phase was increased by addition of 150 µl microprep buffer. Following 200 µl aqueous phases containing DNA was pipetted into new sterile 96-deep well plates. For DNA precipitation the aqueous phase of each sample was submerged with 200 µl ice cold isopropanole. DNA was pelleted by centrifugation (30 min., see above). The pellets were washed with 100 µl 70% ethanol, centrifugated (30 min., see above) and dried at 60°C (60 min.). The final DNA pellets were suspended in 200 µl ddH_2O at 60°C (60 min). The DNA stock solution was stored at -80°C.
The quality and quantity of extracted DNA was determined by a 1.0% agarose gel. The DNA was separated (100 V, 60 min.) in agarose gel including ethidium bromide using a horizontal electrophoresis chamber (Pharmacia GNA 200, Pharmacia Biotech, München, Germany). The DNA bands were visualised using a ultraviolet transilluminator (Gel Doc 1000) and the software package Molecular Analyst from Bio-Rad Laboratories (München, Germany). Finally, the DNA working solution was water-diluted 1:10, resulting in an approximately 20 ng μl^{-1}.

2.3 Marker set

A total marker set of 451 SSR (simple sequence repeats) markers (for convenience abbreviated as markers) were screened for polymorphism between the crossing parents (Triso, Devon and Syn-84) of both advanced backcross populations (Gloss based on Appendix 1.
Appendix 3). The following prefixes of marker names indicate the published sources: BARC (Song et al. 2005), CFA and CFD (Sourdille et al. 2001), GDM (Pestsova et al. 2000a), GWM (Röder et al. 1998a) and WMC (Gupta et al. 2002). Initially, the markers were selected from the genetic map of Ward (2003) and finally from the consensus map developed by Somers et al. (2004). The chromosomal position of the markers obtained from the consensus map of Somers et al. (2004) or estimated either from flanking markers of the genetic map of Ward (2003) or after identification of linkage association from the individuals of each population by means of a Chi-square test using SAS/STAT 9.1 (SAS Institute 2003). The genotyped markers were assigned to deletion bins according to information by Sourdille et al. (2004). The marker set for the polymorphism survey was selected for an even coverage of the three wheat genomes. For genotyping, selected markers had to be polymorphic between the parents, regularly producing amplified PCR products, producing minimal stutter or shadow bands and be repeatable.

The first polymorphism test had been carried out with 195 markers in the laboratory of the IPK (Gatersleben, Germany). These markers were mapped in the ITMI population. The next polymorphism surveys were conducted in the laboratory of the Institute of Crop Science and Resource Conservation (INRES, University of Bonn, Germany). Finally, the graphical maps were computed using the software MapChart (Voorrips 2002) with genetic map positions according to Somers et al. (2004).

2.4 DNA amplification

Polymerase chain reaction was used to amplify the markers with the tailed primer method. Primers for genotyping were infrared dye (IRDye) labelled from LI-COR (LI-COR Biosciences GmbH, Bad Homburg, Germany). One of the unlabelled SSR primers was synthesized with an M13 forward primer sequence on the 5'-end. It was used in combination with a reverse primer without a tail. An IRD-labelled M13 primer was included in the PCR. The IRDye 700 or IRDye 800 labelled M13 primers were incorporated in subsequent cycles, thus labelling the PCR product for visualisation the DNA bands in the automated IR 4200 infrared DNA sequencer (LI-COR Biosciences GmbH, Bad Homburg, Germany).

The polymerisation was performed in thin-walled 96 PCR reaction plates using 20 µl final volume reactions containing 5 µl of template DNA (approximately 50 ng μl^{-1}), 0.5 µl of Taq polymerase (5 Units μl^{-1}, Promega, Mannheim, Germany), 0.75 µl of dNTP (2 mM, Promega, Mannheim, Germany), 0.5 µl of 25 mM $MgCl_2$, 2 µl of 10x PCR buffer (500 mM KCl, 100 mM Tris-HCl, pH 9.0, 1.0% Triton x-100), 0.2 µl of each forward and reverse oligonucleotide primer (10 µM) and 0.5 µl (1 µM) of M13, the IRD-labelled universal forward primer. The PCR was amplified using a thermocycler (either UNO II and T1, Biometra, Göttingen, Germany or Gene Amp PCR System 9600, Perkin Elmer, Applied Biosystems GmbH, Weilerstadt, Germany). The amplification was carried out with cycles that have three temperature steps started with denaturing at 94ºC (hot-start) for 1 min., annealing at 64-55ºC (touch-down) for 1 min. and extension for 1 min. at 72ºC followed by 30 cycles of 1 min. at 94ºC, 1 min. at 55ºC and 1 min. at 72ºC with a final extension step at 72ºC for 5 min. Finally hold was at 4°C for short-term storage of the reaction.

2.5 DNA analysis

Polyacrylamide gel electrophoresis of SSR alleles was carried out using an IR 4200 DNA analyser (LI-COR Biosciences GmbH, Bad Homburg, Germany). The PCR products were prepared by adding one volume of stop solution (95% deionised form amide, 10 mM NaOH, 0.05% fuchsine red) and denaturing at 95°C for 3 min.

The polyacrylamide premixed sequencing gel, 25 cm long and 0.2 mm thick, was prepared by gently mixing 12 ml SequaGel solution (SequaGel XR Extended Range, Biozym, Hess. Oldendorf, Germany) with 3 ml SequaGel Complete Buffer (Biozym, Hess. Oldendorf, Germany) in a beaker and by adding 120 µl 10% ammonium persulphate.

The gel solution was cast between two glass plates and the gel was allowed to polymerise for one hour. After fixing the gel sandwich a 5x TBE buffer (0.45 M Tris, 0.45 M boric acid, 10 mM EDTA, pH = 8.3) was diluted to 1x TBE buffer for filling the buffer chambers. The pre-run was started for 15 min. Afterwards, 0.5 µl of the denatured PCR product was loaded onto the gel and electrophoresed at 1,500 V, 40 mA, 25 W and 51°C. The gel was run for 5-6 hours with up to six loadings each with 48 samples. DNA bands were visualized using LI-COR's e-Seq 2.0 software (LI-COR Biosciences GmbH, Bad Homburg, Germany).

2.6 Investigation of phenotypic traits

The measurement of the phenotypic data sets was ascertained for agronomic traits, quality parameters and disease resistances (Table 1).

Table 1: List of 16 agronomic traits, quality parameters and disease resistances.

	Trait	Abbr.	Unit	Method of measurement	Breeding effort	N-level	Env.
Agronomic traits	Brittleness	BRT		Visual assessment of brittleness as absent (1) or present (2) at BBCH 92	–	N+, N-	D04, D05
	Tillers per square meter	EAR	tillers m^{-2}	Number of tillers counted for 0.5 m (D04, D05) and 1.0 m (remaining environments) at BBCH 75	+	N+, N-	B04, B05, D04, D05, F04, F05, H04
	Grain number per ear	GNE	grains $spike^{-1}$	Number of grains per spike determined from a single row of 0.5 m at BBCH 99	+	N+, N-	D04, D05
	Days until heading	HEA	days	Number of days from sowing until emergence of 75% of ears on main tillers at BBCH 57	–	N+, N-	B04, B05, D04, D05, F04, F05, H04, H05
	Plant height	HEI	cm	Average plant height measured from soil surface to tip of spike (including awns) at BBCH 70	–	N+, N-	B04, B05, D04, D05, F04, F05, H04, H05
	Harvest index	HI		Ratio of tillers to total biomass, computed from a single row of 0.5 m at BBCH 99	+	N+, N-	D04, D05
	Grain test weight	HLW	kg m^{-3}	Kilogram per cubic meter, computed from a sample of 250 ml by a hectolitre weight-measuring funnel (Nr. 6218, Wilhelm Jäger, Königswinter, Germany)	+	N+, N-	B04, D04, D05, H04, H05
	Lodging at harvest	LAH		Visual rating of the severity of lodging between no lodging (1) and total lodging (9) at BBCH 99	–	N+, N-	B04, B05, D04, D05, F05

	Trait	Abbr.	Unit	Method of measurement	Breeding effort	N-level	Env.
	Thousand grain weight	TGW	g 1,000 kernels^{-1}	Average weight of 1,000 kernels computed from two samples of 250 kernels	+	N+, N-	B04, D04, D05, F05, H04, H05
	Grain yield	YLD	dt ha^{-1}	Weight of grain harvested per plot at BBCH 99	+	N+, N-	B04, B05, D04, D05, F05, H04, H05
Quality parameters	Grain hardness	GH	%	Determination of grain hardness using Near Infrared Reflectance (NIR) Spectroscopy measured from whole grain groats	+	N+, N-	D04, H04
Quality parameters	Grain protein content	GPC	%	Determination of grain protein content using NIR Spectroscopy (ICC 2008a)	+	N+, N-	D04, H04, H05
Quality parameters	Sedimentation value	SED	ml	Determination of Sedimentation value according to Zeleny (ICC 2008b)	+	N+, N-	D04, H04
Disease resistances	Leaf rust	LR		Visual rating of *Puccinia recondita* symptoms between no symptoms (1) and maximal infection (9) measured after flowering when infection level was maximal	–	N+	D04, H04
Disease resistances	Powdery mildew	PM		Visual rating of *Blumeria graminis* symptoms (1-9)	–	N+	B04, B05, F04, F05, D04, D05, H04, H05
Disease resistances	*Septoria* leaf blotch	SEP		Visual rating *Septoria tritici* symptoms between no symptoms (1-9)	–	N+	B04, B05, D04, H04

Breeding effort: The breeding purpose for 16 investigated traits were defined according to breeding programmes for spring wheat, where (+) indicates that an increase and (–) that a decrease shall be achieve.

N-level: Mineral nitrogen provided in two or three applications (high N-supply, N+) and only one application (low N-supply, N-). Env.: Environment: Combination of the experimental location [Boldebuck (B), Dikopshof (D), Feldkirchen (F), Hovedissen (H)] and the experimental season [2004 (04), 2005 (05)].

The data collection was carried out under field conditions at four different locations in Germany in the seasons 2004 (04) and 2005 (05) using the $BC_2F_{4:6}$ lines and $BC_2F_{4:7}$ lines. The test locations were the Research Station Dikopshof of the University of Bonn (D04, D05), the breeders' experimental stations in Boldebuck (B04, B05; Deutsche Saatveredelung AG, Lippstadt, Germany), Feldkirchen (F04, F05; Saatzucht Schweiger & Co. OHG, Feldkirchen, Germany) and Hovedissen (H04, H05; W. von Borries - Eckendorf GmbH & Co., Leopoldshöhe, Germany), as described in Table 2.

The advanced backcross lines were grown in a randomised complete block design without replications. The investigation of ten agronomic traits, three quality parameters was carried out using two different N-treatments (N+, N-).

The N-fertilisation in N- (35-90 kg N ha^{-1}) and in N+ (140-190 kg N ha^{-1}) depended on the N min content of the soil and was in accordance with local practice (Table 3). The recurrent parents were tested as a control in each block. Net plot sizes (3.75-7.20 m^2), seed density (400-430 kernels m^{-2}) and field management were in accordance with local practices at the respected breeding station. The grain was harvested with a small plot harvester at maturity.

The investigation of two quality parameters, grain hardness and grain protein content, was carried out at the University of Bonn. Seed samples of BC_2F_4 lines and recurrent parents were collected from field plots in both N-treatments (N+, N-) from the experimental stations Dikopshof (D04) and Hovedissen (H04, H05). In addition, the quality parameter sedimentation value was analysed at the breeding station Hovedissen. Therefore, seed samples of BC_2F_4 lines and recurrent parents were collected from field plots in high N-level (N+) from the experimental stations Dikopshof (D04) and Hovedissen (H04).

Table 2: Climatic and edaphic conditions, listed at four experimental locations and two seasons.

Env.	Longitude/ latitude	Altitude (m)	Soil texture	Valuation index of soil[1]	Temp. min (°C)	Temp. max (°C)	Temp. av. annual (°C)	Annual rainfall (mm)
B04	E 12° 4' 0"/	11	loamy sand	40-42	n.sp.	n.sp.	7.6	688
B05	N 53° 49' 0"				n.sp.	n.sp.	7.6	681
D04	E 6° 59' 0"/	62	humous,	92	-7.3	32.1	10.2	660
D05	N 50° 50' 0"		fine sandy loam		-9.5	33.4	10.7	633
F04	E 11° 56' 0"/	420	sandy loam	80	n.sp.	n.sp.	8.6	732
F05	N 48° 28' 0"				n.sp.	n.sp.	8.5	799
H04	E 8° 42' 0"/	110	sandy loam	65	-12.6	32.5	7.4	850
H05	N 52° 1' 0"				-9.8	31.8	10.7	754

Env.: Environment: Combination of the experimental location [Boldebuck (B), Dikopshof (D), Feldkirchen (F), Hovedissen (H)] and the experimental season [2004 (04), 2005 (05)].
(1): German: Ackerzahl
n.sp.: not specified

The measurement of three disease resistances was carried out in experimental plots ranged from 0.5-2.7 m^2. In each plot the diseases, which were occurred under natural infection were investigated and the maximum stage of disease was ranked on a scale from 1 (highly resistant) to 9 (highly susceptible) on the basis of percent leaf or spike damage. Disease resistances were investigated in plots with high N-level (N+), but without applying fungicides (Table 3).

In addition to the recurrent parents certain indicator varieties for each particular disease were included in the experiment as controls and replicated eight times per environment. Indicator varieties were used for leaf rust (Eminent), powdery mildew (Passat), Septoria leaf blotch (Triso) and control (Taifun). If more than 50% data points of a measured trait were missing, then the respective environment was excluded from the QTL analysis.

Table 3: Field management for agronomic traits and quality parameters, listed at eight environments.

Env.	Prec. crop	N min (kg ha^{-1})	N-supply (kg ha^{-1}) N+	N-	Seeds for drilling (m²)	Net plot size (m²)	Herbicide treatment (l or g ha^{-1})	Growth regulator treatment (l ha^{-1})	Fungicide treatment (l or kg ha^{-1})	Insecticide treatment (ml or g ha^{-1})
B04	WR	21	150	40	400	4.50	Primus (0.1)	CCC (0.8)	Opus-Top (1.0)	n.a.
B05	WR	21	150	40	400	4.50	Primus (0.1)	CCC (0.8)	Opus-Top (1.0)	n.a.
D04	SB	44	150	35	400	6.00	Azur (2.5), Starane XL (1.5)	Moddus (0.3+0.15)	Acanto (0.6), Agent (0.6), Caramba (1.2), Pronto Plus (1.5)	Karate (75+75+75)
D05	SB	28	150	35	400	6.00	Azur (2.5)	Moddus (0.4)	Bravo (1.0), Folicur (0.4), Juwel Forte (0.5), Opus Top (0.5), Taspa (0.4), Unix (0.8[2])	Karate (75)
F04	WW	10	190	90	400	7.20	Basagran (2.25), Lotus (0.2)	CCC (0.4+0.2)	Radius (1.0[2]), Folicur (1.0), Opus Top (0.7)	Karate (75)
F05	WW	25	190	90	400	7.20	2.4 D (0.25), Concert (25[1]), Duplosan (1.0), Ralon (1.0)	CCC (0.5)	Impulse (0.8), Proline (0.8)	Trafo (150[1])
H04	WW	35	140	45	430	3.75	Basagran DP (3.0)	CCC (1.0)	Juwel Top (0.5), Taspa (0.25)	n.a.
H05	WW	40	150	50	430	3.75	Basagran DP (3.0), Pointer (20[1])	CCC (1.0)	Impulse (0.6), Proline (0.6)	n.a.

Table 3: Continued.

Env.: Environment: Combination of the experimental location [Boldebuck (B), Dikopshof (D), Feldkirchen (F), Hovedissen (H)] and the experimental season [2004 (04), 2005 (05)].
Prec. crop: Preceding crop: SB (sugar beat), WR (winter rape), WW (winter wheat).
N min: Mineral N-content in soil measured at up tp 90 cm in February.
N-supply: Mineral N-fertilisation provided as Calcium Ammonium Nitrate (27% N, 12% Ca) and/or liquid N-fertiliser (28% N) by unsing two or three applications (high N-supply, N+) and single application (low N-supply, N-) after sowing.
n.a.: Data not known.

2.7 Statistical analyses of phenotypic data

The statistical analyses were performed with the Statistical Analysis System SAS (SAS Institute 2003).

Comparison of mean values

Following statistical tests were conducted using the GLM procedure. The significance threshold of tests was defined by $P = 0.05$. Means and LS-means of advanced backcross lines were computed across tested environments for each trait performance and N-level, separately. The Student-Newman-Keuls test was applied for describing significant differences between tested environments. This comparison was conducted with the means. For characterisation, the significant differences between two N-levels were computed with the Tukey-Kramer test. Further, LS-means were computed for each trait, measured in each N-level and population.

Estimation of heritability

The ratio of the genetic variance over the phenotypic variance is defined as broad sense heritability. The heritability of the investigated traits across all environments and separately for each N-supply was estimated from REML variance components using the VARCOMP procedure and the following model:

$$Y_{ijk}=\mu+L_i+E_j+\varepsilon_{k(ij)},$$

with phenotypic observations Y_{ijk}, general mean μ, fixed effect L_i of the *i* th BC_2F_4 line, random effect E_j of the *j* th environment and error $\varepsilon_{k(ij)}$.
Then the heritability follows from:

$$h^2=VC_g/(VC_g+(VC_e/N_{env})),$$

whereas VC_g = variance component of the BC_2F_4 lines, VC_e = variance component of the error and N_{env} = number of tested environments.

Genetic correlations of traits

LS-means of investigated traits across BC_2F_4 lines tested environments and separately for each N-level were included for the calculation of the Pearson correlation coefficients (r). The genetic correlations between trait performances were computed using the correlation procedure (PROC CORR).

2.8 QTL mapping

Statistical analysis was performed by different mixed model analyses of multi-environmental QTL detections. These QTL mapping methods using SAS software were considered in analysis of variance method (ANOVA) using the general linear models procedure (PROC GLM) and restricted maximum likelihood method (REML) using the mixed procedure (PROC MIXED). The ANOVA method was computed as a single-locus analysis. Further, the REML method was classified in a single-locus and a multi-locus analysis. In addition, three QTL mapping methods were refined in three-way (including phenotypic data from the high N-supply plots) and four-way (including phenotypic data from high and low N-supply plots) analyses.

2.8.1 Models

Three-way analyses

The following three-way analyses of variance were specified in two single-locus methods and one multi-locus method. These analyses were carried out to detect significant QTL effects for trait performance in high N-level. These three-way QTL mapping methods revealed significant marker main effects and marker×environment interaction effects.

ANOVA single-locus analysis (ANOVA I)

The ANOVA I method was conducted using the following mixed hierarchical model using the GLM procedure according to von Korff et al. (2006):

$$Y_{ijkm}=\mu+M_i+L_j(M_i)+E_k+M_i*E_k+\varepsilon_{m(ijk)},$$

with phenotypic observations Y_{ijkm}, general mean μ, fixed effect M_i of the *i* th marker genotype, random effect $L_j(M_i)$ of the *j* th line nested in the *i* th marker genotype, random effect E_k of the *k* th environment, random interaction effect M_i*E_k of the *i* th marker genotype and the *k* th environment, residue $\varepsilon_{m(ijk)}$ of Y_{ijkm}.

REML single-locus analysis (REML I)

The REML method was computed by unsing the MIXED procedure applying the same mixed hierarchical model, as described above (ANOVA I). Considering Bauer et al. (2009), the random factor $L_j(M_i)$ is a kind of a genetic background effect in this analysis. In addition, the residuals were assumed to be identically and independently normally distributed.

REML multi-locus analysis using a forward selection method (REML II)

The REML II method was conducted using the mixed hierarchical model, as described above (REML I) and here implemented for stepwise variable selection in the MIXED procedure, according to Bauer et al. (2009). Thus, the marker with the most significant effect (based on the P-value of test type 3 F-statistic) was chosen as a fixed cofactor in the model of the following estimation round.

Using this extended model, the marker effects were estimated again. This procedure was repeated until no further significant markers could be found.

Four-way analysis

The four-way analyses of variance were specified in two single-locus methods and one multi-locus method. These analyses were conducted to detect significant QTL effects for trait performance under both N-levels (N+, N-). An environment was included if there was a significant difference of LS-means of each trait between both N-levels. These QTL mapping methods revealed significant marker main effects, marker×environment and marker×nitrogen interaction effects.

ANOVA single-locus analysis (ANOVA II)

The ANOVA II method was conducted using the following mixed hierarchical model using the GLM procedure. The model ANOVA I was amplified by the fixed effect nitrogen and its interaction effects according to Kunert (2007a):

$$Y_{ijkmn}=\mu+M_i+L_j(M_i)+E_k+N_m+M_i*E_k+M_i*N_m+E_k*N_m+M_i*E_k*N_m+\varepsilon_{n(ijkm)},$$

with Y_{ijkmn}, μ, M_i, $L_j(M_i)$, E_k, M_i*E_k as above-mentioned and fixed effects N_m of the *m* th N-supply, fixed interaction effect M_i*N_m of the *i* th marker genotype and the *m* th N-supply, random interaction effect E_k*N_m of the *k* th environment and the *m* th N-supply, random interaction effect $M_i*E_k*N_m$ of the *i* th marker genotype with the *k* th environment and the *m* th N-supply and residue $\varepsilon_{n(ijkm)}$ of Y_{ijkmn}.

REML single-locus analysis (REML III)

The REML III was computed using the REML method of the MIXED procedure according to Bauer et al. (2009). Further, the model REML I was extended by the fixed effect nitrogen and its interaction effects.

REML multi-locus analysis using a forward selection method (REML IV)

The REML IV method comprised the mixed hierarchical model (REML III) and was applied here for stepwise variable selection in the MIXED procedure, following Bauer et al. (2009).

2.8.2 Definition of a QTL

Following Pillen et al. (2003), at each marker locus only the homozygous genotypes were included in the calculation, because the repeated selfing of heterozygous genotypes leads to a mix of both homozygous genotypes in derived $BC_2F_{4:6}$ and $BC_2F_{4:7}$ field plots, resulting in a false estimate of the performance of true heterozygous genotypes. A significant marker×trait association was specified as a QTL, if a marker main effect, a marker×environment interaction effect and/or a marker×nitrogen interaction effect, was significant with at least $P = 0.01$ (P-value computed by the test type 3 sum of squares) using the ANOVA or REML mapping method.

A group of linked markers with a ≤ 20 cM distance and the same marker effect were interpreted as a single QTL with the same QTL labelling. For groups of linked markers, the significant marker with the highest F-statistics was defined as the closest marker to the QTL.

2.8.3 Evaluation of favourable QTL effects

The marker main effects (three-way analysis) and marker×nitrogen interaction effects (four-way analysis) were divided in favourable or unfavourable QTL effects characterised through the relative performance of the homozygous exotic genotype (RP[aa]). The exotic genotype (Syn-84) improved or impaired the trait performance in regard to the breeding effort across all environments at a given marker locus.
Following Pillen et al. (2003) the relative performance of the homozygous exotic genotype (RP[aa]) was computed by

RP[aa]=(([aa]-[AA])/[AA])*100,

where [aa] represents LS-means of the homozygous exotic genotype and [AA] LS-means of the elite genotype.

In three-way analyses, significant marker main effects were accepted as QTLs with favourable exotic effects if [aa] < [AA] at a significant marker locus, where [aa] and [AA] indicates LS-means of the homozygous exotic genotype and homozygous elite genotype, respectively.

In four-way analyses, significant marker×nitrogen interaction effects were described as N-responsive QTLs. These N-responsive QTLs were classified according to the trait performance of the exotic genotype in the two different N-treatments, N+ and N-. An N-responsive QTL effect was evaluated as favourable regarding the trait performance of the exotic genotype under low N-supply.
The following QTL categories were distinguished: (1) N-responsive QTL with a favourable exotic effect under both N-levels; (2) N-responsive QTL with a favourable exotic effect only under low N-supply; (3) N-responsive QTL with a favourable exotic effect only under high N-supply; (4) N-responsive QTL with an unfavourable exotic effect under both N-levels.

2.8.4 Calculation of the coefficient of determination

The coefficient of determination explained marker (R^2_M), marker×environment interaction (R^2_{M*E}) and marker×nitrogen interaction (R^2_{M*N}) were computed according to Bauer et al. (2009):

Three-way analysis	Four-way analysis
$R^2_M=(SS_M/(SS_M+SS_{L(M)}))*100$	$R^2_M=(SS_M/(SS_M+SS_{L(M)}))*100$
$R^2_{M*E}=(SS_{M*E}/(SS_{M*E}+SS_{L(M*E)}))*100$	$R^2_{M*N}=(SS_{M*N}/(SS_{M*N}+SS_{L(M*N)}))*100$

where SS_M, SS_{M*E} and SS_{M*N} represent sums of squares of test type 3 for marker main effect (M), marker×environment interaction effect (M*E) and marker×nitrogen interaction effect (M*N). $SS_{L(M)}$, $SS_{L(M*E)}$ and $SS_{L(M*N)}$ were computed as sums of squares of test type 3 for the BC_2F_4 lines, BC_2F_4 lines nested in marker×environment interaction effect (L(M*E)) and BC_2F_4 lines nested in marker×nitrogen interaction effect (L(M*N)).

2.8.5 Determination of the proportion of the exotic genome

The proportion of the exotic genome (P[aa]) revealed by synthetic wheat Syn-84 was computed as the percentage of exotic alleles present in a single BC_2F_4 line according to the formula given by Pillen et al. (2003):

P[aa]=(2[aa]+[Aa])/(2([AA]+[Aa]+[aa])),

where [AA], [Aa] and [aa] represent the frequencies of the homozygous elite genotype, the heterozygous genotype and the homozygous exotic genotype, determined from all investigated marker loci. Deviations of the observed ratio of elite to heterozygous to exotic genotype (AA:Aa:aa) from the expected ratio of 85.9 : 3.1 : 10.9 in BC_2F_4 generation were computed by the Chi-square test.

3 Results

Ten agronomic traits, three quality parameters and three disease resistances were investigated in advanced backcross populations T84 and D84 in BC_2F_4 generation by applying the advanced backcross quantitative trait locus strategy. The aim of this study was to identify QTL effects of exotic alleles on agronomic traits, quality parameters and disease resistances, which were introgressed from the exotic wheat accession Syn-84 into BC_2F_4 lines and which eventually improve the trait performances. For this objective the study involved genetic analysis, field experiments and subsequently statistical analyses. In the following chapter, the polymorphism test with SSR markers between the advanced backcross parents, the generation of both advanced backcross populations and their genetic constitution are described. Next, the data sets of phenotypic traits are presented and clarified using the genetic correlations between investigated traits from both N-levels. Then, the detection of QTLs investigated under high N-supply and N-responsive QTLs determined from both N-levels are depicted using different QTL mapping methods for both populations. Concluding, the ascertained QTLs were verified comparing the QTLs between the two populations and with other QTL analyses.

3.1 Polymorphism test between advanced backcross parents

A total of 451 SSR markers were tested for polymorphism between the parents (Triso, Devon and Syn-84) of the populations T84 and D84 (Appendix 3). The tested markers were taken from five references and varied in number from six (Xcfa) to 230 (Xgwm) markers (Table 4). Among tested markers 141 (31%) with polymorphic fragments between the corresponding parents were determined. A total of 117 markers were used for genotyping.

The proportion of polymorphic markers ranged from 11% (Xgdm) to 50% (Xcfa). The marker screening resulted in 94 (T84) and 106 (D84) markers, which were selected for genotyping the BC_2F_4 lines (Table 5, Appendix 4, Appendix 5). For both populations 86 identical markers were used. The distribution of analysed markers on chromosomes and genomes is listed in (Table 5). The chromosome maps for both populations with the genotyped markers were derived from Somers et al. (2004), as depicted in Figure 2 (T84) and Figure 3 (D84).

Table 4: Characterisation of tested markers, ordered by marker labelling.

Label of SSR marker	Ref.	Tested markers	Polymorphic markers	Proportion of polymorphic markers (%)	Genotyped markers	Genotyped markers per population	
						T84	D84
Xbarc	1	123	40	32.5	29	15	25
Xcfa	2	6	3	50.0	1	1	1
Xcfd	2	20	8	40.0	6	4	4
Xgdm	3	9	1	11.1	1	1	1
Xgwm	4	230	66	28.7	66	61	63
Xwmc	5	63	23	36.5	14	12	12
Total		451	141	31.3	117	94	106

Ref.: References: (1) Song et al. (2005), (2) Sourdille et al. (2001), (3) Pestova et al. (2000), (4) Röder et al. (1998), (5) Gupta et al. (2002).

3.2 Genetic constitution of the BC_2F_4 populations

A total of 94 (T84) and 106 (D84) markers were successfully genotyped in both populations (Table 5). Chromosome 6A was covered with a single marker in each population. Ten markers maximal were genotyped on chromosomes 5D (T84, D84) and 7B (D84). The 94 (T84) and 106 (D84) analysed markers covered 1,556 cM (T84) and 1,753 cM (D84) of the A, B and D genomes. The mean marker density was of 18.3 cM (T84) and 17.3 cM (D84). The genome coverage of markers per chromosome was maximal on chromosome 3B with 148 cM (T84) and 141 cM (D84). Furthermore, the markers were not evenly distributed over the three genomes with 19 (A genome) to 44 (D genome) markers in T84 and 29 (A genome) to 44 (D genome) markers in D84. Several genomic regions contained marker clusters, especially located on chromosomes 2D, 4B and 7B, as mapped in Figure 2 (T84) and Figure 3 (D84).

Table 5: Genotyped markers, chromosome lenght and marker density in T84 and D84, arranged per chromosome and genome.

Chromo-some	T84			D84		
	Genotyped markers	Chromosome lenght (cM)	Marker density (cM marker^{-1})	Genotyped markers	Chromosome lenght (cM)	Marker density (cM marker^{-1})
1A	2	74	37	3	74	25
1B	5	84	17	4	84	21
1D	6	100	17	6	100	17
2A	4	73	18	7	138	20
2B	3	46	15	3	46	15
2D	8	80	10	8	80	10
3A	2	71	36	4	116	29
3B	5	148	30	6	141	24
3D	4	30	8	5	67	13
4A	4	67	17	3	67	23
4B	4	34	9	4	34	9
4D	8	81	10	8	81	10
5A	4	76	19	7	82	12
5B	4	110	28	3	110	37
5D	10	115	12	10	115	12
6A[1]	1	-	-	1	-	-
6B	2	11	6	3	15	5
6D	3	39	13	3	35	12
7A	2	77	39	4	139	35
7B	8	114	14	10	114	11
7D	5	126	25	4	115	29
Genome						
A	19	438	24	29	616	22
B	31	547	18	33	544	17
D	44	571	13	44	593	14
Sum	94	1,556		106	1,753	
Mean			18			17

3.2.1 Distorted segregation in BC_2F_4 lines

The expected distribution of elite to heterozygous to exotic genotype was 85.9 : 3.1 : 10.9. The deviation was computed with the Chi-square test (P = 0.05) in both populations.
In T84, 26% (59 lines) and in D84 25% (44 lines) showed a significantly distorted segregation (Appendix 1, Appendix 2). In T84, the proportion of the exotic genotype ranged from 3.6% to 30.5% with a mean of 12.6%. In D84, the proportion of the exotic genotype varied from 2.5% to 29.3% with a mean of 13.6%. The mean proportion of ambiguous genotyped alleles was 15% (T84) and 13% (D84), respectively. Exotic alleles were present at all genotyped marker loci in both populations. Single exotic introgressions were found in four BC_2F_4 lines (Tri 014, Tri 130, Tri 205 and Tri 213) in T84. In D84, two BC_2F_4 lines (Dev 059 and Dev 169) were detected with two exotic introgressions.

3.2.2 Distorted segregation of SSR markers

Significantly distorted segregation was detected at 24.5% (23 markers) and 21.7% (23 markers) of 94 and 106 markers in T84 and D84, respectively (Table 6). The lowest proportion of distorted segregation with 10.5% (T84) and 13.8% (D84) was computed for the A genome.
Across the three genomes, the proportions of the exotic genotype were similar with variations from 12.7% (A genome) to 15.0% (B genome) in T84 and from 13.5% (B genome) to 14.5% (A genome) in D84 (Appendix 4, Appendix 5). However, means of the exotic genotype were similar with 14.0% (T84) and 13.8% (D94) for each population in comparing with the expected 12.5% of the exotic genotype.

Table 6: Distorted segregation of 94 and 106 genotyped markers, computed in T84 and D84.

Genome	T84			D84		
	Markers	DS	DS (%)	Markers	DS	DS (%)
A	19	2	10.5	29	4	13.8
B	31	10	32.3	33	10	30.3
D	44	11	25.0	44	9	20.5
Sum	94	23		106	23	
Mean			24.5			21.7

DS: Distorted segregation specified the deviation from the expected genotype distribution of cultivar (86%) to heterozygous (3%) to exotic (11%) genotypes were computed with Chi-square test (P = 0.05).

3.3 Phenotypic traits

The populations with 223 (T84) BC_2F_4 lines and 176 (D84) BC_2F_4 lines were investigated at four different experimental locations (Boldebuck, Dikopshof, Feldkirchen, Hovedissen) in two different N-treatments (N+, N-) in two successive seasons (2004, 2005), as listed in Table 7 and Table 8. The investigation of a total of 15 quantitative traits can be grouped in nine agronomic traits (EAR, GNE, HEA, HEI, HI, HLW, LAH, TGW, YLD), three quality parameters (GH, GPC, SED) and three disease resistances (LR, PM, SEP). In addition, the agronomic trait brittleness (BRT) was studied as present or absent.

The investigated traits, corresponding abbreviations, breeding purposes and tested environments are described in Table 1. The phenotypic data were measured in at least two environments per trait. In Appendix 6, LS-means of investigated traits with number of observations per population and recurrent parent for both N-levels are listed. In general, the trait mean was higher under high N-supply compared to low N-supply with the exeption of HEI (T84, D84), HLW (D84), LAH (Triso) and TGW in both populations. As expected the standard deviation was higher in the population compared to recurrent parent exempt from HLW (T84, D84) and YLD (D84) in the high N-supply, respectively. The means and significant differences of each tested environment and both N-levels per trait are presented in Table 7 (T84) and Table 8 (D84).

Table 7: Means of 16 traits in T84, computed by each environment and each N-level, separately.

Trait	N-level	Environment							
		B04	B05	D04	D05	F04	F05	H04	H05
BRT	N+			1.2^{A}	1.2^{A}				
	N-			1.2^{A}	1.1^{A}				
EAR	N+	387.2^{F}	422.7^{E}	683.0^{C}	728.4^{B}	590.6^{D}	764.4^{A}	704.8^{BC}	
	N-	354.6^{F}	462.0^{E}	536.0^{D}	648.0^{B}	476.5^{E}	561.9^{C}	699.0^{A}	
GNE	N+			27.2^{A}	27.7^{A}				
	N-			25.8^{B}	27.4^{A}				
HEA	N+	84.1^{F}	78.6^{G}	94.0^{A}	85.2^{E}	90.8^{B}	78.7^{G}	90.4^{C}	85.9^{D}
	N-	83.5^{F}	78.2^{G}	92.9^{A}	84.7^{E}	90.7^{C}	77.3^{H}	91.3^{B}	85.2^{D}
HEI	N+	86.5^{F}	85.9^{F}	110.9^{A}	110.9^{A}	98.4^{C}	108.5^{B}	90.3^{D}	88.8^{E}
	N-	85.6^{F}	87.7^{E}	104.3^{B}	110.0^{A}	102.8^{B}	100.2^{C}	89.6^{D}	103.0^{B}
HI	N+			0.4^{A}	0.4^{B}				
	N-			0.4^{A}	0.4^{A}				
HLW	N+	76.0^{C}		82.9^{A}	80.7^{B}			75.7^{C}	76.0^{C}
	N-	76.3^{C}		82.2^{A}	79.5^{B}			75.2^{E}	75.6^{D}
LAH	N+	2.8^{C}	2.5^{C}	2.7^{C}	4.5^{B}		6.5^{A}		
	N-	2.9^{A}	2.0^{BC}	1.9^{C}	2.3^{B}		2.2^{BC}		
TGW	N+	45.5^{A}		45.0^{A}	39.6^{C}		39.0^{C}	42.9^{B}	39.7^{C}
	N-	45.2^{B}		46.8^{A}	39.8^{E}		40.7^{D}	42.2^{C}	39.5^{E}
YLD	N+	61.1^{D}	44.4^{F}	89.9^{A}	74.6^{B}		60.6^{D}	68.5^{C}	58.5^{E}
	N-	58.2^{D}	44.1^{E}	75.7^{A}	69.1^{B}		60.2^{C}	57.5^{D}	42.3^{E}
GH	N+			59.4^{A}				50.3^{B}	
	N-			56.3^{A}				48.9^{B}	
GPC	N+			15.2^{A}				12.1^{C}	13.8^{B}
	N-			11.7^{A}				10.8^{C}	11.4^{B}
SED	N+			5.6^{A}				35.1^{B}	
LR	N+			2.9^{A}					2.2^{B}
PM	N+	2.4^{E}	2.3^{E}	4.8^{A}	4.7^{A}	4.2^{B}	3.4^{C}	2.9^{D}	3.7^{C}
SEP	N+	5.0^{B}	7.3^{A}	3.6^{C}				3.2^{D}	

For calculation the means of the phenotypic data of each population of 2004 and 2005 were used and for the recurrent parents only 2004 were included, respectively. Superscript letters were computed with the Student-Newman-Keuls test for description of significant differences between tested environments (P = 0.05). Gray highlighted boxes were computed with the Tukey-Kramer test for characterisation of significant differences between both N-levels (P = 0.05).

Trait: BRT (Brittleness), EAR (Tillers per m²), GNE (Grain number per ear), HEA (Days until heading), HEI (Plant height), HI (Harvest index), HLW (Grain test weight), LAH (Lodging at harvest), TGW (Thousand grain weight), YLD (Grain yield), GH (Grain hardness), GPC (Grain protein content), SED (Sedimentation value), LR (Leaf rust), PM (Powdery mildew), SEP (*Septoria* leaf blotch).

N-level: Two or three mineral N-applications (N+) and single mineral N-application (N-).

Environment: Combination of the experimental location [Boldebuck (B), Dikopshof (D), Feldkirchen (F), Hovedissen (H)] and the experimental season [2004 (04), 2005 (05)].

Table 8: Means of 16 traits in D84, computed by each environment and each N-level, separately.

Trait	N-level	Environment							
		B04	B05	D04	D05	F04	F05	H04	H05
BRT	N+			1.1^{B}	1.2^{A}				
	N-			1.2^{A}	1.3^{A}				
EAR	N+	419.3^{C}	440.7^{C}	606.0^{B}	638.4^{A}	582.3^{B}	649.8^{A}	664.0^{A}	
	N-	355.2^{E}	528.4^{C}	503.6^{C}	559.4^{B}	474.0^{D}	527.8^{C}	697.1^{A}	
GNE	N+			27.7^{A}	27.8^{A}				
	N-			26.7^{B}	28.3^{A}				
HEA	N+	85.6^{D}	78.7^{F}	94.3^{A}	85.0^{E}	90.0^{C}	78.0^{G}	91.4^{B}	86.1^{D}
	N-	83.3^{F}	78.4^{G}	93.6^{A}	85.1^{E}	90.7^{C}	77.7^{H}	91.4^{B}	85.7^{D}
HEI	N+	93.7^{E}	94.5^{E}	119.0^{A}	111.6^{B}	102.4^{D}	106.3^{C}	94.3^{E}	92.0^{F}
	N-	92.9^{E}	95.3^{D}	112.1^{A}	112.2^{A}	108.7^{B}	103.2^{C}	94.7^{D}	108.4^{B}
HI	N+			0.4^{A}	0.4^{B}				
	N-			0.4^{A}	0.4^{B}				
HLW	N+	74.2^{D}		82.5^{A}	80.2^{B}			74.8^{C}	74.0^{D}
	N-	76.5^{C}		82.1^{A}	79.3^{B}			74.2^{E}	75.3^{D}
LAH	N+	5.8^{B}	3.1^{D}	3.3^{D}	4.6^{C}		6.3^{A}		
	N-	4.2^{A}	2.6^{C}	1.6^{E}	2.1^{D}		3.2^{B}		
TGW	N+	46.7^{B}		49.7^{A}	43.8^{C}		44.0^{C}	43.0^{C}	40.0^{D}
	N-	47.0^{B}		50.0^{A}	42.7^{D}		44.5^{C}	43.4^{D}	42.7^{D}
YLD	N+	58.6^{C}	45.4^{E}	92.4^{A}	75.1^{B}		58.9^{C}	51.5^{D}	52.8^{D}
	N-	57.4^{C}	46.2^{EF}	80.4^{A}	70.1^{B}		53.7^{D}	47.7^{E}	45.1^{F}
GH	N+			60.1^{A}				51.1^{B}	
	N-			55.6^{A}				50.2^{B}	
GPC	N+			15.0^{A}				12.7^{C}	13.2^{B}
	N-			12.0^{A}				11.3^{B}	11.3^{B}
SED	N+			57.2^{A}					41.5^{B}
LR	N+			2.5^{A}					3.3^{A}
PM	N+	2.3^{F}	1.9^{F}	4.4^{B}	5.2^{A}	4.0^{BC}	2.7^{E}	3.1^{D}	3.7^{C}
SEP	N+	4.1^{B}	6.0^{A}	3.2^{D}				3.5^{C}	

Gloss based on Table 7.

In both populations the means were mostly different between experimental locations and seasons. The highest diversity of means was measured for HEA (N-) with significant variations for each environment and population, respectively. Significant distinctions between both N-levels were observed for EAR and GPC in all tested environments for each population. In contrast no significant difference was detected for HI (D84) and BRT (T84, D84) in both environments. Noticeable, converse values were compared to the prospects of EAR and YLD between both N-levels for the environment B05 in each population. Furthermore, phenotypic data for HEI were specified with no tendency for both N-levels across tested environments.

LS-means for 16 investigated traits under high and low N-levels were compared between populations T84, D84 and their recurrent parents Triso and Devon (Table 9). Within the agronomic traits only HEA (T84, D84) and TGW (D84) were significantly favourable in the population compared to the recurrent parent in both N-treatments. In T84, only GPC as the representative of the three quality parameters measured under low N-supply showed a significantly advantageous opposite to the recurrent parent Triso. The traits GPC and SED were superior to the recurrent parent Devon in each N-supply. LS-means of the three disease resistances showed no significant differences between the population and the recurrent parent.

Table 9: LS-means of 16 investigated traits for each N-level in T84, D84 and their recurrent parents Triso and Devon.

Trait	N+			N-			N+			N-		
	T84	Triso	Sig.	T84	Triso	Sig.	D84	Devon	Sig.	D84	Devon	Sig.
BRT	1.2	1.0	n.s.	1.2	1.0	n.s.	1.2	1.0	*	1.2	1.1	n.s.
EAR	611.0	590.6	n.s.	533.4	518.9	n.s.	571.7	587.4	n.s.	520.7	537.5	n.s.
GNE	27.5	31.2	**	26.6	31.0	**	27.7	30.6	*	27.5	29.9	*
HEA	86.0	92.1	***	85.5	91.2	***	86.2	91.8	***	85.7	90.9	***
HEI	97.5	98.1	n.s.	97.9	96.7	n.s.	101.7	91.6	***	103.4	89.9	***
HI	0.4	0.4	*	0.4	0.5	***	0.4	0.5	***	0.4	0.4	**
HLW	78.4	77.9	n.s.	78.0	77.6	n.s.	77.2	78.3	n.s.	77.7	78.1	n.s.
LAH	3.3	1.7	**	2.1	1.9	n.s.	4.0	2.6	**	2.6	1.8	**
TGW	42.0	43.7	**	42.4	45.0	***	44.5	42.5	**	45.1	42.4	**
YLD	65.4	81.6	***	58.2	69.5	***	62.1	76.2	***	57.3	67.7	***
GH	55.1	56.3	n.s.	52.7	53.1	n.s.	55.8	56.6	n.s.	53.3	52.5	n.s.
GPC	13.8	13.2	n.s.	11.3	10.6	***	13.7	13.2	*	11.6	10.8	***
SED	47.5	47.3	n.s.	30.3	29.7	n.s.	51.3	46.8	*	33.6	30.4	**
LR	1.8	1.7	n.s.				1.8	2.0	n.s.			
PM	3.6	3.5	n.s.				3.4	3.5	n.s.			
SEP	4.3	4.0	n.s.				3.7	3.7	n.s.			

For calculation LS-means of phenotypic data of each population of 2004 and 2005 were used and for the recurrent parents only 2004 were included, respectively.

Trait: BRT (Brittleness), EAR (Tillers per square meter), GNE (Grain number per ear), HEA (Days until heading), HEI (Plant height), HI (Harvest index), HLW (Grain test weight), LAH (Lodging at harvest), TGW (Thousand grain weight), YLD (Grain yield), GH (Grain hardness), GPC (Grain protein content), SED (Sedimentation value), LR (Leaf rust), PM (Powdery mildew), SEP (*Septoria* leaf blotch).

N+ or N-: N-level: Two or three mineral N-applications (N+) and only one mineral N-application (N-) after sowing.

Sig.: Significance were determined with the Tukey-Kramer test (*** P = 0.0001, ** P = 0.001,*P = 0.05, n.s. not significant).

Table 10: Heritability of 16 investigated traits in T84 and D84, computed in each N-level.

Trait	h^2 in T84		h^2 in D84	
	N+	N-	N+	N-
BRT	0.75	0.87	0.62	0.65
EAR	0.32	0.28	0.32	0.36
GNE	0.45	0.44	0.57	0.58
HEA	0.90	0.91	0.89	0.90
HEI	0.91	0.92	0.89	0.89
HI	0.67	0.67	0.58	0.51
HLW	0.59	0.61	0.64	0.73
LAH	0.64	0.77	0.64	0.74
TGW	0.87	0.89	0.85	0.81
YLD	0.80	0.84	0.73	0.74
GH	0.86	0.86	0.83	0.78
GPC	0.54	0.53	0.46	0.44
SED	0.77	-	0.68	-
LR	0.12	-	0.47	-
PM	0.91	-	0.87	-
SEP	0.19	-	0.31	-

Trait: BRT (Brittleness), EAR (Tillers per m²), GNE (Grain number per ear), HEA (Days until heading), HEI (Plant height), HI (Harvest index), HLW (Grain test weight), LAH (Lodging at harvest), TGW (Thousand grain weight), YLD (Grain yield), GH (Grain hardness), GPC (Grain protein content), SED (Sedimentation value), LR (Leaf rust), PM (Powdery mildew), SEP (*Septoria* leaf blotch).

h^2: The heritability of the traits obtained by REML variance component estimation using the VARCOMP procedure.

N+ or N-: N-level, two or three mineral N-applications (N+) and only one mineral N-application (N-) after sowing.

For a detailed description of investigated traits, the heritability was computed (Table 10). Heritability is the proportion of phenotypic variation in a population that is attributable to genetic variation among individuals. In this study the estimation of heritability applied estimation of variance components. The heritability of traits obtained by the REML variance component estimation using the VARCOMP procedure. The supremely heritability was detected in HEA, HEI, TGW, YLD, GH and PM in T84 and D84, simultaneously. However, the least heritability was computed in EAR, LR and SEP.

3.4 Genetic correlations

The genetic correlations between measured traits were computed using the LS-mean of a trait for each BC_2F_4 line averaged across tested environments and separately for high and low N-level, as listed in Table 11 (T84) and Table 12 (D84). A total of 63 (T84) and 54 (D84) in high N-level (N+) as well as 52 (T84) and 38 (D84) in low N-level significant correlations were determined. Strong correlations were detected between YLD and HI with 0.76 (T84) and 0.59 (D84) under high N-supply and 0.66 (T84) and 0.54 (D84) under low N-supply. In T84 and D84 other strong positive correlations were computed between HI and GNE (N+, N-) and HEI and LAH (N-). BRT was strong negative correlated with HI (0.63) and YLD (0.67) under low N-supply in T84. The quality parameters were significantly correlated with agronomic traits ranged between -0.29 and 0.23 in each population and each N-level. The disease resistances were significantly correlated with EAR (up to -0.19, T84) and HEA (up to -0.34, T84, D84).
Furthermore, the proportion of exotic genotype was strongest correlated with LAH (0.33, N+) and TGW (0.35, N+) in T84. In D84, the proportion of exotic genotype was strongest correlated with YLD (-0.38, N-) and GPC (0.33, N-).

Table 11: Correlation coefficients (r) according to Pearson in T84, computed between 16 traits measured in each N-supply.

Trait	BRT	EAR	GNE	HEA	HEI	HI	HLW	LAH	TGW	YLD	GH	GPC	SED	LR	PM	SEP	[aa]
BRT		-0.14 *	-0.45 ***	-0.02	0.03	-0.54 ***	-0.09	0.10	-0.12	-0.55 ***	-0.01	-0.04	0.12	-0.02	-0.03	0.01	-0.02
EAR	-0.12		0.04	0.18 **	-0.27 ***	0.26 ***	-0.20 **	-0.06	-0.38 ***	0.25 ***	-0.21 **	-0.18 **	-0.15 *	-0.19 **	-0.17 **	0.06	-0.10
GNE	-0.39 ***	0.06		0.15 *	-0.04	0.63 ***	0.01	-0.25 ***	-0.13 *	0.48 ***	0.18 **	-0.04	-0.15 *	-0.04	0.16 *	0.02	-0.12
HEA	-0.08	0.02	0.16 *		0.19 **	0.07	-0.10	-0.15 *	-0.30 ***	0.15 *	-0.01	-0.28 ***	-0.29 ***	-0.25 ***	-0.14 *	-0.34 ***	-0.24 ***
HEI	0.09	-0.20 **	-0.05	0.17 *		-0.24 ***	0.04	0.46 ***	0.29 ***	-0.08	0.18 **	0.11	-0.04	0.08	0.09	-0.17 *	0.10
HI	-0.63 ***	0.31 ***	0.54 ***	0.09	-0.20 **		0.04	-0.27 ***	-0.06 ***	0.66 ***	-0.02	-0.16 *	-0.20 **	-0.07	0.08	0.00	-0.20 **
HLW	0.15 *	-0.18 **	-0.16 *	0.21 **	0.17 **	-0.23 **		0.07	0.26 ***	0.16 *	0.11	-0.02	0.07	0.07	0.10	-0.09	-0.19 **
LAH	0.16 *	0.02	-0.13 *	-0.10	0.52 ***	-0.16 *	-0.17 *		0.11	-0.27 ***	0.05	0.21 **	0.13	0.11	-0.14 *	-0.02	0.33 ***
TGW	-0.10	-0.24 ***	-0.06	-0.22 **	0.31 ***	0.03	0.21 **	0.05		0.05	0.13	0.17 *	0.06	0.16 *	0.12	-0.02	0.35 ***
YLD	-0.67 ***	0.33 ***	0.46 ***	0.04	-0.09	0.76 ***	-0.16 *	-0.15 *	0.11		-0.08	-0.21 **	-0.28 ***	-0.09	0.09	-0.01	-0.20 **
GH	0.02	-0.17 *	-0.01	-0.06	0.16 *	-0.14 *	0.23 **	0.06	0.18 **	-0.05		0.30 ***	0.41 ***	0.12	0.06	0.01	0.06
GPC	0.00	-0.19 **	-0.13	-0.24 ***	-0.05	-0.24 ***	0.08	-0.04	0.07	-0.22 ***	0.12		0.47 ***	0.10	0.02	0.08	0.21 **
SED	0.10	-0.10	-0.21 **	-0.29 ***	-0.08	-0.23 ***	0.18 **	-0.02	0.01	-0.17 **	0.31 ***	0.44 ***		0.11	-0.04	0.10	0.08
LR															0.10	0.21 **	0.15 *
PM																0.15 *	0.10
SEP																	0.07
[aa]	-0.01	-0.18 **	-0.04	-0.24 ***	0.13 *	-0.20 **	0.01	0.27 ***	0.27 ***	-0.06	0.09	0.21 **	-0.02				

For computing the genetic correlations the LS-mean of a trait for each BC_2F_4 line and each N-supply was averaged across all tested environments. The non and gray highlighted r values were referred to N-supply N+ and N-, respectively. The significance thresholds for r values were (***) P = 0.001, (**) P = 0.01, (*) P = 0.05.

Trait: BRT (Brittleness), EAR (Tillers per square meter), GNE (Grain number per ear), HEA (Days until heading), HEI (Plant height), HI (Harvest index), HLW (Grain test weight), LAH (Lodging at harvest), TGW (Thousand grain weight), YLD (Grain yield), GH (Grain hardness), GPC (Grain protein content), SED (Sedimentation value), LR (Leaf rust), PM (Powdery mildew), SEP (*Septoria* leaf blotch).

[aa]: Proportion of exotic genotype in each BC_2F_4 line.

Table 12: Correlation coefficients (r) according to Pearson in D84, computed between 16 traits measured in each N-supply.

Trait	BRT	EAR	GNE	HEA	HEI	HI	HLW	LAH	TGW	YLD	GH	GPC	SED	LR	PM	SEP	[aa]
BRT		0.03	-0.40 ***	-0.14	-0.06	-0.43 ***	0.06	0.07	0.03	-0.39 ***	0.09	0.01	0.14	0.00	-0.06	0.19 *	0.09
EAR	-0.14 *		-0.13	0.04	-0.21 **	-0.03	0.02	0.16 *	-0.38 ***	-0.11	-0.15 *	0.01	-0.06	-0.06	0.06	0.05	-0.05
GNE	-0.47 ***	0.01		0.25 **	0.02	0.58 ***	-0.05	-0.23 **	-0.23 **	0.35 ***	-0.02	-0.28 ***	-0.23 **	0.04	-0.21 **	-0.21 **	-0.25 ***
HEA	0.01	0.07	0.20 **		0.05	0.08	-0.17 *	-0.15 *	-0.33 ***	0.01	-0.03	-0.14 ***	-0.31 ***	-0.28 ***	-0.23 **	-0.34 ***	-0.18 *
HEI	0.00	-0.27 ***	-0.06	0.05		-0.20 **	-0.05	0.49 ***	0.33 ***	-0.12	0.09	0.07	0.01	0.18 *	-0.11	-0.06	0.20 **
HI	-0.45 ***	0.19 *	0.59 ***	0.14	-0.25 ***		-0.06	-0.33 ***	-0.03	0.54 ***	-0.03	-0.20 **	-0.17 *	0.02	-0.08	-0.18 *	-0.28 ***
HLW	-0.03	0.08	-0.10	-0.13	0.01	0.09		-0.06	0.07	0.03	0.17 *	-0.09	0.09	0.09	0.00	-0.04	-0.06
LAH	0.11	-0.01	-0.17 *	-0.14	0.53 ***	-0.26 ***	-0.21 **		-0.02	-0.34 ***	-0.15 *	0.12	0.09	0.15 *	-0.02	0.15 *	0.20 **
TGW	-0.03	-0.30 ***	-0.29 ***	-0.30 ***	0.31 ***	-0.05	0.16 *	0.03		0.07	0.15 *	0.02	0.03	0.16 *	0.07	-0.02	0.14
YLD	-0.48 ***	0.15 *	0.52 ***	0.03	-0.06	0.59 ***	0.13 **	-0.16 *	0.02		0.11	-0.16 *	0.00	0.05	0.02	-0.04	-0.37 ***
GH	0.01	-0.19 *	-0.10	-0.05	0.07	-0.18 *	0.13	-0.11	0.07	-0.05		0.14 ***	0.44 ***	-0.07	-0.16 *	-0.02	0.07
GPC	-0.05	-0.06	-0.15	-0.03	0.09	-0.26 ***	0.07	0.07	0.09	-0.27 ***	0.18 *		0.37 ***	0.09	0.05	0.19 *	0.31 ***
SED	0.04	0.05	-0.08	-0.03	0.14	-0.16 *	0.22 **	0.17 *	0.01	-0.02	0.13	0.31 ***		0.08	0.03	0.22 **	0.15
LR															0.06	0.25 **	0.11
PM																0.30 ***	0.08
SEP																	0.22 *
[aa]	0.13	-0.18 *	-0.20 **	-0.19 *	0.14	-0.30 ***	-0.08	0.18 *	0.15	-0.38 ***	0.15 *	0.33 ***	0.03				

Gloss based on Table 11.

3.5 Detection of QTLs

Marker analyses using two different types of estimates of variance components in SAS procedures were conducted to calculate significant marker×trait associations. The different methods of multi-environmental QTL detection were considered in analysis of variance (ANOVA) and restricted maximum likelihood (REML) methods. The ANOVA analyses were computed using the PROC GLM procedure through three-way (high N-level, ANOVA I) and four-way (high and low N-levels, ANOVA II) models. The REML analyses were determined through three-way (high N-level, REML I, REML II) and four-way (high and low N-levels, REML III, REML IV) models using the PROC MIXED procedure.
Using three-way QTL detection marker main effects and marker×environment interaction effects were computed. Furthermore, marker×nitrogen interaction effects were detected using four-way QTL analyses. A significant marker×trait association was specified as a QTL, if a marker main effect, a marker×environment interaction effect or a marker×nitrogen interaction effect, was significant with at least $P = 0.01$ using the ANOVA or REML mapping method. The marker main effects were divided in favourable or unfavourable QTL effects, where the exotic genotype (Syn-84) improved or impaired the trait performance in regard to the breeding effort across all environments at a given marker locus.

A group of linked QTLs with a ≤ 20 cM distance and the identical QTL effect were interpreted as one QTL with the identical QTL designation. For groups of linked QTLs, the significant marker with the highest F-value was defined for the closest marker to the QTL. Along with QTLs of different mapping methods, groups of linked significant markers showing the identical effect were interpreted as an identical QTL, which was given the identical designation.
In the following chapters a detailed characterisation of the significant marker×trait associations included QTLs with the corresponding chromosome position and basic data were listed for each population and each mapping method, respectively.

3.6 Localisation of QTLs - Three-way analyses

Three-way analyses were used to identify QTL effects on agronomic traits, quality parameters and disease resistances in high N-level. Thus, ANOVA single-locus analysis (ANOVA I), REML single-locus analysis using a mixed hierarchical model (REML I) and REML multi-locus analysis by a forward selection method applying a mixed hierarchical model (REML II) were conducted. Three-way QTL mapping methods revealed marker main effects and marker×environment interaction effects, which are depicted in genetic maps in Figure 2 (T84) and Figure 3 (D84).

3.6.1 ANOVA I - QTLs in T84

A total of 1,504 marker×trait combinations under high N-supply were tested in T84 using the three-way ANOVA single-locus analysis (ANOVA I). A set of 128 significant marker×trait associations were detected for 16 traits. Seventy marker main effects were computed, of which 16 marker loci given additional marker×environment interaction effects (Table 13). Fifty-eight significant associations showed marker×environment interaction effects (Appendix 7). Among significant marker×trait associations 105 QTLs were detected. In detail, 57 QTLs were significant as marker main effects, 48 marker×environment interaction effects and eleven QTLs with both effects (Figure 2, Table 13, Appendix 7). Overall 24 QTLs showed favourable effects derived from the presence of exotic alleles. Out of 41 QTLs only 15 (36.6%) QTLs for agronomic traits were identified with favourable effects. Six (66.7%) QTLs showed favourable effects for quality parameters. Seven QTLs found in disease resistances, thereof three (43%) QTLs showed favourable effects.
In Appendix 9, relative performances of exotic alleles (Syn-84) of marker main effects and marker×environment interaction effects were detailed listed according to traits and chromosomes. In the following, QTLs are described for each trait separately.

Brittleness (BRT)

For the agronomic trait BRT, tested in two environments, four QTLs were revealed the analysis. Two QTLs were significant for marker main effects on chromosomes 3A and 3B. Marker×environment interaction effects were significant on chromosomes 2A and 6D. Exotic alleles were responsible at all identified QTLs. The QTL, *QBrt.T84-3A*, explained 33.6% of the genetic variance and increased BRT by 69.8%.

Tillers per square meter (EAR)

EAR were measured in seven environments. The analysis revealed four QTLs for EAR. The QTL, *QEar.T84-7A*, was significant for a marker main effect and explained 8.9% of the genetic variance. The presence of exotic alleles at this QTL reduced EAR by 50.4 tillers. The remaining three QTLs were located on chromosomes 2A, 5B and 7B with significant marker×environment interaction effects.

Grain number per ear (GNE)

Five QTLs were ascertained for GNE, tested in two environments. Significant marker main effects were computed at four loci. One of them showed a favourable effect derived from exotic alleles. But this QTL, *QGne.T84-1D*, explained only 1.6% of the genetic variance. Otherwise, at the QTL, *QGne.T84-3A*, explaining 20.6% of the genetic variance, the presence of exotic alleles decreased GNE by 7.4 grains per ear. The marker×environment interaction effect was significant at one QTL on chromosome 1B. This locus explained 12.6% of the genetic variance.

Days until heading (HEA)

Measured in eight environments, ten QTLs were determined for HEA. Six QTLs were significant for marker main effects. One QTL was significant for a marker main effect as well as for a marker×environment interaction effect, located on chromosome 5A. Six QTLs were associated with a favourable HEA by up to 1.9 days. Thereof, at the QTL, *QHea.T84-4*, exotic alleles explained 20.4% of the genetic variance. The remaining three loci were significant for marker×environment interaction effects on chromosomes 6B, 1D and 2D.

Plant height (HEI)

Altogether, ten QTLs were identified for HEI, tested in eight environments. Six QTLs were significant as marker main effects. One QTL showed marker main and marker×environment interaction effect on chromosome 5A. The only favourable QTL, *QHei.T84-4Ab*, was identified on chromosome 4B. This locus explained 10.2% of the exotic variance and exotic alleles revealed a shorting of HEI by 6.2 cm. The strongest unfavourable effect showed the QTL, *QHei.T84-4D*, explaining a genetic variance by 13.7%. At this locus, the absence of exotic alleles released an extension of HEI by 7.0 cm. Marker×environment interaction effects were significant at three QTLs on chromosomes 5B, 7B and 6D.

Harvest index (HI)

HI was measured in two environments. Four QTLs were detected for HI. Three QTLs were located with significant marker main effects on chromosomes 3B, 4B and 7D. These QTLs explained up to 5.4% of the genetic variance. The presence of exotic alleles reduced HI by up to 9.0%. For one QTL, a significant marker×environment effect was mapped on chromosome 1B.

Grain test weight (HLW)

Five QTLs were localised for HLW across five environments. Three QTLs were significant for marker main effects on chromosomes 5A, 5B and 7D. Two QTLs presented significant marker×environment interaction effects on chromosomes 2A and 5B. At one QTL, *QHlw.T84-5Aa*, exotic alleles suggested an increase of HLW. Marker×environment interaction effects revealed stronger genetic variance by 7.2% in comparison with the marker main effects.

Lodging at harvest (LAH)

LAH was measured in five environments. Seven QTLs were identified for LAH. One QTL was detected with a significant marker main effect on chromosome 4D. The QTL, *QLah.T84-4D*, explained 7.2% of the genetic variance and exotic alleles increased LAH by 32.7% with 1.3 rating units. Six QTLs were localised with significant marker×environment interaction effects on chromosomes 5A, 5B, 5D, 7A and 7B. At these loci the exotic allele showed controversial effects across environments as an indication of crossover interactions. The strongest explained genetic variance was 16.3% at the QTL *QLah.T84-5B*.

Thousand grain weight (TGW)

For TGW 12 QTLs were detected across six environments. Six loci showed significance for marker main effects, whereas four loci revealed significant marker×environment interaction effects. Two QTLs combined marker main effects and a marker×environment interaction effects on chromosomes 2A and 7A. Six favourable QTL effects were influenced by the presence of exotic alleles. The QTL, *QTgw.T84-4A*, revealed the strongest effect by explaining 17.2% of the genetic variance. In addition, exotic alleles increased TGW by 7.3 g at the QTL *QTgw.T84-4D*.

Grain yield (YLD)

In seven environments YLD was tested. Eight QTLs were identified. Five QTLs were computed with significant marker main effects. Two of them also exhibited marker×environment interaction effects on chromosomes 3A and 3B. At all QTLs, exotic alleles revealed an unfavourable effect in terms of the breeding effort. The exotic genotype was responsible for an unfavourable decreasing of YLD. The QTL, *QYld.T84-3A*, showed the strongest unfavourable effect with an explained genetic variance of 33.1%. At this locus, exotic alleles reduced YLD by 27.4% with 18.3 dt ha^{-1}. The remaining three QTLs were significant for marker×environment interaction effects on chromosomes 5A, 2B and 4B.

Grain hardness (GH)

Four QTLs were determined for the quality parameter GH, tested in two environments. Three QTLs exhibited significant marker main effects on chromosomes 3B, 5B and 3D. One QTL showed a significant marker×environment interaction effect on chromosome 6B. The QTL, *QGh.T84-3B*, was associated with a favourable effect for GH. This locus explained 2.9% of the genetic variance. In addition, exotic alleles increased GH by 3.6%. The locus, *QGh.T84-5D*, explained 54.5% of the genetic variance. At this QTL exotic alleles possessed an unfavourable effect with a decrease of GH by 15.7%.

Grain protein content (GPC)

The trait GPC was measured in three environments, seven QTLs were identified. Three QTLs were detected with significant marker main effects, where exotic alleles revealed an increasing of GPC at all loci. The QTL, *QGpc.T84-4D*, explained 4.0% of the genetic variance and the exotic alleles increased GPC by 0.8%. The remaining four QTLs showed significant marker×environment interaction effects. Relative performances of the exotic genotype ranged between -0.7% and 11.4%, thus these loci were crossover interactions.

Sedimentation value (SED)

Seven QTLs were ascertained for SED in two tested environments. While three QTLs exhibited significant marker main effects, four QTL showed significant marker×environment interaction effects. At two QTLs, *QSed.T84-5A* and *QSed.T84-6B*, the presence of exotic alleles revealed a favourable increase of SED by 14.0% and 19.2%, respectively.

Leaf rust (LR)

LR was measured in two environments. Two QTLs were identified for the disease resistance against LR. Both QTLs were significant for marker×environment interaction effects. Exotic alleles showed controversial effects between -22.3% and 216.0% as crossover interaction.

Powdery mildew (PM)

Across eight environments, a total of eleven QTLs were localised for PM leaf symptoms. Marker main effects were present at seven QTLs, whereas five concurrently showed marker×environment interaction effects. Two QTLs were found on chromosomes 2B and 7D, where exotic alleles led to favourable decrease in PM. At the QTL, *QPm.T84-7D*, exotic alleles explained 20.9% of the genetic variance and favourably reduced PM leaf symptoms by 35.4%. On chromosomes 2A, 4A and 5D exotic alleles caused the susceptibility to PM by 26.0%, 25.2% and 28.3%, respectively. The strongest susceptibility to PM was found at the QTL, *QPm.T84-7B*, which explained 7.2% of the genetic variance. At this locus, the presence of exotic alleles increased PM leaf symptoms by 38.0%.

Septoria leaf blotch (SEP)

SEP was measured in three environments. Five QTLs were detected with significant marker×environment interaction effects. The QTLs explained up to 8.6% of the genetic variance. The relative performance ranged between -25.4% and 20.6% due to the appearance of crossover interactions.

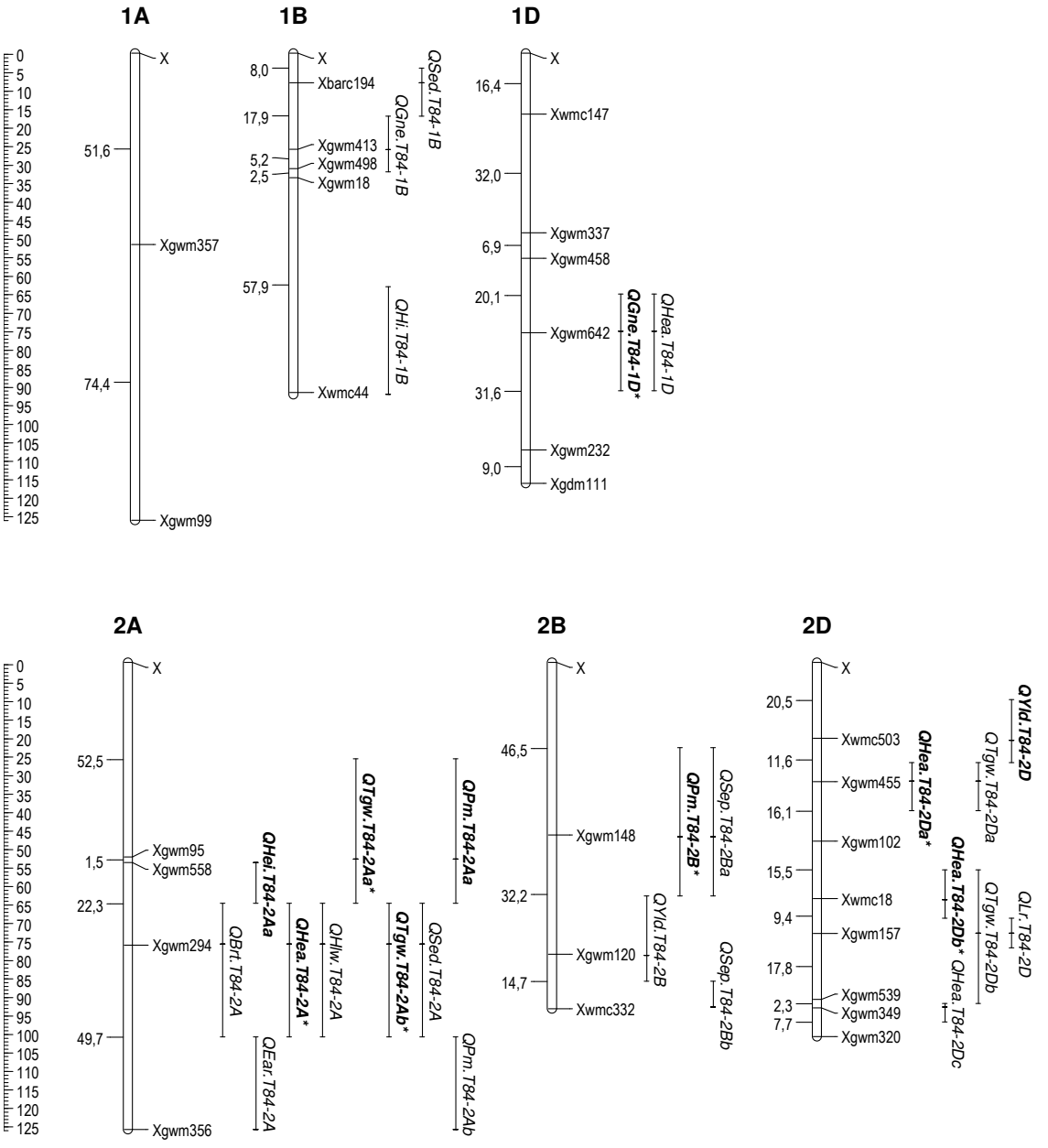

Figure 2: Localisation of 105 QTLs (P = 0.01) including 23 favourable QTL effects for agronomic traits, quality parameters and disease resistances in T84, detected in high N-level using a three-way ANOVA single-locus analysis (ANOVA I).

This graphical map was computed using MapChart (Voorrips 2002) in the high N-supply using 94 markers with genetic map positions according Somers et al. (2004). The ruler (in cM) was on the left. Mapped markers were indicated on the right and their corresponding genetic distances (cM) were indicated on the left. QTL confidence interval was indicated by a vertical bar, whereas F-value maximal of a significant marker×trait association (P = 0.01) was pointed by a horizontal bar. Bold QTLs were marker main effects and not bold QTLs were marker×environment interaction effects. QTLs marked with an asterisk were specified as favourable QTLs, where the exotic genotype (Syn-84) improved the trait performance in regard to the breeding effort.

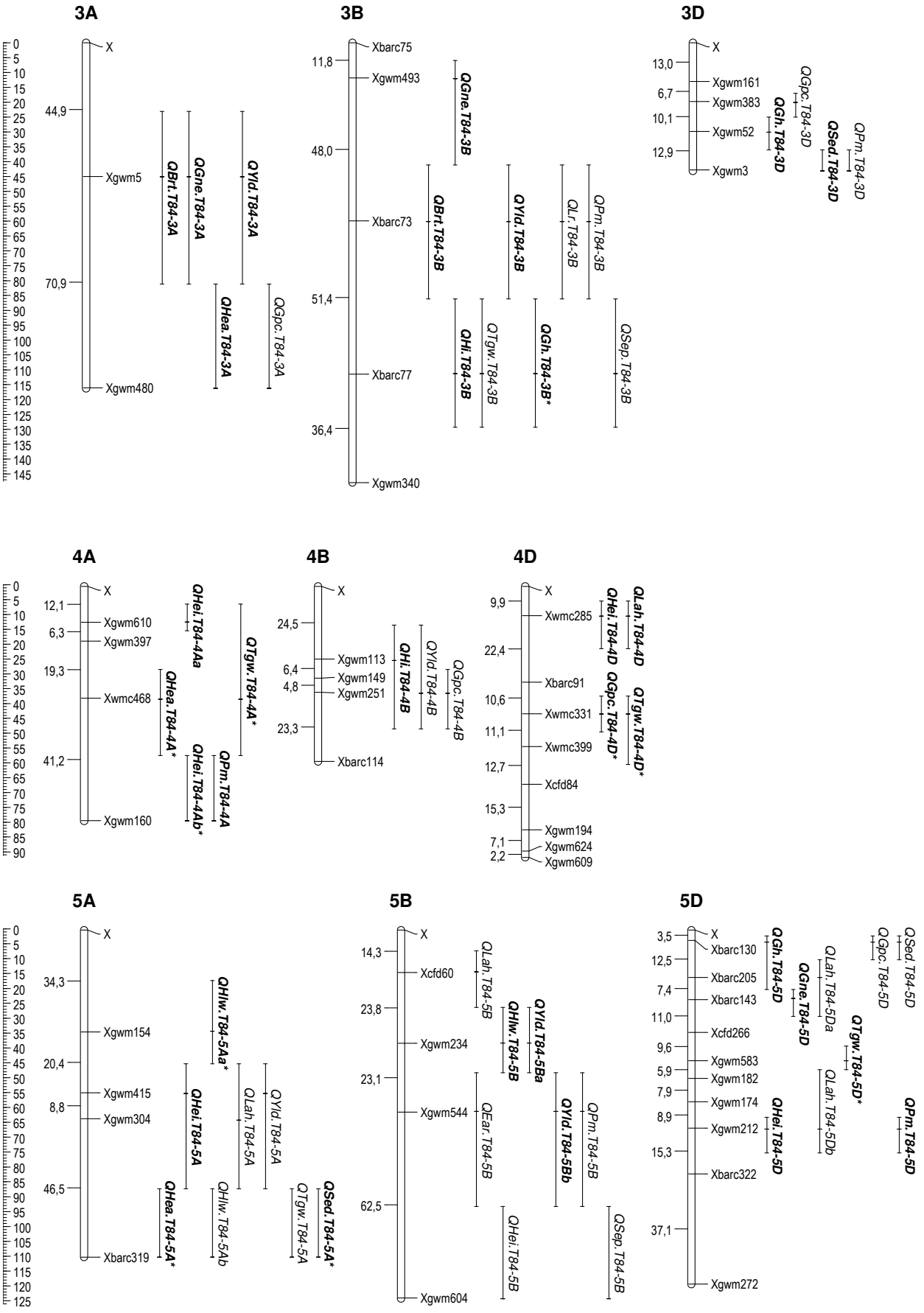

Figure 2: Continued.

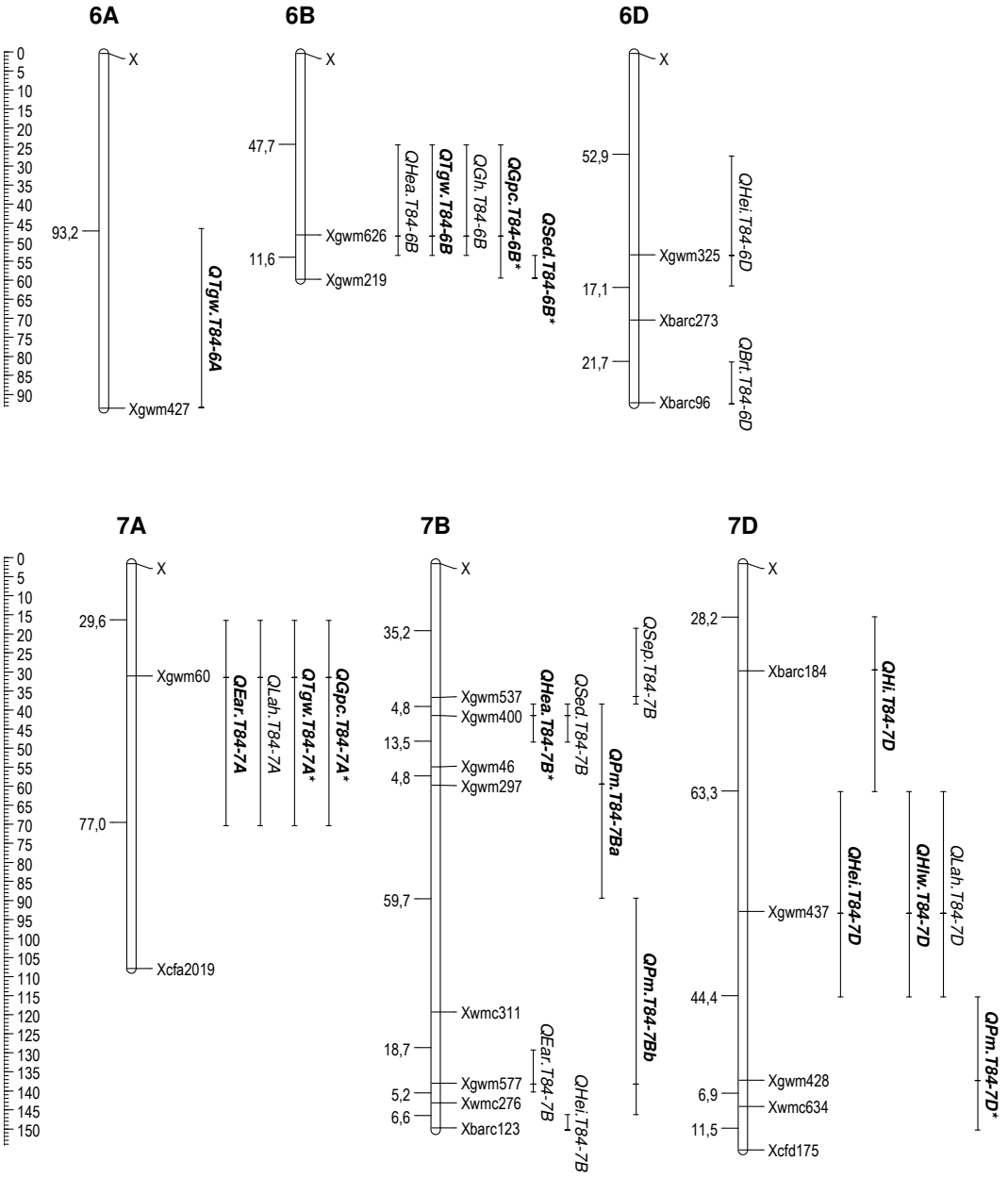

Figure 2: Continued.

Table 13: Localisation of 57 QTLs as marker main effects (P = 0.01) in T84, computed in high N-level with 94 markers using a three-way ANOVA single-locus analysis (ANOVA I).

Trait	Marker	Chr.	Pos. (cM)	n [aa]	Effect	Sign.	F-val.	R^2 (%)	RP [aa]	N+ [AA]	N+ [aa]	Diff. [aa]	QTL	QTL effect
BRT	Xgwm5	3A	45	13	M	**	158.5	33.6	69.8	1.1	1.9	0.8	*QBrt.T84-3A*	-
BRT	Xbarc73	3B	60	7	M	**	51.9	17.9	68.7	1.1	1.9	0.8	*QBrt.T84-3B*	-
EAR	Xgwm60	7A	30	28	M	*	16.3	8.9	-8.1	619.6	569.2	-50.4	*QEar.T84-7A*	-
GNE	Xgwm642	1D	75	21	M	*	7.8	1.6	6.2	27.3	29.0	1.7	*QGne.T84-1D*	+
GNE	Xgwm5	3A	45	13	M	**	137.0	20.6	-26.5	28.0	20.6	-7.4	*QGne.T84-3A*	-
GNE	Xgwm493	3B	12	10	M	*	11.4	3.0	-11.5	27.6	24.4	-3.2	*QGne.T84-3B*	-
GNE	Xbarc143	5D	23	30	M	*	10.0	2.1	-4.8	28.0	26.6	-1.4	*QGne.T84-5D*	-
HEA	Xgwm294	2A	76	34	M	*	6.9	3.6	-1.1	86.1	85.2	-0.9	*QHea.T84-2A*	+
HEA	Xgwm455	2D	32	23	M	*	7.8	3.9	-1.4	86.2	85.0	-1.2	*QHea.T84-2Da*	+
HEA	Xwmc18	2D	64	17	M	*	7.5	3.7	-1.5	86.1	84.7	-1.4	*QHea.T84-2Db*	+
HEA	Xgwm480	3A	116	10	M	*	7.3	3.5	1.9	85.9	87.5	1.6	*QHea.T84-3A*	-
HEA	Xwmc468	4A	38	19	M	**	20.3	20.4	-2.3	86.3	84.4	-1.9	*QHea.T84-4A*	+
HEA	Xbarc319[1]	5A	110	20	M/M×E	**	13.9	8.7	-2.0	86.0	84.2	-1.8	*QHea.T84-5A*	+
HEA	Xgwm400	7B	40	35	M	*	7.2	3.2	-1.0	86.1	85.2	-0.9	*QHea.T84-7B*	+
HEI	Xgwm558	2A	54	24	M	*	7.9	4.7	3.6	96.6	100.1	3.5	*QHei.T84-2Aa*	-
HEI	Xgwm610	4A	12	23	M	**	11.7	5.9	4.4	96.7	100.9	4.2	*QHei.T84-4Aa*	-
HEI	Xgwm160	4A	79	21	M	**	21.5	10.2	-6.3	98.3	92.1	-6.2	*QHei.T84-4Ab*	+
HEI	Xwmc285	4D	10	8	M	*	10.4	13.7	7.2	96.8	103.8	7.0	*QHei.T84-4D*	-
HEI	Xgwm415×	5A	55	20	M/M×E	*	9.7	5.3	4.5	97.0	101.4	4.4	*QHei.T84-5A*	-
HEI	Xgwm304	5A	64	19	M/M×E	*	8.8	4.9	4.5	97.0	101.4	4.4	"	-
HEI	Xgwm212	5D	67	23	M	*	7.4	3.5	3.5	97.1	100.5	3.4	*QHei.T84-5D*	-
HEI	Xgwm437	7D	92	22	M	*	8.9	4.2	3.9	97.2	101.0	3.8	*QHei.T84-7D*	-
HI	Xbarc77	3B	111	39	M	**	15.0	5.4	-6.2	0.4	0.4	0.0	*QHi.T84-3B*	-
HI	Xgwm113×	4B	25	22	M	**	17.2	5.2	-8.8	0.4	0.4	0.0	*QHi.T84-4B*	-
HI	Xgwm251	4B	36	13	M	*	11.7	3.2	-9.0	0.4	0.4	0.0	"	-
HI	Xbarc184	7D	28	42	M	*	7.5	2.3	-4.5	0.4	0.4	0.0	*QHi.T84-7D*	-
HLW	Xgwm154	5A	34	13	M	*	8.2	2.7	0.9	78.2	78.9	0.7	*QHlw.T84-5Aa*	+
HLW	Xgwm234	5B	38	13	M	*	10.9	5.1	-1.3	78.4	77.4	-1.0	*QHlw.T84-5B*	-
HLW	Xgwm437	7D	92	22	M	*	9.0	2.6	-0.7	78.3	77.8	-0.5	*QHlw.T84-7D*	-
LAH	Xwmc285	4D	10	8	M	*	8.3	7.2	32.7	3.9	5.2	1.3	*QLah.T84-4D*	-
TGW	Xgwm95	2A	53	30	M	*	7.7	3.9	3.8	41.7	43.3	1.6	*QTgw.T84-2Aa*	+
TGW	Xgwm294	2A	76	34	M/M×E	**	17.5	11.8	6.2	41.5	44.1	2.6	*QTgw.T84-2Ab*	+
TGW	Xgwm610	4A	12	23	M	*	8.2	4.3	4.2	41.8	43.6	1.8	*QTgw.T84-4A*	+
TGW	Xgwm397	4A	18	23	M	*	9.0	4.5	4.2	41.9	43.7	1.8	"	+
TGW	Xwmc468×	4A	38	19	M	**	17.9	17.2	6.3	42.0	44.6	2.6	"	+
TGW	Xwmc331×	4D	43	8	M	*	10.5	5.1	7.3	41.7	44.8	3.1	*QTgw.T84-4D*	+
TGW	Xwmc399	4D	54	13	M	*	9.3	4.5	5.5	41.7	44.0	2.3	"	+
TGW	Xgwm583	5D	44	29	M	*	8.0	3.7	3.6	41.7	43.2	1.5	*QTgw.T84-5D*	+
TGW	Xgwm427	6A	93	27	M	**	15.6	6.9	-5.2	42.2	40.0	-2.2	*QTgw.T84-6A*	-
TGW	Xgwm626	6B	48	23	M	**	16.0	8.2	-6.0	42.2	39.7	-2.5	*QTgw.T84-6B*	-
TGW	Xgwm60	7A	30	28	M/M×E	**	17.4	10.2	6.2	41.6	44.2	2.6	*QTgw.T84-7A*	+

Table 13: Continued.

Trait	Marker	Chr.	Pos. (cM)	n [aa]	Effect	Sign.	F-val.	R^2 (%)	RP [aa]	N+ [AA]	N+ [aa]	Diff. [aa]	QTL	QTL effect
YLD	Xwmc503	2D	21	9	M	*	8.9	9.3	-11.7	66.3	58.5	-7.8	*QYld.T84-2D*	-
YLD	Xgwm5	3A	45	13	M/M×E	*	16.2	33.1	-27.4	66.6	48.3	-18.3	*QYld.T84-3A*	-
YLD	Xbarc73	3B	60	7	M/M×E	*	10.8	7.1	-16.7	65.9	54.9	-11.0	*QYld.T84-3B*	-
YLD	Xgwm234	5B	38	13	M	**	15.7	7.9	-12.0	66.2	58.3	-7.9	*QYld.T84-5Ba*	-
YLD	Xgwm544	5B	61	8	M	*	9.9	5.3	-14.0	65.7	56.5	-9.2	*QYld.T84-5Bb*	-
GH	Xbarc77	3B	111	39	M	*	7.2	2.9	3.6	54.4	56.3	1.9	*QGh.T84-3B*	+
GH	Xgwm52	3D	30	25	M	*	10.4	3.5	-4.8	55.4	52.8	-2.6	*QGh.T84-3D*	-
GH	Xbarc130×	5D	4	35	M	**	432.4	54.5	-15.7	56.5	47.7	-8.8	*QGh.T84-5D*	-
GH	Xbarc205[1]	5D	16	37	M	*	11.2	3.8	-4.2	55.5	53.2	-2.3	"	-
GPC	Xwmc331	4D	43	8	M	*	12.3	4.0	5.8	13.7	14.5	0.8	*QGpc.T84-4D*	+
GPC	Xgwm626×	6B	48	23	M	**	22.1	5.0	4.2	13.6	14.2	0.6	*QGpc.T84-6B*	+
GPC	Xgwm219	6B	59	19	M	**	15.4	3.4	3.8	13.7	14.2	0.5	"	+
GPC	Xgwm60	7A	30	28	M	*	8.4	2.8	2.8	13.7	14.0	0.3	*QGpc.T84-7A*	+
SED	Xgwm3	3D	43	33	M	*	8.0	1.4	-8.3	45.1	41.3	-3.8	*QSed.T84-3D*	-
SED	Xbarc319[1]	5A	110	20	M	**	12.8	2.3	14.0	44.2	50.4	6.2	*QSed.T84-5A*	+
SED	Xgwm219	6B	59	19	M	*	17.5	4.1	19.2	43.8	52.2	8.4	*QSed.T84-6B*	+
PM	Xgwm95×	2A	53	30	M	*	9.3	4.8	25.1	3.4	4.3	0.9	*QPm.T84-2Aa*	-
PM	Xgwm558	2A	54	24	M	*	8.1	4.8	26.0	3.4	4.3	0.9	"	-
PM	Xgwm160	4A	79	21	M	*	7.2	3.5	25.2	3.5	4.3	0.8	*QPm.T84-4A*	-
PM	Xgwm148	2B	47	45	M/M×E	*	9.8	5.3	-20.3	3.7	3.0	-0.7	*QPm.T84-2B*	+
PM	Xgwm400	7B	40	35	M/M×E	*	7.6	4.3	22.6	3.4	4.2	0.8	*QPm.T84-7Ba*	-
PM	Xgwm46	7B	54	42	M/M×E	*	10.3	6.2	25.0	3.3	4.2	0.9	"	-
PM	Xgwm297×	7B	58	39	M/M×E	**	12.2	6.7	27.7	3.4	4.3	0.9	"	-
PM	Xwmc311	7B	118	19	M/M×E	*	10.0	6.4	34.0	3.4	4.6	1.2	*QPm.T84-7Bb*	-
PM	Xgwm577×	7B	137	18	M	**	13.2	7.2	38.0	3.4	4.7	1.3	"	-
PM	Xwmc276	7B	142	14	M/M×E	*	7.1	5.5	32.7	3.5	4.6	1.1	"	-
PM	Xgwm212	5D	67	23	M/M×E	*	9.0	4.9	28.3	3.4	4.4	1.0	*QPm.T84-5D*	-
PM	Xgwm428×	7D	136	26	M/M×E	**	14.8	9.7	-35.4	3.7	2.4	-1.3	*QPm.T84-7D*	+
PM	Xwmc634	7D	143	21	M/M×E	**	14.7	20.9	-34.6	3.8	2.5	-1.3	"	+

Table 13: Continued.

Trait: BRT (Brittleness), EAR (Tillers per square meter), GNE (Grain number per ear), HEA (Days until heading), HEI (Plant height), HI (Harvest index), HLW (Grain test weight), LAH (Lodging at harvest), TGW (Thousand grain weight), YLD (Grain yield), GH (Grain hardness), GPC (Grain protein content), SED (Sedimentation value), PM (Powdery mildew).

Marker: Label of SSR marker. (×) Significant marker×trait association computed with the highest F-value in a linked QTL cluster with a distance ≤ 20 cM. (1) Marker was not described by Somers et al. (2004) and Sourdille et al. (2004), respectively, estimated position in cM on chromosome by linked marker positions described by Somers et al. (2004) and Song et al. (2005).

Chr.: Chromosomal location of the marker derived from Somers et al. (2004).

Pos.: Position of the marker in cM on chromosome derived from Somers et al. (2004).

n [aa]: Number of markers showing the exotic genotype (Syn-84).

Effect: A significant marker×trait association was specified with marker main effect (M) or marker×environment interaction effect (M×E).

Sign.: Level of significance computed using the GLM procedure of the significant marker×trait associations for marker main effect (M) or marker×environment interaction effect (M×E), (**) P = 0.001, (*) P = 0.01.

F-val.: F-value was computed using the GLM procedure.

R^2 (%): Proportion of the genetic variance computed using the GLM procedure, which was explained the marker main effect (M) or the marker×environment interaction effect (M×E).

RP [aa]: Relative performance of exotic genotype (Syn-84) at a given marker locus across all tested environments computed using the GLM procedure. Relative performance was computed as ([aa] - [AA])×100 / [AA], where [AA] or [aa] were LS-means of BC_2F_4 lines carrying the cultivar genotype (Triso) or the exotic genotype (Syn-84) at the given marker locus.

N+ [AA]: LS-means of trait values for N-supply N+ across all tested environments for BC_2F_4 lines carrying the cultivar genotype (Triso) at the given marker locus.

N+ [aa]: LS-means of trait values for N-supply N+ across all tested environments for BC_2F_4 lines carrying the exotic genotype (Syn-84) at the given marker locus.

Diff. [aa]: Difference between LS-means of the exotic and the cultivar genotype, N+ [aa] - N+ [AA].

QTL: A significant marker×trait association was specified as QTL, if marker main effect (M) or marker×environment interaction effect (M×E), was significant with P = 0.01 in the GLM procedure. Linked QTL with a ≤ 20 cM distance were interpreted as one QTL. The QTL label is consisting of Q (for QTL), YLD (tested trait), T84 (tested population), 4Ab (chromosome, where the QTL was detected and b for the second YLD-QTL on the same chromosome).

QTL effect: Relative performance of exotic genotype (Syn-84) at a given marker locus for N-supply N+ (two or three mineral N-applications) across all tested environments computed using the GLM procedure specified a favourable QTL effect (+) with a improved effect from the exotic genotype (Syn-84) compared with the cultivar genotype (Triso), a not favourable QTL effect (-) with a impaired effect from the exotic genotype (Syn-84) compared with the cultivar genotype (Triso) at a given marker locus.

3.6.2 ANOVA I - QTLs in D84

Altogether, 1,696 marker×trait combinations in high N-level were proved in D84. The three-way ANOVA single-locus analysis (ANOVA I) revealed 92 significant marker×trait associations significant computed as 58 marker main effects (Table 14) and 34 marker×environment interactions effects (Appendix 8). For five marker×trait associations both, marker main effects and marker×environment interaction effects were detected. Due to linkage between markers, these associations were summarised to 78 QTLs for 16 traits (Figure 3). At 48 QTLs marker main effects were significant. Five of them were also identified as marker×environment interaction effects. Marker×environment interaction effects were significant at 30 QTLs. Altogether, eleven QTLs showed favourable effects derived from the presence of exotic alleles. For agronomic traits seven (21%) QTLs with favourable effects were identified. Three (43%) QTLs showed favourable effects for quality parameter. One (15%) QTL revealed a favourable effect for disease resistance.
In Appendix 10, relative performances of the exotic genotype (Syn-84) at marker main effects and marker×environment interaction effects were listed according to traits and chromosomes. In the following, QTLs are presented for each trait separately.

Brittleness (BRT)

Two QTLs were identified for BRT. At one QTL a marker main effect was significant on chromosome 7D. At a QTL, *QBrt.D84-7D*, exotic alleles increased BRT by 12.9%. The significant marker×environment interaction effect was localised on chromosome 3B.

Tillers per square meter (EAR)

The analysis revealed two QTLs for EAR with significant marker×environment interaction effects. The substitution of donor alleles with exotic alleles reduced EAR by 20.4% on chromosome 4A and increased EAR by 20.8% on chromosome 5D, respectively.

Grain number per ear (GNE)

Five QTLs were detected for GNE on chromosomes 3A, 3B, 6B, 2D and 5D. The exotic genotype led to a reduction of up to 12.1% in GNE at four marker main effects. The strongest effect was located at a QTL, *QGne.D84-5D*, which explained 6.6% of the genetic variance.

Days until heading (HEA)

For HEA five QTLs were ascertained. Significant marker main effects were computed at five loci. Four showed favourable effects deriving from exotic alleles. At two loci marker main effects and marker×environment interaction effects were significant. BC_2F_4 lines carrying exotic alleles at the QTL, *QHea.D84-2Ac*, reduced HEA by up to 1.7 days. No marker×environment interaction effect was detected for HEA.

Plant height (HEI)

Eight QTLs were detected for HEI distributed on chromosomes 1A, 2A, 4A, 5A, 7B, 2D and 4D. At four QTLs marker main effects, at three loci marker×environment interaction effects and at one locus both effects were significant. The donor genotype caused a decrease in HEI at all QTLs. At the strongest QTL effect, *QHei.D84-4D*, the exotic genotype increased HEI by up to 7.4%.

Harvest index (HI)

The analysis revealed five QTLs for HI. Four loci were identified as significant marker main effects. At all QTLs exotic alleles reduced HI by up to 10.9%. The strongest effect was at the QTL *QHi.D84-4D*. The remaining locus was identified as a marker×environment interaction effect on chromosome 3A.

Grain test weight (HLW)

For HLW five QTLs were localised on chromosomes 5A, 1B, 6B, 7B and 5D. At three loci marker main effects and at two loci marker×environment interaction effects were significant. The exotic genotype revealed an increase in HLW at the QTL *QHlw.D84-1B*.

Lodging at harvest (LAH)

Three QTLs were identified for LAH as marker main effects. At these QTLs donor alleles contributed the favourable decrease of LAH. The stongest QTL effect at a QTL, *QLah.D84-6B*, explained 9.0% of the genetic variance and exotic alleles increased LAH by 29.2%. No marker× environment interaction effect was detected for LAH.

Thousand grain weight (TGW)

Five QTLs were localised for TGW. Three QTLs were significant for marker main effects on chromosomes 2A, 6B and 2D. Two QTLs presented significant marker×environment interaction effects on chromosomes 2A and 7A. At two QTLs, *QTgw.D84-2A* and *QTgw.D84-2D*, exotic alleles suggested an increasing of TGW by up to 6.6%, which explained 12.7% of the genetic variance.

Grain yield (YLD)

Altogether, eleven QTLs were detected for YLD. Marker main effects were identified at five QTLs. One QTL showed marker main and marker×environment interaction effects. Remaining five QTLs were analysed as significant marker×environment interaction effects on chromosomes 7B, 2D, 4D and 5D. At all loci exotic alleles led to a reduction of up to 13.4% in YLD. The strongest effect was detected at a QTL, *QYld.D84-3A*, which explained 15.4% of the genetic variance.

Grain hardness (GH)

Three QTLs were localised for GH on the D genome. All QTLs were detected as significant marker main effects. Exotic alleles revealed a favourable increasing of GH by 4.6% at the QTL *QGh.D84-2D*. At the QTL, *QGh.D84-5Da*, the exotic genotype explained 40.5% of the genetic variance and reduced GH by 14.6%.

Grain protein content (GPC)

For GPC four QTLs were detected. One significant marker main effect was computed at the QTL *QGpc.D84-4A*, where the favourable effect derived from exotic alleles with increased GPC by 3.0%. The other three loci were identified as significant marker×environment interaction effects on chromosomes 2B, 2D and 4D.

Sedimentation value (SED)

The analysis revealed five QTLs for SED. Three QTLs were significant for marker main effects on chromosomes 6B, 1D and 4D. Two QTLs presented significant marker×environment interaction effects on chromosomes 1A and 2A. At one QTL, *QSed.D84-6B*, the exotic genotype suggested a favourable increasing of SED by 13.4%. The strongest effect was identified at the QTL, *QSed.D84-4D*, where exotic alleles reduced SED by 16.1%.

Leaf rust (LR)

One QTL, *QLr.D84-7B*, was detected for resistance against LR as a significant marker main effect. At this locus the presence of exotic alleles unfavourable increased LR by 63.2%. No marker×environment interaction effect was detected for LR.

Powdery mildew (PM)

Nine QTLs were determined for PM leaf symptoms on chromosomes 2A, 6A, 7B, 2D, 3D, 5D and 7D. At three QTLs marker main effects, at five loci marker×environment interaction effects and at one locus both effects were significant. At one QTL, *QPm.D84-2A*, the exotic genotype favourable reduced PM by 26.6%. Donor alleles caused a reduction in PM leaf symptoms at three loci by up to 34.3%.

Septoria leaf blotch (SEP)

Five QTLs were ascertained for SEP. Marker main effects were significant at two loci and marker×environment interaction effects were detected at three loci. At all QTLs the presence of the exotic genotype increased SEP symptoms by up to 12.4%.

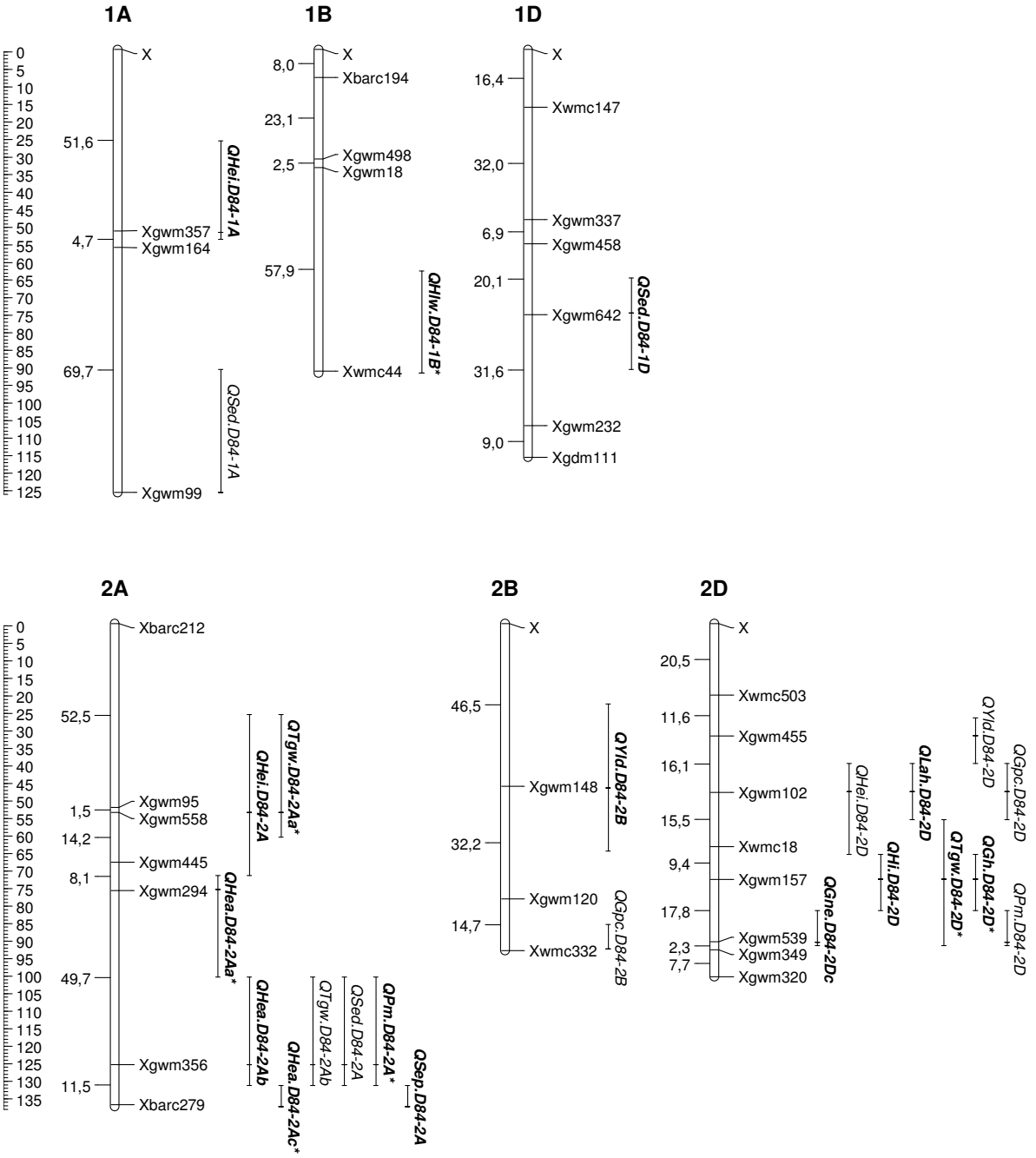

Figure 3: Localisation of 78 QTLs (P = 0.01) including 11 favourable QTL effects for agronomic traits, quality parameters and disease resistances in D84, detected in high N-level using a three-way ANOVA single-locus analysis (ANOVA I).

This graphical map was computed using MapChart (Voorrips 2002) in the high N-supply using 94 markers with genetic map positions according Somers et al. (2004). The ruler (in cM) was on the left. Mapped markers were indicated on the right and their corresponding genetic distances (cM) were indicated on the left. QTL confidence interval was indicated by a vertical bar, whereas F-value maximal of a significant marker×trait association (P = 0.01) was pointed by a horizontal bar. Bold QTLs were marker main effects and not bold QTLs were marker×environment interaction effects. QTLs marked with an asterisk were specified as favourable QTLs, where the exotic genotype (Syn-84) improved the trait performance in regard to the breeding effort.

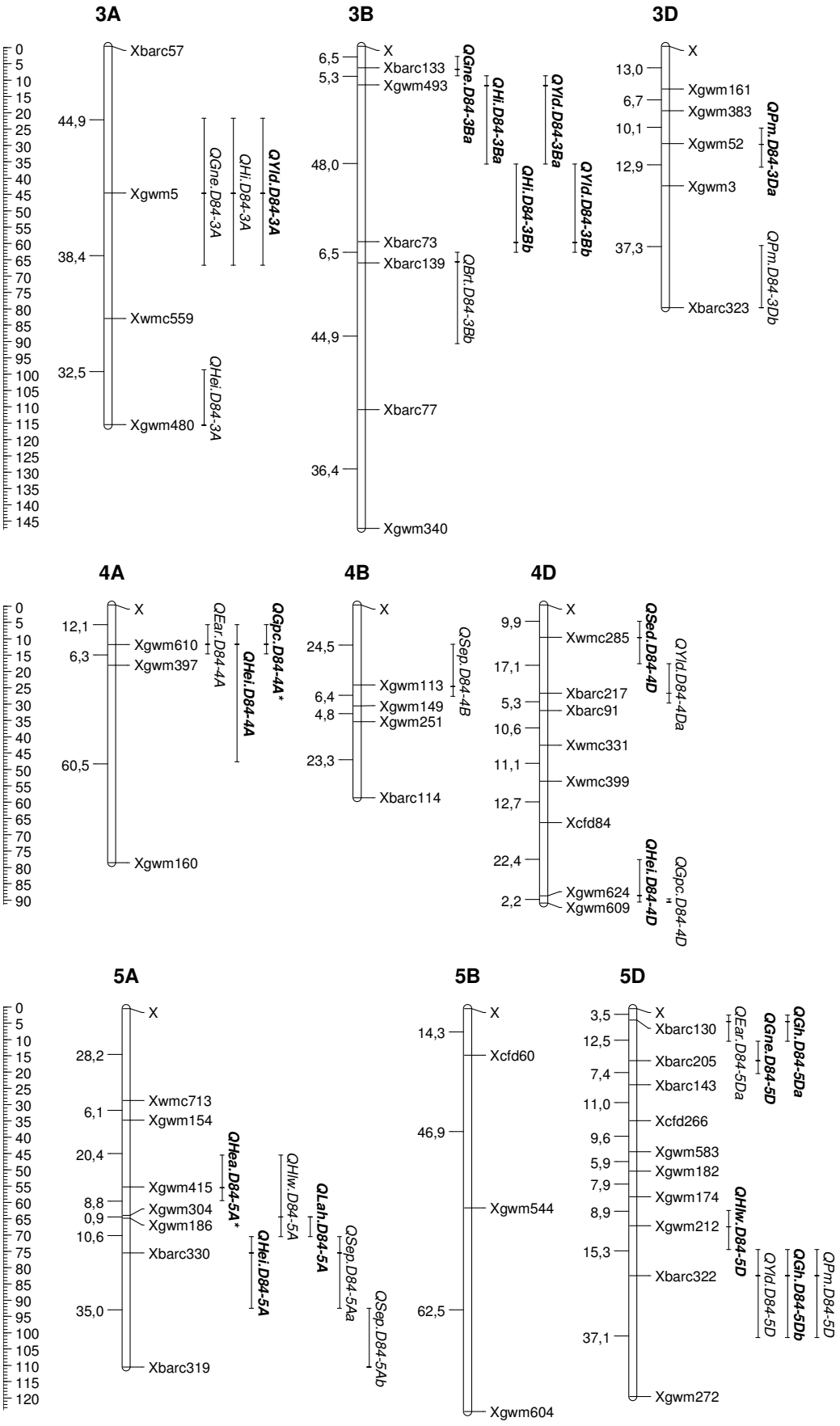

Figure 3: Continued.

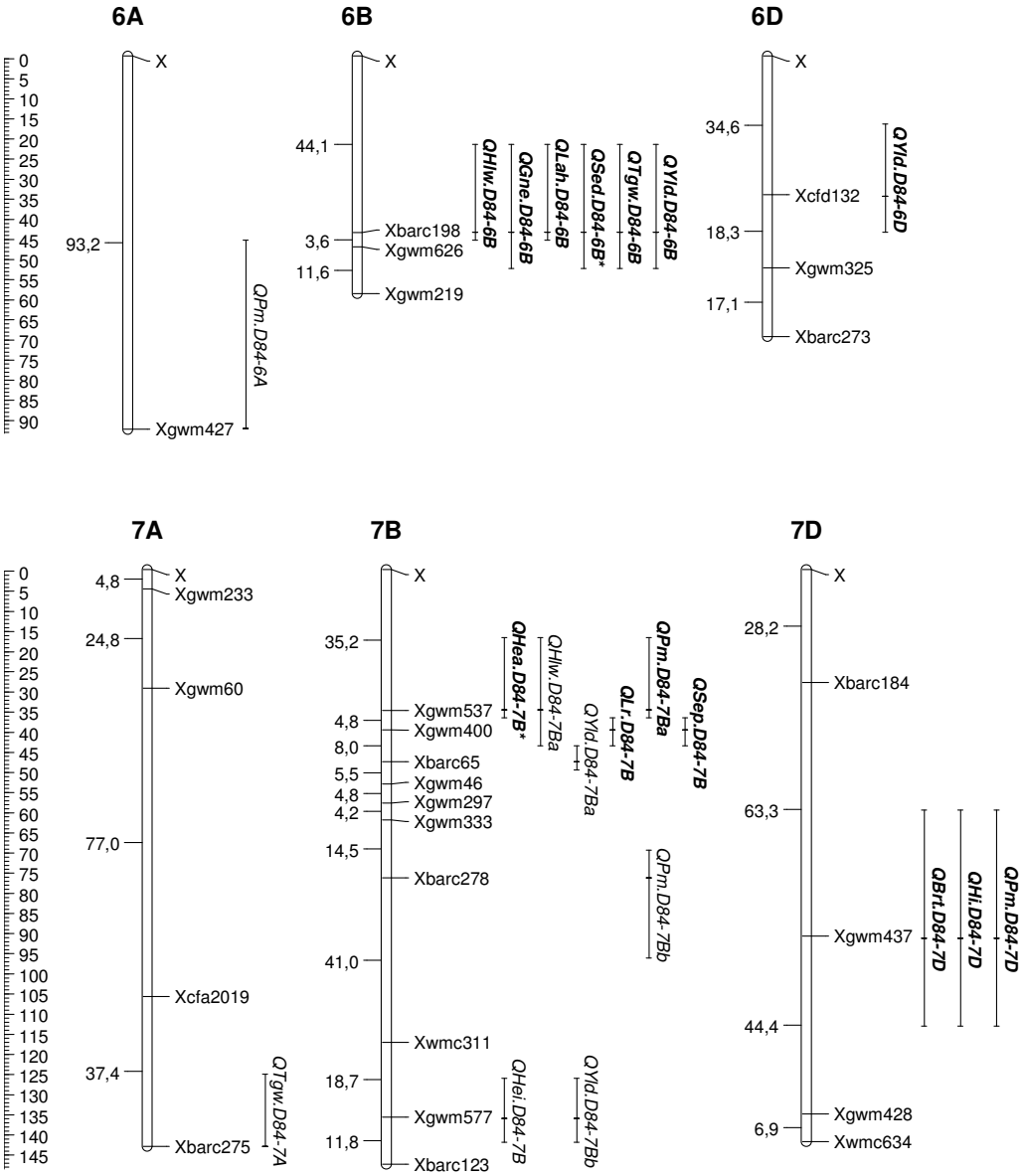

Figure 3: Continued.

Table 14: Localisation of 48 QTLs as marker main effects (P = 0.01) in D84, computed in high N-level with 106 markers using a three-way ANOVA single-locus analysis (ANOVA I).

Trait	Marker	Chr.	Pos. (cM)	n [aa]	Effect	Sign.	F-val.	R^2 (%)	RP [aa]	N+ [AA]	N+ [aa]	Diff. [aa]	QTL	QTL effect
BRT	Xgwm437	7D	92	27	M	*	8.3	3.2	12.9	1.1	1.3	0.2	*QBrt.D84-7D*	-
GNE	Xgwm539	2D	91	22	M	**	17.2	5.5	-10.6	28.1	25.1	-3.0	*QGne.D84-2Dc*	-
GNE	Xbarc133[1]	3B	7	11	M	*	8.5	3.2	-10.8	28.1	25.1	-3.0	*QGne.D84-3Ba*	-
GNE	Xbarc205[1]	5D	16	20	M	*	14.2	6.6	-12.1	28.2	24.8	-3.4	*QGne.D84-5D*	-
GNE	Xbarc198×	6B	44	22	M	**	14.9	4.8	-9.9	28.0	25.2	-2.8	*QGne.D84-6B*	-
GNE	Xgwm626	6B	48	15	M	*	10.8	4.4	-11.5	28.0	24.8	-3.2	"	-
HEA	Xgwm294	2A	76	23	M	*	7.1	4.2	-1.4	86.3	85.1	-1.2	*QHea.D84-2Aa*	+
HEA	Xgwm356	2A	126	26	M	*	7.3	4.9	1.3	86.1	87.3	1.2	*QHea.D84-2Ab*	-
HEA	Xbarc279[1]	2A	138	17	M/MxE	*	10.7	7.3	-2.0	86.4	84.7	-1.7	*QHea.D84-2Ac*	+
HEA	Xgwm415	5A	55	24	M/MxE	*	9.3	6.4	-1.7	86.4	84.9	-1.5	*QHea.D84-5A*	+
HEA	Xgwm537	7B	35	20	M	*	9.5	6.1	-1.8	86.3	84.8	-1.5	*QHea.D84-7B*	+
HEI	Xgwm357	1A	52	18	M	*	8.9	5.7	4.1	101.2	105.4	4.2	*QHei.D84-1A*	-
HEI	Xgwm95	2A	53	14	M/MxE	*	11.2	8.9	5.7	101.1	106.9	5.8	*QHei.D84-2A*	-
HEI	Xgwm558×	2A	54	17	M	**	15.4	9.7	5.6	101.1	106.7	5.6	"	-
HEI	Xgwm445	2A	68	7	M	*	7.4	4.6	5.3	101.3	106.7	5.4	"	-
HEI	Xgwm610×	4A	12	20	M	*	10.9	6.3	4.1	101.2	105.4	4.2	*QHei.D84-4A*	-
HEI	Xgwm397	4A	18	18	M	*	10.7	6.5	4.3	101.1	105.4	4.3	"	-
HEI	Xgwm624×	4D	89	5	M	*	9.7	5.7	7.4	101.5	109.0	7.5	*QHei.D84-4D*	-
HEI	Xgwm609	4D	91	9	M	*	8.1	4.3	5.0	101.4	106.4	5.0	"	-
HEI	Xbarc330[1]	5A	75	19	M	**	16.3	14.7	4.6	101.0	105.7	4.7	*QHei.D84-5A*	-
HI	Xgwm157	2D	73	26	M	*	14.1	6.5	-7.2	0.4	0.4	0.0	*QHi.D84-2D*	-
HI	Xgwm493	3B	12	8	M	**	13.6	4.6	-10.9	0.4	0.4	0.0	*QHi.D84-3Ba*	-
HI	Xbarc73	3B	60	10	M	*	9.7	3.5	-8.5	0.4	0.4	0.0	*QHi.D84-3Bb*	-
HI	Xgwm437	7D	92	27	M	*	10.7	3.7	-5.5	0.4	0.4	0.0	*QHi.D84-7D*	-
HLW	Xwmc44	1B	92	14	M	*	10.5	8.8	1.5	76.9	78.0	1.1	*QHlw.D84-1B*	+
HLW	Xgwm212	5D	67	19	M	*	10.4	6.0	-1.4	77.3	76.2	-1.1	*QHlw.D84-5D*	-
HLW	Xbarc198	6B	44	22	M	*	9.2	3.4	-1.1	77.2	76.4	-0.8	*QHlw.D84-6B*	-
LAH	Xgwm102	2D	48	31	M	*	12.0	6.3	21.5	4.4	5.3	0.9	*QLah.D84-2D*	-
LAH	Xgwm186	5A	64	25	M	*	11.4	6.9	24.0	4.4	5.5	1.1	*QLah.D84-5A*	-
LAH	Xbarc198	6B	44	22	M	**	16.7	9.0	29.2	4.4	5.7	1.3	*QLah.D84-6B*	-
TGW	Xgwm95	2A	53	14	M	*	7.7	5.0	5.7	44.3	46.8	2.5	*QTgw.D84-2Aa*	+
TGW	Xgwm558×	2A	54	17	M	*	8.0	5.0	5.2	44.2	46.6	2.4	"	+
TGW	Xgwm157×	2D	73	26	M	**	20.0	12.7	6.6	44.1	47.0	2.9	*QTgw.D84-2D*	+
TGW	Xgwm539	2D	91	22	M	**	15.3	8.8	6.0	44.1	46.7	2.6	"	+
TGW	Xbarc198×	6B	44	22	M	**	14.3	9.6	-6.3	45.0	42.1	-2.9	*QTgw.D84-6B*	-
TGW	Xgwm626	6B	48	15	M	*	10.1	6.5	-6.2	44.7	42.0	-2.7	"	-

Table 14: Continued.

Trait	Marker	Chr.	Pos. (cM)	n [aa]	Effect	Sign.	F-val.	R^2 (%)	RP [aa]	N+ [AA]	N+ [aa]	Diff. [aa]	QTL	QTL effect
YLD	Xgwm148	2B	47	13	M	**	13.1	8.1	-9.7	62.7	56.6	-6.1	*QYld.D84-2B*	-
YLD	Xgwm5	3A	45	13	M/M×E	*	12.5	15.4	-13.4	62.6	54.2	-8.4	*QYld.D84-3A*	-
YLD	Xgwm493	3B	12	8	M	*	10.2	5.7	-10.6	62.3	55.7	-6.6	*QYld.D84-3Ba*	-
YLD	Xbarc73	3B	60	10	M	*	8.4	4.1	-7.8	62.2	57.4	-4.8	*QYld.D84-3Bb*	-
YLD	Xbarc198×	6B	44	22	M	**	23.8	12.2	-9.2	63.0	57.3	-5.7	*QYld.D84-6B*	-
YLD	Xgwm626	6B	48	15	M	*	7.4	4.0	-6.6	62.4	58.3	-4.1	"	-
YLD	Xcfd132	6D	35	8	M	*	8.0	9.0	-10.1	62.5	56.2	-6.3	*QYld.D84-6D*	-
GH	Xgwm157	2D	73	26	M	*	8.2	3.8	4.6	55.4	57.9	2.5	*QGh.D84-2D*	+
GH	Xbarc130	5D	4	28	M	**	223.3	40.5	-14.6	57.0	48.7	-8.3	*QGh.D84-5Da*	-
GH	Xbarc322[1]	5D	82	15	M	**	20.5	8.0	-8.2	56.2	51.6	-4.6	*QGh.D84-5Db*	-
GPC	Xgwm610	4A	12	20	M	*	9.9	3.8	3.0	13.5	13.9	0.4	*QGpc.D84-4A*	+
SED	Xgwm642	1D	75	27	M	**	12.8	3.1	-9.5	49.4	44.7	-4.7	*QSed.D84-1D*	-
SED	Xwmc285	4D	10	5	M	*	9.9	2.6	-16.1	50.2	42.1	-8.1	*QSed.D84-4D*	-
SED	Xbarc198×	6B	44	22	M	**	13.8	3.0	10.5	48.0	53.0	5.0	*QSed.D84-6B*	+
SED	Xgwm626	6B	48	15	M	**	13.2	3.4	13.4	47.9	54.3	6.4	"	+
LR	Xgwm400	7B	40	23	M	*	14.4	1.0	63.2	1.7	2.8	1.1	*QLr.D84-7B*	-
PM	Xgwm356	2A	126	26	M	*	8.0	7.9	-26.6	3.5	2.6	-0.9	*QPm.D84-2A*	+
PM	Xgwm52	3D	30	9	M	*	7.2	4.3	34.3	3.3	4.5	1.2	*QPm.D84-3Da*	-
PM	Xgwm537	7B	35	20	M	*	7.6	4.9	26.2	3.3	4.2	0.9	*QPm.D84-7Ba*	-
PM	Xgwm437	7D	92	27	M/M×E	*	7.7	5.5	24.4	3.3	4.1	0.8	*QPm.D84-7D*	-
SEP	Xbarc279[1]	2A	138	17	M	**	34.7	5.3	12.4	4.1	4.6	0.5	*QSep.D84-2A*	-
SEP	Xgwm400	7B	40	23	M	**	27.8	4.2	9.5	4.1	4.5	0.4	*QSep.D84-7B*	-

Table 14: Continued.

Trait: BRT (Brittleness), EAR (Tillers per square meter), GNE (Grain number per ear), HEA (Days until heading), HEI (Plant height), HI (Harvest index), HLW (Grain test weight), LAH (Lodging at harvest), TGW (Thousand grain weight), YLD (Grain yield), GH (Grain hardness), GPC (Grain protein content), SED (Sedimentation value), PM (Powdery mildew).

Marker: Label of SSR marker. (×) Significant marker×trait association computed with the highest F-value in a linked QTL cluster with a distance ≤ 20 cM. (1) Marker was not described by Somers et al. (2004) and Sourdille et al. (2004), respectively, estimated position in cM on chromosome by linked marker positions described by Somers et al. (2004) and Song et al. (2005).

Chr.: Chromosomal location of the marker derived from Somers et al. (2004).

Pos.: Position of the marker in cM on chromosome derived from Somers et al. (2004).

n [aa]: Number of markers showing the exotic genotype (Syn-84).

Effect: A significant marker×trait association was specified with marker main effect (M) or marker×environment interaction effect (M×E).

Sign.: Level of significance computed using the GLM procedure of the significant marker×trait associations for marker main effect (M) or marker×environment interaction effect (M×E), (**) P = 0.001, (*) P = 0.01.

F-val.: F-value was computed using the GLM procedure.

R^2 (%): Proportion of the genetic variance computed using the GLM procedure, which was explained the marker main effect (M) or the marker×environment interaction effect (M×E).

RP [aa]: Relative performance of exotic genotype (Syn-84) at a given marker locus across all tested environments computed using the GLM procedure. Relative performance was computed as ([aa] - [AA])×100 / [AA], where [AA] or [aa] were LS-means of BC_2F_4 lines carrying the cultivar genotype (Triso) or the exotic genotype (Syn-84) at the given marker locus.

N+ [AA]: LS-means of trait values for N-supply N+ across all tested environments for BC_2F_4 lines carrying the cultivar genotype (Triso) at the given marker locus.

N+ [aa]: LS-means of trait values for N-supply N+ across all tested environments for BC_2F_4 lines carrying the exotic genotype (Syn-84) at the given marker locus.

Diff. [aa]: Difference between LS-means of the exotic and the cultivar genotype, N+ [aa] - N+ [AA].

QTL: A significant marker×trait association was specified as QTL, if marker main effect (M) or marker×environment interaction effect (M×E), was significant with P = 0.01 in the GLM procedure. Linked QTL with a ≤ 20 cM distance were interpreted as one QTL. The QTL label is consisting of Q (for QTL), YLD (tested trait), T84 (tested population), 4Ab (chromosome, where the QTL was detected and b for the second YLD-QTL on the same chromosome).

QTL effect: Relative performance of exotic genotype (Syn-84) at a given marker locus for N-supply N+ (two or three mineral N-applications) across all tested environments computed using the GLM procedure specified a favourable QTL effect (+) with a improved effect from the exotic genotype (Syn-84) compared with the cultivar genotype (Triso), a not favourable QTL effect (-) with a impaired effect from the exotic genotype (Syn-84) compared with the cultivar genotype (Triso) at a given marker locus.

3.6.3 ANOVA - Comparison of QTLs detected in T84 and D84

Both analysed BC_2F_4 populations derived from the same exotic accession Syn-84. The donor genotypes of both advanced backcross populations have different genetic backgrounds based on the cultivar Triso and Devon. Hence, a comparison of the identified QTLs and their QTL effects in T84 and D84 may verify QTLs, where exotic alleles are conserved between the donor genotypes.

In total, 16 traits 1,504 marker×trait combinations computed in T84, resulted in 128 (8.5%) significant marker×trait associations, 1,696 marker×trait combinations tested in D84, revealed 92 (5.4%) significant marker×trait associations. The investigation of traits was conducted on 223 (T84) and 176 (D84) BC_2F_4 lines.

Exotic alleles influenced agronomic traits at 32.0% of all identified marker×trait associations tested in T84. In D84, the exotic genotype influenced agronomic traits at 37.0% of all detected marker×trait associations. Exotic alleles enhanced quality parameter at 7.0% and 7.6% of all computed marker×trait associations in T84 and D84, respectively. In T84, the disease resistances were impacted by exotic alleles at 5.5% of all located marker×trait associations. Exotic alleles influenced disease resistances at 7.6% of all tested marker×trait associations tested in D84. As a result of 24 (18.8%) favourable QTL effects in T84 and eleven (12.0%) favourable QTL effects in D84 were identified.

Altogether, 94 (T84) and 106 (D84) markers were simultaneously genotyped and used for the comparison. In order to compare marker×trait associations identical in T84 with D84, the position range of analysed markers was used for overlapping chromosome regions. Consequently, significant marker main effects as well as marker×environment interaction effects were implicated. The combination of marker×trait associations (T84 and D84) resulted in 193 significant marker×trait associations computed from 86 identical markers in both populations. In Appendix 11, a detailed characterisation of the comparison of relative performances of the exotic genotype at these verified marker×trait associations specified as marker main effect and/or marker×environment interaction effect is presented.

A QTL effect is described as common QTL if this effect is computed separately in both populations. Eleven (5.7%) common QTL effects located in T84 were validated in D84 (Table 15). Hence, at eight common QTLs the identical effect of exotic alleles in regard on breeding effort was validated in both populations. At chromosome 2A, agronomic traits TGW and HEA were favourable enhanced by the presence of the exotic genotype at two common QTLs, *QTgw.T84-2Aa* and *QTgw.D84-2Aa*, *QHea.T84-2A* and *QHea.D84-2Aa*. In contrast, at six common QTLs the donor allele controlled favourable QTL effects at these loci. Furthermore, at three common QTLs exotic alleles influenced the relative performance of exotic genotype similarly, while a marker main effect and a marker×environment interaction effect was computed at a common QTL. At common QTLs, *QTgw.T84-2Db* and *QTgw.D84-2D*, *QPm.T84-2Ab* and *QPm.D84-2A*, the exotic genotype revealed a favourable interaction between

TGW and PM. In addition, common QTLs were identified at the identical marker loci on chromosomes 2A (HEI and TGW) and 3A (GNE and YLD), respectively. However, mostly common QTLs (9) were associated with exotic alleles revealed from the A and B genomes. The remaining two common QTLs were influenced by exotic alleles conducted by *Ae. tauschii*.

In similar chromosome regions, further 21 QTLs detected in T84 were validated in D84 for agronomic traits BRT (3B), GNE (3B, 5D), HEA (5A, 7B), HEI (5A, 7B, 4D), HI (3B), HLW (5A), LAH (5A), TGW (7A) and YLD (2B, 3B, 2D), quality parameters GPC (4D) and SED (2A, 6B) and disease resistances PM (3D, 5D) and SEP (7B), listed in Appendix 11.

3.6.4 Pleiotropic effects in T84 and D84

Pleiotropic effects occur when a single gene influences multiple phenotypic traits. Deductive, this gene will have an effect on all traits simultaneously. In the following chapter, marker loci are described, where two or more significant QTL effects were established at the identical marker locus. In Appendix 9 and Appendix 10 the relative performances of the exotic genotype (Syn-84) of QTLs specified as marker main effect or/and marker×environment interaction effect computed using three-way ANOVA single-locus analysis (ANOVA I) for 16 quantitative traits in both populations T84 and D84 were compiled, respectively. In addition, the ascertained QTLs were depicted in genetic maps in Figure 2 (T84) and Figure 3 (D84).

In T84, at 38 marker loci associated with up to five phenotypic QTL effects were identified. Five QTL associated with BRT, HEA, HLW, TGW and SED were coexistent localised at the marker locus Xgwm294. Among these pleiotropic effects, the exotic genotype revealed favourable QTL effects at six marker loci (Xgwm455, Xwmc18, Xwmc468, Xwmc331, Xgwm219) improving two traits and at Xbarc319 improving four traits. Reduced HEA was associated with favourable increased TGW at marker loci Xgwm294, Xgwm455, Xwmc18, Xwmc468 and Xbarc319. At five loci on chromosomes 5A, 4D, 5D and 7D exotic alleles led to favourable increase HEI combined with unfavourable increased LAH. On chromosomes 3A and 3B the exotic genotype increased BRT and reduced GNE and YLD. Quality parameters, GPC and SED, were ascertained with identical QTL effects at two marker loci, Xbarc130 and Xgwm219. Hence, these coherences were in conformance with moderate positive correlations between LAH and HEI, GPC and SED, as well as moderate negative correlations between BRT and YLD, BRT and GNE and HEA and TGW.

In D84, 23 marker loci showed up to six phenotypic QTL effects simultaneously. Six QTL effects associated with reduced GNE, HLW, TGW, YLD and increased LAH and SED were mapped at the marker locus Xbarc198. Furthermore, alleles influenced four, three and two QTL effects at two, eight and 12 marker loci. At the same genomic region on chromosomes 3A and 3B the genotype revealed a decrease of GNE, YLD and HI. On chromosomes 5A and 2D alleles for HEI were associated with unfavourable increased LAH. These results were in agreement with moderate positive correlations between GNE and HI, HI and YLD and HEI and LAH.

Table 15: Eleven common QTLs (P = 0.01) in T84, validated in D84, computed using a three-way ANOVA single-locus analysis (ANOVA I).

Trait	QTL	Marker	Chr.	Range (cM)	Bin range	Effect	Sign.	F-val.	R^2 (%)	RP [aa]	N+ [aa]	QTL effect
GNE	*QGne.T84-3A*	Xgwm5	3A	45	C-3AL3-0.42	M	**	137.0	20.6	-26.5	20.6	-
	QGne.D84-3A	Xgwm5	3A	45	C-3AL3-0.42	M×E	*	8.1	2.0	-26.5	20.6	○
HEA	*QHea.T84-2A*	Xgwm294	2A	76	C-2AL1-0.85	M	*	6.9	3.6	-1.1	85.2	+
	QHea.D84-2Aa	Xgwm294	2A	76	C-2AL1-0.85	M	*	7.1	4.2	-1.4	85.1	+
HEI	*QHei.T84-2Aa*	Xgwm558	2A	54	C-2AL1-0.85	M	*	7.9	4.7	3.6	100.1	-
	QHei.D84-2A	Xgwm558	2A	53-68	C-2AS5-0.78-C-2AL1-0.85	M	**	15.4	9.7	5.6	106.7	-
	QHei.T84-4Aa	Xgwm610	4A	12	C-4AS1-0.20	M	**	11.7	5.9	4.4	100.9	-
	QHei.D84-4A	Xgwm610	4A	12-18	C-4AS1-0.20-4AL13-0.59-0.66	M	*	10.9	6.3	4.1	105.4	-
TGW	*QTgw.T84-2Aa*	Xgwm95	2A	53	C-2AS5-0.78	M	*	7.7	3.9	3.8	43.3	+
	QTgw.D84-2Aa	Xgwm95	2A	53	C-2AS5-0.78	M	*	7.7	5.0	5.7	46.8	+
	QTgw.T84-6B	Xgwm626	6B	48	C-6BS5-0.76	M	**	16.0	8.2	-6.0	39.7	-
	QTgw.D84-6B	Xgwm626	6B	44-48	C-6BS5-0.76	M	*	10.1	6.5	-6.2	42.0	-
	QTgw.T84-2Db	Xgwm157	2D	64-91	2DL3-0.49-0.76-C-2DL3-0.49	M×E	**	9.8	2.8	5.3	43.9	○
	QTgw.D84-2D	Xgwm157	2D	73-91	2DL3-0.49-0.76-C-2DL3-0.49	M	**	20.0	12.7	6.6	47.0	+
YLD	*QYld.T84-3A*	Xgwm5	3A	45	C-3AL3-0.42	M/M×E	*	16.2	33.1	-27.4	48.3	-
	QYld.D84-3A	Xgwm5	3A	45	C-3AL3-0.42	M/M×E	*	12.5	15.4	-13.4	54.2	-
	QYld.T84-3B	Xbarc73	3B	60	3BS1-0.33-0.57	M/M×E	*	10.8	7.1	-16.7	54.9	-
	QYld.D84-3Bb	Xbarc73	3B	60	3BS1-0.33-0.57	M	*	8.4	4.1	-7.8	57.4	-
GH	*QGh.T84-5D*	Xbarc130	5D	4-16	5DS2-0.78-1.00	M	**	432.4	54.5	-15.7	47.7	-
	QGh.D84-5Da	Xbarc130	5D	4	5DS2-0.78-1.00	M	**	223.3	40.5	-14.6	48.7	-
PM	*QPm.T84-2Ab*	Xgwm356	2A	126	C-2AL1-0.85	M×E	*	3.3	1.0	-22.9	2.8	○
	QPm.D84-2A	Xgwm356	2A	126	C-2AL1-0.85	M	*	8.0	7.9	-26.6	2.6	+

Table 15: Continued.

Trait: GNE (Grain number per ear), HEA (Days until heading), HEI (Plant height), TGW (Thousand grain weight), YLD (Grain yield), GH (Grain hardness), PM (Powdery mildew).

QTL: A significant marker×trait association was specified as QTL, if marker main effect (M) or marker×environment interaction effect (M×E), was significant with P = 0.01 in the GLM procedure. Linked QTLs with a ≤ 20 cM distance were interpreted as one QTL. The QTL label is consisting of Q (for QTL), YLD (tested trait), D84 (tested population), 4Ab (chromosome, where the QTL was detected and b for the second YLD-QTL on the same chromosome).

Marker: Label of SSR marker. (×) Significant marker×trait association computed with the highest F-value in a linked QTL cluster with a ≤ 20 cM distance. (1) Marker was not described by Somers et al. (2004) and Sourdille et al. (2004), respectively, estimated position in cM on chromosome by linked marker positions described by Somers et al. (2004) and Song et al. (2005).

Chr.: Chromosomal location of the marker derived from Somers et al. (2004).

Range: Position range of the marker in cM on chromosome derived from Somers et al. (2004).

Bin range: Marker was assigned to deletion bins described by Sourdille et al. (2004).

Effect: A significant marker×trait association (P = 0.01) was specified with marker main effect (M) or marker×environment interaction effect (M×E).

Sign.: Level of significance computed using the GLM procedure of the significant marker×trait associations for marker main effect (M) or marker×environment interaction effect (M×E), (**) P = 0.001, (*) P = 0.01.

F-val.: F-value was computed using the GLM procedure.

R^2 (%): Proportion of the genetic variance computed using the GLM procedure, which was explained the marker main effect (M) or the marker×environment interaction effect (M×E).

RP [aa]: Relative performance of exotic genotype (Syn-84) at a given marker locus across all tested environments computed using the GLM procedure. Relative performance was computed as ([aa] - [AA])×100 / [AA], where [AA] or [aa] were LS-means of BC_2F_4 lines carrying the cultivar genotype (Devon) or the exotic genotype (Syn-84) at the given marker locus.

N+ [aa]: LS-means of trait values for high N-supply across all tested environments for BC_2F_4 lines carrying the exotic genotype (Syn-84) at the given marker locus.

QTL effect: Relative performance of exotic genotype (Syn-84) at a given marker locus for high N-supply across all tested environments computed using the GLM procedure specified a favourable QTL effect (+) with a positive effect from the exotic genotype (Syn-84) compared with the cultivar genotype (Devon), unfavourable QTL effect (-) with a negative effect from the exotic genotype (Syn-84) compared with the cultivar genotype (Devon) at a given marker locus. (°) QTLs, where marker×environment interaction effects revealed crossover interactions, where the exotic genotype [aa] was favourable in some environments, but unfavourable in others.

3.6.5 REML I and REML II - QTLs in T84 and D84

These three-way QTL analyses were computed through a REML single-locus analysis using a mixed hierarchical model (REML I) and a REML multi-locus analysis by a forward selection method applying a mixed hierarchical model (REML II). Altogether, in both populations 14 QTLs were identified using the REML I method (Table 16).

Hence, REML analyses detected marker×trait associations specified as marker×environment interaction effects, but these effects were not significant (P = 0.01). Thus, no QTLs classified as marker×environment interaction effects were established. Only significant marker main effects were detected using REML I and REML II method. These QTLs were identical computed by using the ANOVA I method.

In T84, ten QTLs were associated with six favourable effects enhanced by the presence of exotic alleles. One strong QTL effect explained 21.9% of the genetic variance. This effect was detected at the QTL, *QPm.T84-7D*, where exotic alleles reduced sensitivity to PM by 34.7%. Two favourable QTLs were identified for TGW on chromosomes 2A and 7A.

Table 16: Localisation of 14 QTLs as marker main effects (P = 0.01) in T84 and D84, computed in high N-level using a REML single-locus analysis (REML I) and a REML multi-locus analysis (REML II).

Pop	Trait	QTL	Marker	Chr.	Pos. (cM)	n [aa]	F-val.	R^2 (%)	RP [aa]	N+ [AA]	N+ [aa]	Diff. [aa]	QTL effect	REML analysis I	REML analysis II
T84	EAR	*QEar.T84-7A*	Xgwm60	7A	30	28	16.1	24.2	-8.0	619.1	569.7	-49.4	-	M	M
T84	HEA	*QHea.T84-4A*	Xwmc468	4A	38	19	20.4	22.2	-2.3	86.3	84.4	-1.9	+	M	M
T84	HEA	*QHea.T84-5A*	Xbarc319[1]	5A	110	20	13.9	9.4	-2.0	86.0	84.2	-1.7	+	M	
T84	HEI	*QHei.T84-4Ab*	Xgwm160	4A	79	21	21.8	11.1	-6.3	98.3	92.1	-6.2	+	M	M
T84	TGW	*QTgw.T84-2Ab*	Xgwm294	2A	76	34	17.4	12.4	6.1	41.6	44.1	2.6	+	M	M
T84	TGW	*QTgw.T84-7A*	Xgwm60	7A	30	28	17.2	10.8	6.2	41.6	44.2	2.6	+	M	
T84	YLD	*QYld.T84-3A*	Xgwm5	3A	45	13	16.3	38.7	-27.4	66.6	48.3	-18.3	-	M	M
T84	YLD	*QYld.T84-5Ba*	Xgwm234	5B	38	13	15.6	9.6	-12.0	66.2	58.3	-7.9	-	M	M
T84	PM	*QPm.T84-7Bb*	Xgwm577	7B	137	18	13.5	7.2	37.9	3.4	4.7	1.3	-	M	
T84	PM	*QPm.T84-7D*	Xgwm428	7D	136	26	14.5	10.1	-22.9	3.7	2.4	-1.3	+	M	M
T84	PM	"	Xwmc634×	7D	143	21	14.3	21.9	-34.7	3.9	2.5	-1.3	+	M	
D84	HEI	*QHei.D84-2A*	Xgwm558	2A	54	17	15.4	10.3	5.6	101.1	106.7	5.6	-	M	M
D84	HEI	*QHei.D84-5A*	Xbarc330[1]	5A	75	19	15.3	16.0	4.6	101.0	105.7	4.7	-	M	
D84	TGW	*QTgw.D84-2D*	Xgwm157	2D	73	26	20.0	14.2	6.6	44.1	47.0	2.9	+	M	M
D84	YLD	*QYld.D84-6B*	Xbarc198	6B	44	22	22.4	16.6	-9.2	63.0	57.3	-5.8	-	M	

Table 16: Continued.

Trait: EAR (Tillers per square meter), HEA (Days until heading), HEI (Plant height), TGW (Thousand grain weight), YLD (Grain yield), PM (Powdery mildew).

Marker: Label of SSR marker. (×) Significant marker×trait association computed with the highest F-value in a linked QTL cluster with a ≤ 20 cM distance. (1) Marker was not described by Somers et al. (2004) and Sourdille et al. (2004), respectively, estimated position in cM on chromosome by linked marker positions described by Somers et al. (2004) and Song et al. (2005).

Chr.: Chromosomal location of the marker derived from Somers et al. (2004).

Pos.: Position of the marker in cM on chromosome derived from Somers et al. (2004).

n [aa]: Number of markers showing the exotic genotype (Syn-84).

Sign.: Level of significance computed using the MIXED procedure of the significant marker×trait associations for marker main effect (M, P = 0.01).

F-val.: F-value was computed using the MIXED procedure.

R^2 (%): Proportion of the genetic variance computed using the MIXED procedure, which was explained the marker main effect (M).

RP [aa]: Relative performance of exotic genotype (Syn-84) at a given marker locus across all tested environments computed using the MIXED procedure. Relative performance was computed as ([aa]-[AA])×100 / [AA], where [AA] or [aa] were LS-means of BC_2F_4 lines carrying the cultivar genotype (Triso or Devon) or the exotic genotype (Syn-84) at the given marker locus.

N+ [AA]: LS-means of trait values for N-supply N+ for BC_2F_4 lines carrying the cultivar genotype (Triso or Devon) at the given marker locus.

N+ [aa]: LS-means of trait values for N-supply N+ for BC_2F_4 lines carrying the exotic genotype (Syn-84) at the given marker locus.

Diff. [aa]: Difference between LS-means of the exotic and the cultivar genotype, N+ [aa] - N+ [AA].

QTL: A significant marker×trait association was specified as QTL, if marker main effect (M), was significant with P = 0.01 in the MIXED procedure. Linked QTL with a ≤ 20 cM distance were interpreted as one QTL. The QTL label is consisting of Q (for QTL), YLD (tested trait), T84 (tested population), 4Ab (chromosome, where the QTL was detected and b for the second YLD-QTL on the same chromosome).

QTL effect: Relative performance of exotic genotype (Syn-84) at a given marker locus in the high N-supply (two or three mineral N-applications) across all tested environments computed using the MIXED procedure specified a favourable QTL effect (+) with a positive effect from the exotic genotype (Syn-84) compared with the cultivar genotype (Triso or Devon), a not favourable QTL effect (-) with a negative effect from the exotic genotype (Syn-84) compared with the cultivar genotype (Triso or Devon) at a given marker locus.

The exotic genotype increased TGW by 6.2%. These QTLs *QTgw.T84-2Ab* and *QTgw.T84-7A*, explained 12.4% and 10.8% of the genetic variance. Furthermore, the QTL *QHea.T84-4A*, explained 22.2% of the genetic variance. This locus reduced HEA by 2.3%, which resulted in an earlier heading by 1.9 days. At the QTL *QHei.T84-4Ab*, exotic alleles reduced HEI by 6.3% corresponding to 6.2 cm and accounting for 11.1% of the genetic variance. The strongest unfavourable QTL effect was conducted by exotic alleles at the QTL *QYld.T84-3A*, which explained 38.7% of the genetic variance and reduced YLD by 27.4% according to 18.3 dt ha^{-1}.

In D84, four QTLs were ascertained. One QTL *QTgw.D84-2D* was improved by the presence of the exotic genotype. This locus explained 14.2% of the genetic variance and increased TGW by 6.6%. At the QTL *QYld.D84-6B*, exotic alleles explained 16.6% of the genetic variance and led to decrease by 9.2% YLD. In addition, QTLs identified in T84 were not validated in D84.

Using the REML II method seven (T84) and two (D84) QTLs were detected (Table 16). These QTLs were identical computed by using the REML I method, which were detected with the highest F-value. Six QTLs were located on the A genome for EAR, HEA, HEI, TGW and YLD. The remaining three QTLs were identified on the B and D genomes. However, mostly QTLs were associated with exotic alleles conducted by the wild emmer germplasm.

3.6.6 REML - Comparison of QTLs detected in T84 and D84

A comparison of QTLs and their QTL effects in T84 and D84 detected using the REML I analysis may validate common QTLs with exotic alleles, which are conserved between the donor genotypes (Table 17).

Three QTLs might be validated with marker×trait associations at identical marker loci and same exotic allele's effects detected in the other population. At these common QTLs for plant height (*QHei.D84-2A*), grain yield (*QYld.T84-3A*) and powdery mildew (*QPm.T84.7D*), significances for marker×trait associations ranged between 0.012 and 0.037. Six marker×trait associations validated effects conducted by identical synthetic wheat alleles in close vicinity to QTLs in the other population. The remaining five QTLs could not be validated in the other population.

3.6.7 Comparison of selected BC_2F_4 lines in T84 carrying exotic alleles

Advanced backcross lines will contain practically all of the recurrent parent genome except for the chromosomal region containing a QTL of interest. These nearly-isogenic lines (NILs) were utilised for validation of QTLs or fine mapping. Furthermore, NILs containing different genes revealing the same trait were used directly in breeding programmes. Additionally, BC_2F_4 lines carrying exotic introgression were selected in regard to breeding efforts. The breeding efforts were defined according to breeding programmes for spring wheat (Table 1). Accordingly, a favourable QTL for an investigated trait included exotic alleles, which preferably improved the trait performance.

Based on this marker analysis no NILs were found. The analysed marker set was not sufficient to absolutely cover the A, B and D genomes. Despite that, four BC_2F_4 lines contained a single exotic introgression in T84 (Tri 014, Tri 130, Tri 205, Tri 213). The proportion of the exotic genotype ranged between 2.4% and 4.3%. By using REML I method only QTLs detected as significant marker main effects were taken into account.

Exotic alleles revealed a favourable QTL effect for HEI in Tri 213 at the single introgression locus Xgwm160. At this locus the exotic genotype reduced HEI by 9.8% and explained 11.1% of the genetic variance. The remaining three BC_2F_4 lines carrying one exotic introgression, exotic introgressions caused no QTL effect.

In addition, BC_2F_4 lines carrying more than one exotic introgression were selected (Table 18). The QTL that explained the highest genetic variance in the trait performance was chosen. In the following, selected BC_2F_4 lines are described for each trait separately.

Days until heading (HEA)

For HEA, two QTLs were detected with favourable effects revealed from exotic alleles. The QTL *QHea.T84-4A* accounted for 22.2% of the genetic variance. The exotic genotype reduced HEA by 13.0% in Tri 125. At the second QTL, *QHea.T84-4A*, exotic alleles explained 9.4% of the genetic variance. In Tri 022 exotic alleles improved the trait performance by 11.7%.

Table 17: Validation of nine QTLs as marker main effects (P = 0.01) in T84 and D84, computed in high N-level using a REML single-locus analysis (REML I).

Pop	Trait	QTL/ association	Sign.	Marker	Chr.	Pos. (cM)	n [aa]	F-val.	R^2 (%)	RP [aa]	N+ [AA]	N+ [aa]	Diff. [aa]	QTL effect
T84	HEA	*QHea.T84-4A*	0.003	Xwmc468	4A	38	19	20.4	22.2	-2.3	86.3	84.4	-1.9	+
D84	HEA	*association*	0.045	Xgwm160	4A	79	17	6.0	3.2	-1.4	86.2	85.0	-1.2	+
T84	HEA	*QHea.T84-5A*	0.007	Xbarc319[1]	5A	110	20	13.9	9.4	-2.0	86.0	84.2	-1.7	+
D84	HEA	*association*	0.019	Xgwm415	5A	55	24	9.3	6.5	-1.7	86.4	85.0	-1.4	+
T84	HEI	*QHei.T84-4Ab*	0.002	Xgwm160	4A	79	21	21.8	11.1	-6.3	98.3	92.1	-6.2	+
D84	HEI	*association*	0.013	Xgwm610	4A	12	20	10.8	6.4	4.1	101.2	105.4	-4.2	-
T84	TGW	*QTgw.T84-2Ab*	0.009	Xgwm294	2A	76	34	17.4	12.4	6.1	41.6	44.1	2.6	+
D84	TGW	*association*	0.037	Xgwm558	2A	54	17	8.0	5.2	5.3	44.2	46.6	2.4	+
T84	YLD	*QYld.T84-3A*	0.007	Xgwm5	3A	45	13	16.3	38.7	-27.4	66.6	48.3	-18.3	-
D84	YLD	*association*	0.012	Xgwm5	3A	45	13	12.7	19.8	-13.4	62.6	54.2	-8.4	-
T84	PM	*QPm.T84-7Bb*	0.008	Xgwm577	7B	137	18	13.5	7.2	37.9	3.4	4.7	1.3	-
D84	PM	*association*	0.026	Xgwm537	7B	35	20	7.9	4.9	26.2	3.3	4.2	-0.9	-
T84	PM	*QPm.T84-7D*	0.007	Xwmc634×	7D	143	21	14.3	21.9	-34.7	3.9	2.5	-1.3	+
D84	PM	*association*	0.037	Xwmc634×	7D	143	14	6.6	8.8	-27.5	3.6	2.6	-1.0	+
T84	HEI	*association*	0.026	Xgwm558	2A	54	24	7.9	4.4	3.6	96.6	100.1	3.5	-
D84	HEI	*QHei.D84-2A*	0.006	Xgwm558	2A	54	17	15.4	10.3	5.6	101.1	106.7	5.6	-
T84	HEI	*association*	0.017	Xgwm415	5A	55	20	9.6	5.3	4.5	97.0	101.4	4.4	-
D84	HEI	*QHei.D84-5A*	0.006	Xbarc330[1]	5A	75	19	15.3	16.0	4.6	101.0	105.7	4.7	-

Gloss based on Table 16.

Table 18: List of selected BC_2F_4 lines carrying QTLs with favourable exotic alleles in T84, detected using REML I method.

Trait	QTL	Marker	R^2 (%)	BC_2F_4 line	[aa] (%)	RP [Line:Triso]	Line	Triso	Sign.
HEA	*QHea.T84-4A*	Xwmc468	22.2	Tri 114	30.5	-11.1	81.9	92.1	*
				Tri 125	13.4	-13.0	80.1	92.1	*
				Tri 176	23.1	-12.1	81.0	92.1	*
				Tri 194	10.0	-9.8	83.1	92.1	*
HEA	*QHea.T84-5A*	Xbarc319	9.4	Tri 022	18.8	-11.7	81.3	92.1	*
				Tri 027	14.6	-10.9	82.1	92.1	*
				Tri 039	11.9	-11.3	81.7	92.1	*
				Tri 043	17.1	-10.3	82.6	92.1	*
HEI	*QHei.T84-4Ab*	Xgwm160	11.1	Tri 018	13.3	-13.7	84.6	98.1	n.s.
				Tri 027	14.6	-15.3	83.1	98.1	n.s.
				Tri 190	9.4	-15.0	83.4	98.1	n.s.
				Tri 191	11.0	-16.7	81.8	98.1	*
TGW	*QTgw.T84-2Ab*	Xgwm294	12.4	Tri 007	11.1	13.5	49.5	43.6	n.s.
				Tri 114	30.5	17.2	51.1	43.6	*
				Tri 118	17.7	14.9	50.1	43.6	*
				Tri 122	21.8	10.3	48.1	43.6	n.s.
TGW	*QTgw.T84-7A*	Xgwm60	11.5	Tri 114	30.5	17.2	51.1	43.6	*
				Tri 118	17.7	14.9	50.1	43.6	*
				Tri 122	21.8	10.3	48.1	43.6	n.s.
				Tri 176	23.1	8.3	47.2	43.6	n.s.
PM	*QPm.T84-7D*	Xwmc634	21.9	Tri 018	13.3	-39.3	2.1	3.5	n.s.
				Tri 047	11.3	-42.9	2.0	3.5	n.s.
				Tri 048	6.0	-51.4	1.7	3.5	n.s.
				Tri 065	12.4	-42.9	2.0	3.5	n.s.

Gray highlighted BC_2F_4 line carrying more than one favourable QTL effects revealed from exotic alleles.
Trait: HEA (Days until heading), HEI (Plant height), TGW (Thousand grain weight), PM (Powdery mildew).
QTL: QTL for a trait, where exotic alleles improved the trait performance.
Marker: Label of SSR marker.
R^2 (%): Proportion of the genetic variance computed using the GLM procedure, which was explained the marker main effect (M).
BC_2F_4 line: Advanced backcross line in the generation BC_2F_4 was developed from a cross between the exotic genotype (Syn-84) and the recurrent parent Triso.
[aa] (%): Proportion of the exotic genotype in BC_2F_4 line.
RP [Line:Triso]: Relative performance of the selected BC_2F_4 line: (Line - Triso)×100 / Triso, where Line and Triso are LS-means of the BC_2F_4 line and the recurrent parent.
Line: LS-means of trait values for high N-supply across environments for lines carrying the exotic genotype.
Triso: LS-means of trait values for high N-supply across tested environments for the recurrent parent.
Sign.: Significant differences between relative performances of BC2F4 line and Triso were tested with a Dunnett multiple comparison of LS-means differences using the recurrent parent as the control: (*) significance threshold at P = 0.05, n.s. not significant.

Plant height (HEI)

The QTL *QHei.T84-4Ab* for HEI explained 11.1% of the genetic variance. Exotic alleles caused a decrease of HEI by 6.3%. The exotic genotype shortened HEI between 13.7% and 16.7% in selected BC_2F_4 lines. The least proportion of the exotic genotype was detected with 9.4% in Tri 190. The selected BC_2F_4 line Tri 027 advanced HEI (4A) and HEA (5A) simultaneously.

Thousand grain weight (TGW)

Exotic alleles revealed an increase in TGW at two loci on chromosome 2A and 7A. At the QTL *QTgw.T84-2Ab* the exotic genotype increased TGW up to 17.2% in Tri 114. Exotic alleles explained 12.4% of the genetic variance at this locus, Xgwm294. The second QTL, *QTgw.T84-7A*, was explained with 11.5% of the genetic variance at Xgwm60. The exotic genotype increased TGW by 17.2% in Tri 114. In the selected BC_2F_4 line Tri 114 exotic alleles improved two traits at three loci (HEA on 4A, TGW on 2A and 7A) simultaneously. Among selected BC_2F_4 lines, Tri 114 carried the highest proportion of the exotic genotype with 30.5%.

Powdery mildew (PM)

For PM, exotic alleles explained 21.9% of the genetic variance at the QTL *QPm.T84-7D*. In Tri 018, exotic alleles reduced leaf symptoms for PM by 51.6%. The exotic genotype revealed favourable QTL effects for two traits (HEI on 4A, PM on 7D) simultaneously in Tri 018. The least proportion of the exotic genotype (6.0%) was detected in Tri 048.

3.7 Localisation of N-responsive QTLs - Four-way analyses

Four-way analyses were conducted to identify N-supply effects on agronomic traits and quality parameters. Thus, ANOVA single-locus analysis (ANOVA II), REML single-locus analysis using a mixed hierarchical model (REML III) and REML multi-locus analysis by a forward selection method applying a mixed hierarchical model (REML IV) were used to detect N-responsive QTLs. An environment was included if there was a significant difference of LS-means of each trait between two different N-levels (N+ and N-). In Table 19, nine traits across seven environments for both populations (T84 and D84) provided data to compute four-way analyses.

These QTL mapping methods revealed significant marker×nitrogen interaction effects, which are described as N-responsive QTLs. Further, N-responsive QTLs were classified according to the trait performance of the exotic genotype in two N-treatments. An N-responsive QTL effect was evaluated as favourable regarding the trait performance of the exotic genotype under low and high N-supply according to a QTL category.

QTL categories: (1) favourable N-responsive QTL effect with a positive effect from the exotic genotype compared with the cultivar genotype in both N-levels; (2) favourable N-responsive QTL effect with a positive effect from the exotic genotype compared with the cultivar genotype in the low N-supply and was unfavourable in the high N-supply; (3) unfavourable N-responsive QTL effect with a positive effect from the exotic genotype compared with the cultivar genotype in the high N-supply and a degradation of trait performance of the exotic genotype in the low N-supply; (4) unfavourable N-responsive QTL effect from the exotic genotype compared with the cultivar genotype in both N-levels.

Table 19: Nine traits for detection of N-responsive QTLs in T84 and D84, measured in up to seven environments.

Pop	Trait	Environment
T84	EAR	B04, B05, D04, D05, F04, F05
	HEA	B04, D04, D05, F05, H04, H05
	HEI	D04, F04, F05, H05
	HLW	D04, D05, H04
	LAH	B05, D04, D05, F05
	TGW	D04, F05, H04
	YLD	B04, D04, D05, H04, H05
	GH	D04, H04
	GPC	D04, H04, H05
D84	EAR	B04, B05, D04, D05, F04, F05, H04
	HEA	B04, D04, F04, H05
	HEI	D04, F04, F05, H05
	HLW	B04, D05, H05
	LAH	B04, B05, D04, D05, F05
	TGW	D05, H05
	YLD	D04, D05, F05, H04, H05
	GPC	D04, H04, H05

Trait: EAR (Tillers per square meter), HEA (Days until heading), HEI (Plant height), HLW (Grain test weight), LAH (Lodging at harvest), TGW (Thousand grain weight), YLD (Grain yield), GH (Grain hardness), GH (Grain hardness), GPC (Grain protein content).

Environment: Combination of the experimental location [Boldebuck (B), Dikopshof (D), Feldkirchen (F), Hovedissen (H)] and the experimental season [2004 (04), 2005 (05)]

3.7.1 ANOVA II - N-responsive QTLs in T84

The ANOVA II analysis computed 1,222 marker×trait combinations. Sixteen significant marker×trait associations classified as marker×nitrogen interaction effects were identified, revealing eleven N-responsive QTLs for 13 traits in T84 (Figure 4, Table 20). At six (54.5%) N-responsive QTLs, exotic alleles improved the trait performance under low N-supply. Furthermore, a total of 58 significant marker×trait associations were significant for marker main effects (Appendix 12). Hence, 48 QTLs were described as marker main effects uninfluential of different N-supplies. In the following, N-responsive QTLs are described for each trait separately.

Plant height (HEI)

A single N-responsive QTL was established for HEI. The N-responsive QTL, *QHei-N.T84-7B*, was classified as QTL category 4. At this locus the exotic genotype revealed an increased HEI under both N-levels by 1.0% (N-) and 2.6% (N+).

Harvest index (HI)

One N-responsive QTL was detected for HI accounting for 0.8% of the genetic variance. At this locus, *QHi-N.T84-6B*, exotic alleles presented an increase in harvest index under low N-supply by 4.2%. Hence, this N-responsive QTL was considered as QTL category 2.

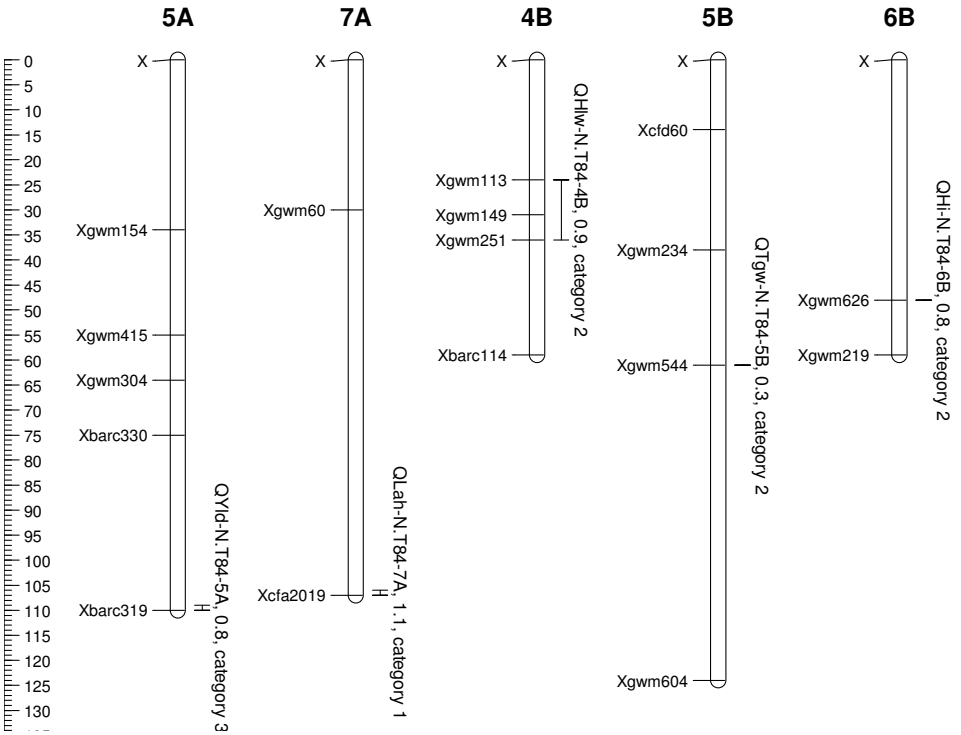

Figure 4: Localisation of 11 N-responsive QTLs (P = 0.01) for agronomic traits and quality parameters in T84, detected under high and low N-levels using a four-way ANOVA single-locus analysis (ANOVA II).

This graphical map was computed using MapChart (Voorrips 2002) in the high N-supply using 94 markers with genetic map positions according Somers et al. (2004). Mapped markers were indicated on the left. N-responsive QTL confidence interval was indicated by a vertical bar, whereas F-value maximal of a significant marker×nitrogen interaction effect (P = 0.01) was pointed by a horizontal bar. QTL description: QTL designation, number (R^2 as explained genetic variance in %) and QTL category.

Grain test weight (HLW)

Three QTLs were identified for HLW as QTL category 2. At these N-responsive QTLs the presence of the exotic genotype caused an increase in HLW by up to 1.3% (N-). The strongest N-responsive QTL effect was explained with 1.9% of the genetic variance at the locus *QHlw-N.T84-4D*.

Lodging at harvest (LAH)

Two N-responsive QTLs were identified for LAH. At the locus, *QLah-N.T84-7A*, exotic alleles explained 1.1% of the genetic variance and decreased LAH under both N-levels by 24.5% (N-) and 13.5% (N+). This N-responsive QTL was described as QTL category 1 with favourable N-responsive QTL effects improving the trait performance by the presence of the exotic genotype. On chromosome 4D the N-responsive QTL was specified as QTL category 4 and explained 1.3% of the genetic variance. Exotic alleles led to a disadvantageous increase of LAH by 34.0% (N-) and 15.5% (N+).

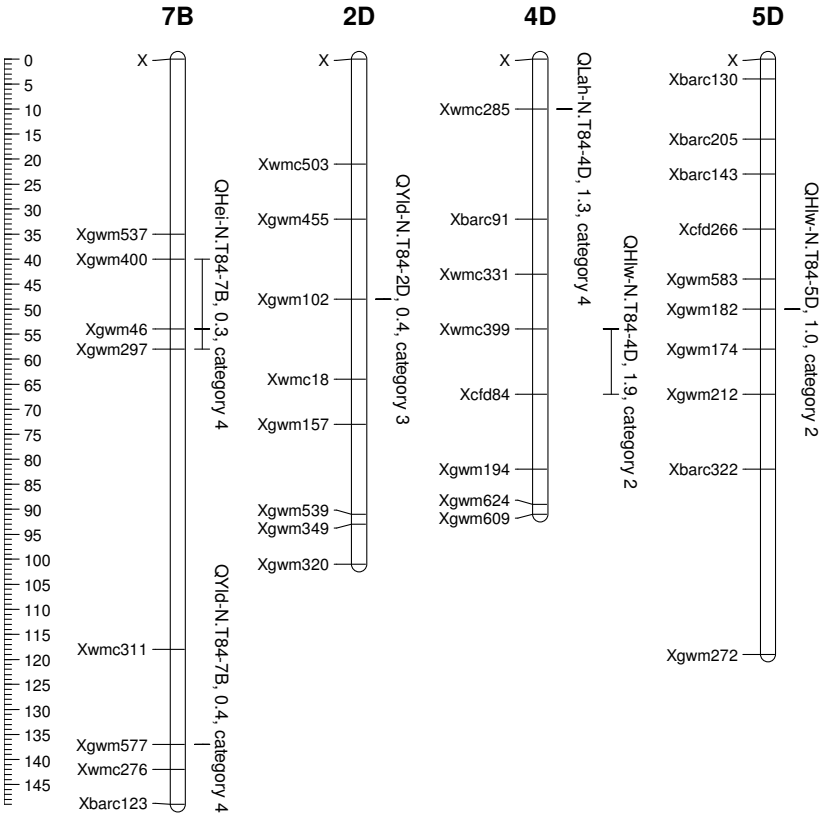

Figure 4: Continued.

Thousand grain weight (TGW)

One N-responsive QTL, *QTgw-N.T84-5B*, was ascertained for TGW. At this locus exotic alleles revealed an increase in TGW by 2.7% under low N-supply and a decrease in the high N-supply by 0.8%. Thus, the N-responsive QTL was classified as QTL category 2.

Grain yield (YLD)

Three QTLs were detected for YLD specified as QTL categories 3 and 4. The presence of the exotic genotype caused a decrease in YLD by up to 4.2% (N-) and led to a favourable increase by up to 3.6% (N+), specified as QTL category 3. The strongest N-responsive QTL effect was determined at the locus *QYld-N.T84-5A*. At the locus, *QYld-N.T84-7B*, exotic alleles influenced unfavourable reduction in YLD by 1.5% (N-) and 7.6% (N+). Consequentially, this N-responsive QTL was specified as QTL category 4.

Table 20: Localisation of 11 N-responsive QTLs (P = 0.01) in T84, computed in high and low N-level with 94 markers using a four-way ANOVA single-locus analysis (ANOVA II).

Trait	Marker	Chr.	Pos. (cM)	n [aa]	Sign.	F-val.	R^2 (%)	RP_{N-} [aa]	N- [AA]	N- [aa]	RP_{N+} [aa]	N+ [AA]	N+ [aa]	QTL	QTL category
HEI	Xgwm400	7B	40	35	*	9.6	0.2	0.0	97.5	98.9	1.4	97.4	97.4	*QHei-N.T84-7B*	4
HEI	Xgwm46×	7B	54	42	**	12.9	0.3	1.0	97.1	99.6	2.6	97.1	98.0	"	4
HEI	Xgwm297	7B	58	39	*	8.8	0.2	1.1	97.4	99.8	2.4	97.2	98.3	"	4
HI	Xgwm626	6B	48	23	*	7.9	0.8	4.2	0.4	0.4	-2.0	0.4	0.4	*QHi-N.T84-6B*	2
HLW	Xgwm113	4B	25	22	*	7.4	0.9	0.2	77.7	77.9	-0.5	78.3	77.9	*QHlw-N.T84-4B*	2
HLW	Xgwm149	4B	31	14	**	11.1	1.3	0.2	77.7	77.9	-0.9	78.3	77.6	"	2
HLW	Xgwm251×	4B	36	13	**	12.7	1.4	0.3	77.7	78.0	-0.9	78.3	77.7	"	2
HLW	Xwmc399×	4D	54	13	**	14.6	1.9	1.3	77.7	78.7	0.0	78.3	78.3	*QHlw-N.T84-4D*	2
HLW	Xcfd84	4D	67	11	*	7.7	1.1	1.1	77.7	78.5	0.0	78.3	78.3	"	2
HLW	Xgwm182	5D	50	12	*	8.7	1.0	0.4	77.7	78.0	-0.7	78.3	77.8	*QHlw-N.T84-5D*	2
LAH	Xwmc285	4D	10	8	*	6.7	1.3	34.0	2.4	2.8	15.5	3.9	5.2	*QLah-N.T84-4D*	4
LAH	Xcfa2019	7A	107	17	*	6.7	1.1	-24.5	2.1	1.9	-13.5	3.8	2.8	*QLah-N.T84-7A*	1
TGW	Xgwm544	5B	61	8	*	9.9	0.3	2.7	42.4	42.0	-0.8	41.9	43.0	*QTgw-N.T84-5B*	2
YLD	Xgwm102	2D	48	22	*	8.7	0.4	-1.5	57.9	60.0	3.6	65.4	64.4	*QYld-N.T84-2D*	3
YLD	Xbarc319[1]	5A	110	20	**	12.5	0.8	-4.2	58.7	59.8	1.7	66.3	63.5	*QYld-N.T84-5A*	3
YLD	Xgwm577	7B	137	18	*	9.1	0.4	-1.5	58.3	53.9	-7.6	65.3	64.2	*QYld-N.T84-7B*	4

Table 20: Continued.

Trait: HEI (Plant height), HI (Harvest index), HLW (Grain test weight), LAH (Lodging at harvest), TGW (Thousand grain weight), YLD (Grain yield).

Marker: Label of SSR marker. (×) Significant marker×trait association computed with the highest F-value in a linked QTL cluster with a ≤ 20 cM distance. (1) Marker was not described by Somers et al. (2004) and Sourdille et al. (2004), respectively, estimated position in cM on chromosome by linked marker positions described by Somers et al. (2004) and Song et al. (2005).

Chr.: Chromosomal location of the marker derived from Somers et al. (2004).

Pos.: Position of the marker in cM on chromosome derived from Somers et al. (2004).

n [aa]: Number of markers showing the exotic genotype (Syn-84).

Sign.: Level of significance computed using the GLM procedure of the significant marker×trait associations for marker×nitrogen interaction effects, (**) P = 0.001, (*) P = 0.01.

F-val.: F-value was computed using the GLM procedure.

R^2 (%): Proportion of the genetic variance computed using the GLM procedure, which was explained the marker×nitrogen interaction effects.

RP_{N+} or $_{N-}$ [aa]: Relative performance (for N-levels N+ or N-) of exotic genotype (Syn-84) at a given marker locus across all tested environments computed using the GLM procedure. Relative performance was computed as ([aa]-[AA])×100 / [AA], where [AA] or [aa] were LS-means of BC_2F_4 lines carrying the cultivar genotype (Triso) or the exotic genotype (Syn-84) at the given marker locus.

N+ or N- [AA]: LS-means of trait values for N-supply N+ or N- for BC_2F_4 lines carrying the cultivar genotype (Triso) at the given marker locus.

N+ or N- [aa]: LS-means of trait values for N-supply N+ or N- for BC_2F_4 lines carrying the exotic genotype (Syn-84) at the given marker locus.

QTL: A significant marker×trait association was specified as N-responsive QTL, if marker×nitrogen interaction effect was significant with P = 0.01 in the GLM procedure. Linked QTLs with a ≤ 20 cM distance were interpreted as one N-responsive QTL. The N-responsive QTL label is consisting of Q (for QTL), YLD (tested trait), N (computed for two N supplies), T84 (tested population), 4Ab (chromosome, where the QTL was detected and b for the second YLD-QTL on the same chromosome).

QTL category: Relative performance of the exotic genotype (Syn-84) at a given marker locus for N supplies N+ and N- across all tested environments computed using the GLM procedure specified as (1) N-responsive QTL with a favourable exotic effect under both N-levels; (2) N-responsive QTL with a favourable exotic effect only under low N-supply; (3) N-responsive QTL with a favourable exotic effect only under high N-supply; (4) N-responsive QTL with an unfavourable exotic effect under both N-levels.

3.7.2 ANOVA II - N-responsive QTLs in D84

A total of 1,378 marker×trait combinations revealed 14 significant marker×trait associations classified as marker×nitrogen interaction effects using the four-way ANOVA single-locus analysis (ANOVA II). Thus, 13 N-responsive QTLs were identified in D84 (Figure 5, Table 21). At four (30.8%) N-responsive QTLs, exotic alleles improved the trait performance under low N-supply. Further, 62 significant marker×trait associations were specified as marker main effects, including three QTLs with two effects, marker main effects and marker×nitrogen interaction effects at the same locus (Appendix 13). Hence, 48 QTLs were appointed as marker main effects uninfluenced of different N-supplies. In the following, N-responsive QTLs are described for each trait separately.

Table 21: Localisation of 13 N-responsive QTLs (P = 0.01) in D84, computed in high and low N-level with 106 markers using a four-way ANOVA single-locus analysis (ANOVA II).

Trait	Marker	Chr.	Pos. (cM)	n [aa]	Sign.	F-val.	R^2 (%)	RP_{N-} [aa]	N- [AA]	N- [aa]	RP_{N+} [aa]	N+ [AA]	N+ [aa]	QTL	QTL category
BRT	Xgwm356	2A	126	26	*	6.7	0.8	8.3	1.2	1.3	-8.3	1.2	1.1	*QBrt-N.D84-2A*	3
EAR	Xgwm5	3A	45	13	*	7.8	2.5	-4.1	521.2	499.7	4.8	568.7	596.3	*QEar-N.D84-3A*	2
HEI	Xgwm583	5D	44	22	*	7.4	0.3	-0.6	103.6	103.0	1.0	101.6	102.6	*QHei-N.D84-5D*	3
HLW	Xgwm52	3D	30	9	*	10.8	1.3	-1.2	77.6	76.7	0.4	77.2	77.5	*QHlw-N.D84-3D*	3
HLW	Xgwm154	5A	34	19	*	8.0	0.9	0.9	77.4	78.1	0.0	77.1	77.1	*QHlw-N.D84-5Aa*	2
HLW	Xgwm415×	5A	55	24	*	9.0	0.9	1.3	77.3	78.3	0.3	77.1	77.3	*QHlw-N.D84-5Ab*	1
HLW	Xgwm304	5A	64	22	*	7.6	0.8	1.3	77.3	78.3	0.4	77.1	77.4	"	1
HLW	Xbarc65[1]	7B	48	9	*	7.0	1.0	-0.4	77.6	77.3	0.8	77.2	77.8	*QHlw-N.D84-7Ba*	3
HLW	Xgwm297	7B	58	31	*	7.7	0.8	-1.0	77.7	76.9	-0.3	77.2	77.0	*QHlw-N.D84-7Bb*	4
YLD	Xwmc503	2D	21	17	**	11.0	1.0	0.5	57.2	57.5	-5.1	62.4	59.2	*QYld-N.D84-2Da*	3
YLD	Xwmc18	2D	64	32	*	7.6	0.8	-0.5	57.3	57.0	-4.0	62.6	60.1	*QYld-N.D84-2Db*	4
YLD	Xgwm400	7B	40	23	*	10.3	0.9	-2.0	57.6	56.4	3.1	61.9	63.8	*QYld-N.D84-7B*	2
GH	Xgwm182	5D	50	14	*	7.4	0.4	0.2	52.9	53.0	-3.7	55.7	53.6	*QGh-N.D84-5D*	3
GPC	Xwmc147	1D	16	14	*	7.1	3.2	4.3	11.6	12.1	0.0	13.6	13.6	*QGpc-N.D84-1D*	3

Gloss based on Table 20.

Brittleness (BRT)

Two N-responsive QTLs were detected for BRT. At the locus, *QBrt-N.D84-2A*, exotic alleles revealed an increase in BRT by 4.1% (N-), but a reduction by 8.2% under high N-supply. This N-responsive QTL was considered as QTL category 3. A second QTL, *QBrt.D84-3A*, was analysed with two effects, marker main effect and marker×nitrogen interaction effect, simultaneously. At this locus the exotic genotype explained 40.3% of the genetic variance.

Tillers per square meter (EAR)

One N-responsive QTL, *QEar-N.D84-3A*, was determined for EAR, explaining 2.5% of the genetic variance. Exotic alleles revealed an increase in EAR by 4.9% under low N-supply and a decrease by 4.1% under high N-supply. Thus, the N-responsive QTL was classified as QTL category 2.

Plant height (HEI)

A single N-responsive QTL as QTL category 3 was detected for HEI. The presence of the exotic genotype caused an increase in HEI by 0.9% (N-) and led to a favourable increase by 0.6% (N+).

Grain test weight (HLW)

Five N-responsive QTLs were established for HLW, present in each QTL category. The N-responsive QTL, *QHlw-N.D84-5Ab*, was classified as QTL category 1. At this locus, exotic alleles revealed an increased HLW under both N-levels by 1.2% (N-) and 0.3% (N+). At the same chromosome, a category 2 QTL was located explaining 0.9% of the genetic variance. Two QTL effects were classified as QTL category 3 at the loci *QHlw-N.D84-3D* and *QHlw-N.D84-7Ba*. In addition, one QTL was specified as category 4 on chromosome 7B.

Lodging at harvest (LAH)

Two QTLs, *QLah.D84-6B* and *QLah.D84-2D*, were identified for LAH with two effects, marker main effects and marker×nitrogen interaction effects at the same locus. The exotic genotype explained 8.4% and 5.2% of the genetic variance. Under both N-levels exotic alleles unfavourably increased LAH by 27.5% and 19.0%.

Grain yield (YLD)

Three QTLs were identified for YLD explaining up to 1.0% of the genetic variance. At the locus, *QYld-N.D84-7B*, exotic alleles revealed an increase in YLD by 3.0% (N-) and a decrease by 2.0% (N+). Thus, this N-responsive QTL was classified as QTL category 2. On chromosome 2D two loci were defined as category 3 and 4.

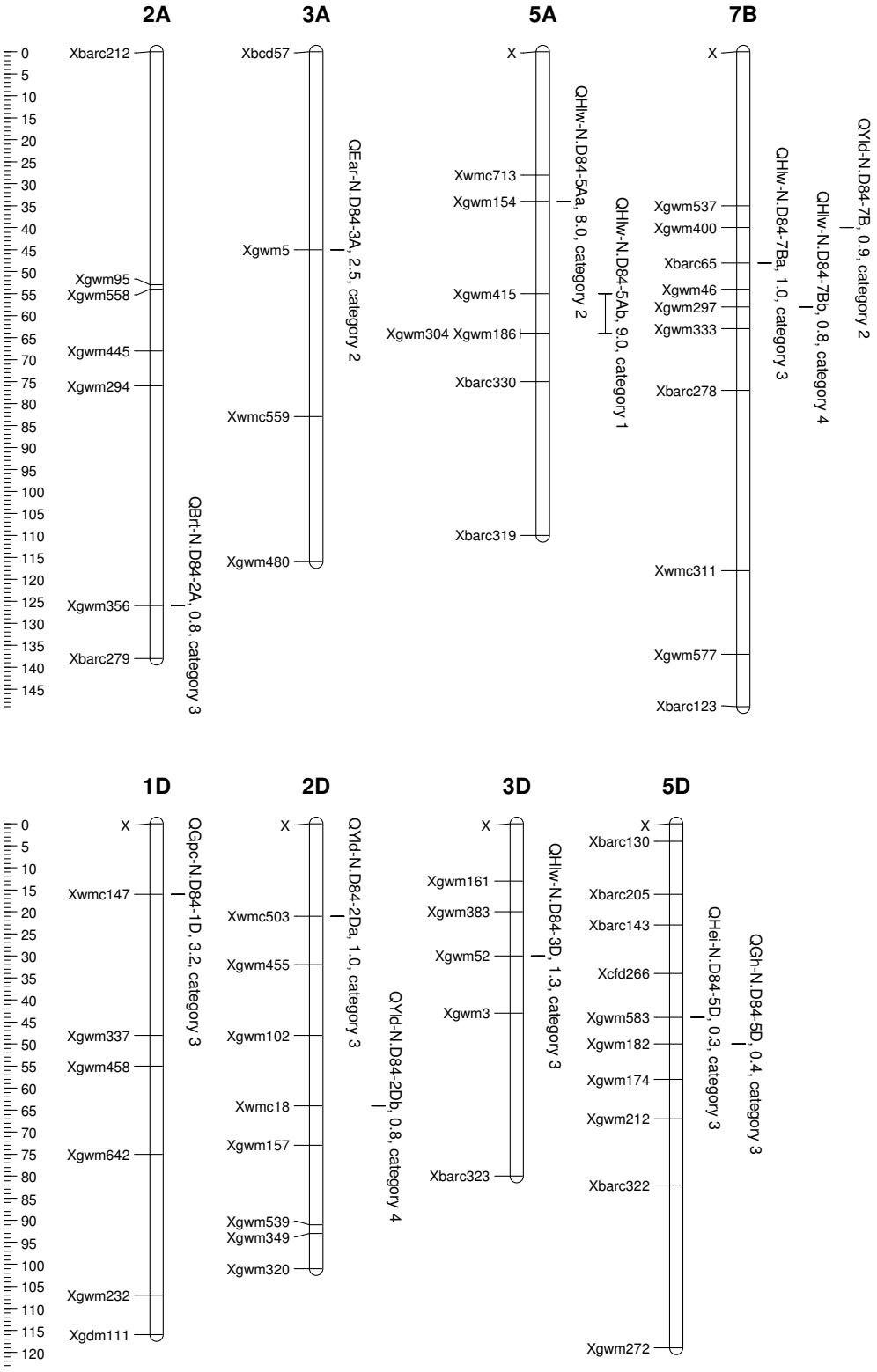

Figure 5: Localisation of 13 N-responsive QTLs (P = 0.01) for agronomic traits and quality parameters in D84, detected under high and low N-levels using a four-way ANOVA single-locus analysis (ANOVA II).

This graphical map was computed using MapChart (Voorrips 2002) in the high N-supply using 94 markers with genetic map positions according Somers et al. (2004). Mapped markers were indicated on the left. N-responsive QTL confidence interval was indicated by a vertical bar, whereas F-value maximal of a significant marker×nitrogen interaction effect (P = 0.01) was pointed by a horizontal bar. QTL description: QTL designation, number (R^2 as explained genetic variance in %) and QTL category.

Grain hardness (GH)

The analysis revealed a single N-responsive QTL for GH. The QTL, *QGh-N.D84-5D*, explained 0.4% of the genetic variance. The presence of exotic alleles at this N-responsive QTL reduced GH by 3.8% (N-) and raised GH by 0.1% (N+). Hence, this N-responsive QTL was classified as QTL category 3.

Grain protein content (GPC)

One N-responsive QTL was detected for GPC, identified as QTL category 3. At this locus, *QGpc-N.D84-1D,* exotic alleles led to a reduction in GPC by 3.8% under low N-supply and an increase by 4.3% under high N-supply.

3.7.3 Comparison of N-responsive QTLs detected in T84 and D84

A four-way ANOVA single-locus analysis (ANOVA II) was used to compare N-supply effects on agronomic traits and quality parameters in T84 and D84.

A total of 1,222 marker×trait combinations were computed for 13 traits in T84, resulted in 64 (5.2%) significant marker×trait associations. In D84, 1,378 marker×trait combinations were analysed and revealed 76 (5.5%) significant marker×trait associations. Hence, in T84 and D84, 16 and 14 significant marker×nitrogen interaction effects including eleven and 13 N-responsive QTLs were ascertained.

By using this analysis no N-responsive QTLs detected in T84 were validated in D84. However, one N-responsive QTL (T84) was localised at two similar chromosome regions in D84. The QTL *QYld-N.T84-2D* was mapped between *QYld-N.D84-2Da* and *QYld-N.D84-2Db*. Thus, exotic alleles revealed the same effect in both populations with reduced YLD by 1.5% and 5.1% under low N-supply. These N-responsive QTLs were classified as QTL categories 3 and 4.

3.7.4 REML III and REML IV - N-responsive QTLs in T84 and D84

The QTL mapping method for N-responsive QTLs were devided in a four-way REML single-locus analysis (REML III) and a four-way REML multi-locus analysis by a forward selection method applying a mixed hierarchical model (REML IV). The REML III method revealed 12 associations as marker×nitrogen interaction effects, listed in Table 22. Thus, no significant marker×nitrogen interaction effects were identified. Hence, no N-responsive QTLs were ascertained.

In both populations nine QTLs were identified as marker main effects (Table 23). In T84, at the QTL *QHea.T84-4A* and *QHei.T84-4Ab*, the exotic genotype preferable reduced HEA by 2.2% and HEI by 6.6%, respectively. In addition, at three QTLs donor alleles favourable influenced trait performances of TGW and YLD. The strongest effect was identified at the locus *QYld.T84-3A*, where alleles explained 40.0% of the genetic variance.

In D84, one favourable QTL *QTgw.D84-2D* explained 12.3% of the genetic variance. At this locus exotic alleles increased TGW by 6.1%. At three other loci the presence of the exotic genotype unfavourable increased HEI by up to 5.9% and reduced YLD by 13.2%.

Table 22: Localisation of 12 associations as marker×nitrogen interaction effects in T84 and D84, computed in high and low N-level using a four-way REML single-locus analysis (REML III).

Pop	Trait	Marker	Chr.	Pos. (cM)	Sign.	F-val.	$RP_{N+,N-}$ [aa]	N+,N- [AA]	N+,N- [aa]
T84	HEI	Xgwm400	7B	40	0.017	9.7	0.6	97.5	98.2
T84	HEI	Xgwm46	7B	54	0.011	13.0	1.8	97.1	98.8
T84	TGW	Xgwm544	5B	61	0.026	9.8	2.9	42.1	42.5
T84	YLD	Xbarc319	5A	110	0.019	10.0	5.6	62.5	61.7
T84	YLD	Xgwm413	1B	26	0.050	6.0	3.7	58.9	53.1
T84	YLD	Xgwm577	7B	137	0.034	7.4	2.9	61.8	59.1
D84	EAR	Xgwm5	3A	45	0.032	7.8	2.9	544.9	548.0
D84	EAR	Xbarc77	3B	111	0.046	6.3	61.8	546.0	543.7
D84	YLD	Xbarc133	3B	7	0.044	6.5	4.5	59.9	55.0
D84	YLD	Xgwm400	7B	40	0.018	10.3	3.9	59.7	60.1
D84	YLD	Xwmc503	2D	21	0.050	6.0	-9.7	59.8	58.4
D84	YLD	Xbarc323	3D	80	0.042	6.6	-1.4	59.6	58.3

Trait: EAR (Tillers per square meter), HEI (Plant height), TGW (Thousand grain weight), YLD (Grain yield).
Marker: Label of SSR marker.
Chr.: Chromosomal location of the marker derived from Somers et al. (2004).
Pos.: Position of the marker in cM on chromosome derived from Somers et al. (2004).
Sign.: Level of significance computed using the MIXED procedure of the marker×nitrogen interaction effect.
F-val.: F-value was computed using the MIXED procedure.
$RP_{N+,N-}$ [aa]: Mean of relative performances (RP_{N+}, RP_{N-}) of exotic genotype (Syn-84) at a given marker locus across all tested environments computed using the MIXED procedure. Relative performance was computed as ([aa]-[AA])×100 / [AA], where [AA] or [aa] were LS-means of BC_2F_4 lines carrying the cultivar genotype (Triso or Devon) or the exotic genotype (Syn-84) at the given marker locus.
N+, N- [AA]: Mean of LS-means of trait values for both N-levels for BC_2F_4 lines carrying the cultivar genotype (Triso or Devon) at the given marker locus.
N+, N- [aa]: Mean of LS-means of trait values for both N-levels for BC_2F_4 lines carrying the exotic genotype (Syn-84) at the given marker locus.

3.7.5 REML - Comparison of marker main effects detected in T84 and D84

A comparison of marker main effects in T84 and D84 detected using the REML III analysis may validate common marker main effects with exotic alleles, which are conserved between the donor genotypes (Table 23).

Five QTLs might be validated with marker×trait associations at identical marker loci and same exotic allele's effects detected in the other population. At these common QTLs for plant height (*QHei.D84-2A*), thousand grain weight (*QTgw.T84-6B*, *QTgw.D84-2D*) and grain yield (*QYld.T84-3A*, *QYld.T84-3A*), significances for marker×trait associations ranged between 0.013 and 0.022. Two marker×trait associations validated effects conducted by identical synthetic wheat alleles in close vicinity to QTLs in the other population. The remaining two QTLs could not be validated in the other population.

Table 23: Localisation of nine QTLs as marker main effects (P = 0.01) in T84 and D84, computed in high and low N-level using four-way REML single-locus analysis analysis (REML III) and REML multi-locus analysis (REML IV).

Pop	Trait	QTL	Marker	Chr.	Pos. (cM)	n [aa]	F-val.	R^2 (%)	$RP_{N+,N-}$ [aa]	N+,N- [AA]	N+,N- [aa]	QTL effect	REML III	REML IV
T84	HEA	*QHea.T84-4A*	Xwmc468	4A	38	19	15.7	20.5	-2.2	86.3	84.4	+	M	M
T84	HEI	*QHei.T84-4Ab*	Xgwm160	4A	79	21	25.0	9.7	-6.6	98.5	92.0	+	M	M
T84	TGW	*QTgw.T84-6B*	Xgwm626	6B	48	23	24.6	11.5	-6.6	42.5	39.7	-	M	M
T84	YLD	*QYld.T84-3A*	Xgwm5	3A	45	13	23.7	40.0	-30.2	63.0	44.0	-	M	M
T84	YLD	*QYld.T84-3B*	Xbarc73	3B	60	7	14.1	5.1	-18.6	62.3	50.7	-	M	
D84	HEI	*QHei.D84-2A*	Xgwm558	2A	54	17	13.2	7.3	5.9	102.0	108.0	-	M	M
D84	HEI	*QHei.D84-5A*	Xbarc330[1]	5A	75	19	13.0	11.4	4.3	101.9	106.3	-	M	
D84	TGW	*QTgw.D84-2D*	Xgwm157	2D	73	26	16.5	12.3	6.1	44.4	47.1	+	M	M
D84	YLD	*QYld.D84-3Ba*	Xgwm493	3B	12	8	18.5	7.6	-13.2	59.9	52.0	-	M	M

Table 23: Continued.

Trait: HEA (Days until heading), HEI (Plant height), TGW (Thousand grain weight), YLD (Grain yield).

QTL: A significant marker×trait association was specified as QTL, if marker main effect was significant with P = 0.01 in the MIXED procedure. Linked QTL with a ≤ 20 cM distance were interpreted as one QTL. The QTL label is consisting of Q (for QTL), YLD (tested trait), D84 (tested population), 4Ab (chromosome, where the QTL was detected and b for the second YLD-QTL on the same chromosome).

Marker: Label of SSR marker. (×) Significant marker×trait association computed with the highest F-value in a linked QTL cluster with a ≤ 20 cM distance. (1) Marker was not described by Somers et al. (2004) and Sourdille et al. (2004), respectively, estimated position in cM on chromosome by linked marker positions described by Somers et al. (2004) and Song et al. (2005).

Chr.: Chromosomal location of the marker derived from Somers et al. (2004).

Pos.: Position of the marker in cM on chromosome derived from Somers et al. (2004).

n [aa]: Number of markers showing the exotic genotype (Syn-84).

F-val.: F-value was computed using the MIXED procedure.

R^2 (%): Proportion of the genetic variance computed using the MIXED procedure, which was explained the marker main effect (M).

$RP_{N+,N-}$ [aa]: Mean of relative performances (RP_{N+}, RP_{N-}) of exotic genotype (Syn-84) at a given marker locus across all tested environments computed using the MIXED procedure. Relative performance was computed as ([aa]-[AA])×100 / [AA], where [AA] or [aa] were LS-means of BC_2F_4 lines carrying the cultivar genotype (Triso or Devon) or the exotic genotype (Syn-84) at the given marker locus.

N+, N- [AA]: Mean of LS-means of trait values for high and low N-supply for BC_2F_4 lines carrying the cultivar genotype (Triso or Devon) at the given marker locus.

N+, N- [aa]: Mean of LS-means of trait values for high and low N-supply for BC_2F_4 lines carrying the exotic genotype (Syn-84) at the given marker locus.

QTL effect: Relative performance of exotic genotype (Syn-84) at a given marker locus for N supplies N+ and N- across all tested environments computed using the MIXED procedure specified a favourable QTL effect (+) with a positive effect from the exotic genotype (Syn-84) compared with the cultivar genotype (Triso or Devon), a not favourable QTL effect (-) with a negative effect from the exotic genotype (Syn-84) compared with the cultivar genotype (Triso or Devon) at a given marker locus.

REML: Four-way REML single-locus analysis (REML III) and four-way REML multi-locus analysis (REML IV).

3.8 Comparison of QTLs detected in ANOVA and REML analyses

The QTL analyses revealed QTLs detected through three-way (ANOVA I, REML I, REML II) and four-way (ANOVA II, REML III, REML IV) methods, which were used to compare the QTL effects (Table 25). Principally, each QTL was proved using the different methods of multi-environmental QTL detection.

Only significant marker main effects were detected using REML mapping methods, whereas marker main effects (ANOVA I, ANOVA II), marker×environment (ANOVA I) and marker×nitrogen interaction effects (ANOVA II) were ascertained using ANOVA methods.

Altogether, 130 (T84) and 109 (D84) QTLs were established across QTL mapping methods (Appendix 14, Appendix 15). A QTL effect is described as common QTL if this effect is computed separately in different QTL mapping methods. Hence, 40 (T84) and 31 (D84) common QTLs were validated in two or more QTL mapping methods, which are described in the following.

Table 24: Validation of seven QTLs as marker main effects (P = 0.01) in T84 and D84, computed in high and low N-level using four-way REML single-locus analysis analysis (REML III).

Pop	Trait	QTL/ association	Sign.	Marker	Chr.	Pos. (cM)	n [aa]	F-val.	R^2 (%)	$RP_{N+,N-}$ [aa]	N+,N- [AA]	N+,N- [aa]	Diff. [aa]	QTL effect
T84	HEI	*QHei.T84-4Ab*	0.002	Xgwm160	4A	79	21	21.8	11.1	-6.6	98.5	92.0	-5.5	+
D84	HEI	*association*	0.014	Xgwm397	4A	18	18	10.5	5.6	4.3	101.9	106.3	4.4	-
T84	TGW	*QTgw.T84-6B*	0.004	Xgwm626	6B	48	23	24.6	11.5	-6.6	42.5	39.7	2.6	-
D84	TGW	*association*	0.020	Xgwm626	6B	48	15	11.2	6.2	-6.4	45.0	42.1	-2.9	-
T84	YLD	*QYld.T84-3A*	0.007	Xgwm5	3A	45	13	23.7	40.0	-30.2	63.0	44.0	-19.0	-
D84	YLD	*association*	0.013	Xgwm5	3A	45	13	12.0	15.7	-13.4	62.6	54.2	-8.4	-
T84	YLD	*QYld.T84-3B*	0.009	Xbarc73	3B	60	7	14.1	5.1	-18.6	62.3	50.7	-11.6	-
D84	YLD	*association*	0.015	Xbarc73	3B	60	10	11.6	4.3	-9.5	59.9	54.2	-5.7	-
D84	HEI	*QHei.D84-2A*	0.008	Xgwm558	2A	54	17	13.2	7.3	5.9	102.0	108.0	6.0	-
T84	HEI	*association*	0.022	Xgwm558	2A	54	24	8.5	4.4	3.6	96.6	100.1	3.5	-
D84	HEI	*QHei.D84-5A*	0.006	Xbarc330[1]	5A	75	19	13.0	11.4	4.3	101.9	106.3	4.4	-
T84	HEI	*association*	0.012	Xgwm415	5A	55	20	11.2	5.3	4.5	97.0	101.4	4.4	-
D84	TGW	*QTgw.D84-2D*	0.009	Xgwm157	2D	73	26	16.5	12.3	6.1	44.4	47.1	2.7	+
T84	TGW	*association*	0.013	Xgwm157	2D	73	22	14.1	6.7	5.5	41.9	44.2	2.3	+

Gloss based on Table 23.

Common QTLs stable across QTL mapping methods

Common QTLs were identical established using all three-way and four-way QTL mapping methods, simultaneously. Only these QTLs were involved, which were significant as marker main effects. Three (T84) and two (D84) common QTLs were detected.
In T84, at common QTLs *QHea.T84-4A*, *QHei.T84-4Ab* and *QYld.T84-3A*, exotic alleles explained 20.4%, 10.2% and 33.1% of the genetic variance, respectively. In D84, at common QTLs *QHei.D84-2A* and *QTgw.D84-2D*, the exotic genotype revealed 9.7% and 12.7% of the genetic variance. In both populations, common QTLs showed the highest genetic variance computed by using ANOVA methods.

Three-way analyses

Three-way QTL mapping methods (ANOVA I, REML I) revealed ten (T84) and four (D84) common QTLs, which were identical in both QTL analyses, respectively (Appendix 14, Appendix 15). QTLs were included, which were significant as marker main effects and/or marker×environment interaction effects.
By using REML I, five (T84) and four (D84) QTLs were analysed as significant marker main effects in ANOVA I. In T84, further five QTLs were significant for both, marker main effect and marker×environment interaction effect.
Altogether, strongest QTL effects detected by using ANOVA I were validated in REML I. Eight (T84) and four (D84) common QTLs were computed with a level of significance less than 0.001 in ANOVA I. In T84, exotic alleles explained the genetic variance of 7.2% and 33.1% at common QTLs, *QPm.T84-7Bb* and *QYld.T84-3A*, respectively. In D84, at common QTLs, *QHei.D84-2A* and *QHei.D84-5A*, the exotic genotype explained the least genetic variance by 9.7% and the highest genetic variance by 14.7%. Thus, using ANOVA I the genetic variance was estimated higher than 10% at 12 (21.5%, T84) and four (10.4%, D84) common QTLs. Using REML I eight (T84) and four (D84) QTLs were analysed with a genetic variance higher than 10%.

Four-way analyses

Four-way QTL mapping methods (ANOVA II, REML III) revealed five (T84) and four (D84) common QTLs, which were identical in both QTL analyses (Appendix 14, Appendix 15). QTLs were involved, which were significant as marker main effects and/or nitrogen×environment interaction effects.
In T84, using ANOVA II exotic alleles explained the genetic variance of 8.6% and 39.7% at common QTLs *QYld.T84-3B* and *QYld.T84-3A*, respectively (Appendix 12). In D84, at common QTLs, *QYld.D84-3Ba* and *QHei.D84-5A*, the exotic genotype explained the least genetic variance by 9.4% and the highest genetic variance by 14.7% (Appendix 13).

Table 25: Comparison of QTLs in T84 and D84 across QTL mapping methods.

Pop	Effect	three-way model			four-way model		
		ANOVA I	REML I	REML II	ANOVA II	REML III	REML IV
T84	M	57	10	7	48	5	4
	M×E	48	0	0	n.p.	n.p.	n.p.
	M×N	n.c.	n.c.	n.c.	11	0	0
D84	M	48	4	2	48	4	3
	M×E	30	0	0	n.p.	n.p.	n.p.
	M×N	n.c.	n.c.	n.c.	13	0	0

Effect: A significant marker×trait association was specified as QTL, if marker main effect (M), marker×environment (M×E) or marker×nitrogen (M×N) interaction effect was significant with P = 0.01.
ANOVA I and II: These results were computed using a three-way ANOVA single-locus analysis (ANIVA I) and four-way ANOVA single-locus analysis (ANOVA II).
REML I to IV: These results were computed with a three-way REML I single-locus analysis and REML II multi-locus analysis, a four-way REML III single-locus analysis and REML IV multi-locus analysis.
n.c.: Effects were not computed. n.p.: Effects were not presented.

Three-way compared with four-way analyses

QTL mapping methods were compared as followed ANOVA I with ANOVA II, REML I with REML III. The comparison revealed 32 (T84) and 30 (D84) common QTLs, which were identical in two QTL analyses (Appendix 14, Appendix 15). QTLs were involved, which were significant as marker main effects.

Mostly common QTLs were ascertained in HEI (7), HLW (8), TGW (7) and YLD (6) in T84. In D84, mostly common QTLs were established in HEI (5), HEA (4) and YLD (6). In addition, these analyses revealed marker×environment and marker×nitrogen interaction effects at identical marker loci identified for *QHei.T84-7B* and *QHei-N.T84-7B*, *QLah.T84-7A* and *QLah-N.T84-7A*, *QYld.T84-5A* and *QYld-N.T84-5A* and *QHlw.D84-5A* and *QHlw-N.D84-5Ab*. At marker loci *QLah.T84-4D* and *QLah-N.T84-4D* a marker main effect and a marker×nitrogen interaction effect was significant. However, most QTLs were detected in the three-way analyses.

4 Discussion

The present study has been carried out on the basis of field experiments across four widely different locations and two seasons in Germany. The advanced backcross QTL analysis was applied to identify numerous QTLs for ten agronomic traits, three quality parameters and three disease resistances in two advanced backcross populations (T84 and D84). The BC_2F_4 generation was used to localise favourable QTL effects of the exotic alleles for trait improvement. The discussion is subdivided in the following sections. The genetic constitution of the advanced backcross populations as revealed by SSR marker analysis is mentioned, followed by a description of the phenotypic variation and correspondence to correlations between traits. Then, designs of AB-QTL studies are reviewed. In addition, statistical QTL mapping methods for detecting significant marker×trait associations and their potential for detecting QTLs in advanced backcross populations are discussed. Thus, the presence of environment and nitrogen dependent QTL effects in term of marker×environment and marker×nitrogen interaction effects are mentioned. Afterwards, QTLs are compared between both advanced backcross populations and to QTLs and candidate genes published by other QTL studies.

4.1 Designs of AB-QTL studies

Although genotypes that are unadapted to a particular environment are inferior to adapted genotypes, may be contain superior alleles at some loci that could improve specific traits when introgressed into adapted genotypes as elite varieties. Molecular markers have made it possible to identify and introgress favourable QTLs with exotic alleles into elite breeding lines. QTL analysis has produced great advances in plant science and a revolution in quantitative genetics, genetic analysis of complex traits (Asins 2002). Tanksley and Nelson (1996a) proposed the advanced backcross QTL (AB-QTL) strategy to discover and transfer valuable QTL alleles from exotic donor lines (land races, wild species) into cultivated elite breeding lines. Wild species have been widely used as important gene resources for introgressing useful traits into various crops. The backcrossing method has been extensively used in self-pollinating crops to transfer simply inherited characteristics to cultivars which are deficient only in the characteristics being transferred (Blanco et al. 2008).

So far, seven studies used the AB-QTL analysis for detecting QTLs in wheat. Initiating, Huang et al. (2003b) conducted the first advanced backcross QTL analysis in wheat using a BC_2F_2 population derived from a cross between a German winter wheat cultivar and a synthetic wheat line, Prinz×W-7984, developed by CIMMYT. The second advanced backcross QTL analysis published by Huang et al. (2004) and was carried out using a BC_2F_1 population derived from a cross between a German winter wheat cultivar and a synthetic wheat line Flair×XX86, developed in Japan. Later, Liu et al. (2006) developed BC_4F_3 introgression lines from a cross between a Chinese wheat cultivar and an exotic hexaploid wheat genotype, Laizhou953×Am3.

Besides, Narasimhamoorthy et al. (2006) conducted an advanced backcross QTL analysis in a BC_2F_2 population derived from a cross between a hard red winter wheat variety and a synthetic wheat line, Karl92×TA4152-4, provided by CIMMYT. All four advanced backcross QTL analyses were used to identify QTLs for agronomic traits. In addition, Narasimhamoorthy et al. (2006) also investigated baking quality parameters. Besides, Kunert (2007a) and Naz et al. (2008) used two BC_2F_3 populations derived from crosses of two German winter wheat varieties and two synthetic wheat accessions, Batis×Syn-22 and Zentos×Syn-86. In these populations QTLs revealed agronomic traits and quality parameters (Kunert 2007a) and resistances to plant diseases (Naz et al. 2008) were detected. Further, Mohamed (2007) analysed the identical two BC_2F_4 populations derived from crosses, Triso×Syn-84 and Devon×Syn-84, as analysed in the present report. Mohamed (2007) identified QTLs associated with agronomic traits, morphological seedling-root traits and carbon isotope discrimination under well-watered and drought-stress treatments. These results suggested the importance of the following factors which may influence the success of an AB-QTL strategy.

I) The selection of appropriate parents for the backcrossing is a critical step in an AB-QTL strategy. Diverse and more differentiated parents from different genetic backgrounds are favourable for a healthy gene flow from the donor to the recurrent parent (Bernardo 2008). Often for QTL mapping experiments, parents that represent the extreme ends of a trait phenotype are selected. This increases the chance of detecting QTLs because QTL mapping is based on statistically different means of marker groups (Holland 2001). Thus, the genetic background of the advanced backcross population is important in terms of a favourable breeding goal and enriching genetic diversity. Moreover, Gupta et al. (2008) and Kumar at el. (2007) reviewed that the results of latter studies reinforced the realisation that while conducting QTL analysis for an individual complex trait, more than one mapping population should be used. Also, Kunert et al. (2007b) and Naz et al. (2008) used two different genetic background populations, derived from crosses between two winter wheat cultivars with two different synthetic wheat accessions. In the present report, a single synthetic wheat line Syn-84 was used for the development of both advanced backcross populations, derived from two spring wheat cultivars, Triso and Devon.

II) A defined breeding goal should be defined for selection and parents of favourable traits should be taken for the backcrossing. The traits of interest varied from five agronomic traits (Huang et al. 2003b) to eleven agronomic and quality traits (Narasimhamoorthy et al. 2006). So far, only Naz et al. (2008) analysed defence to phytopathogens in two advanced backcross populations. In the current study, ten agronomic traits, three quality parameters and three disease resistances were analysed in each population. Simultaneously, both populations were grown under two different N-treatments to study N-responsive QTLs, according Kunert (2007a).

III) The structure of the population influences the outcome of the AB-QTL analysis in terms of the strength of favourable exotic QTL alleles. Segregation populations as BC_2 were used in AB-QTL analyses published by Kunert et al. (2007b), Mohamed (2007), Naz et al. (2008), Narasimhamoorthy et al. (2006) and Huang et al. (2004, 2003b).

If the dominant effect plays a role, the favourable QTL effect detected in BC_2F_2 generation may be not the true QTL. Thus, a more advanced population like BC_4F_3 is recommendable for AB-QTL analysis, according Liu et al. (2006). However, in this report, BC_2F_4 lines were used which reduced the chance of losing a QTL effect in the next generation.

IV) The population size also plays a crucial role for the detection and selection of QTL effects. Most QTL studies have used small population sizes that limit the power to detect and correctly estimate the location and magnitude of QTL effects (van Ooijen 1992). Due to limited population sizes, genetic effects might be overestimated, QTL localisation might be inaccurate and QTL of minor importance might not be detected (Arbelbide et al. 2006a, Schön 2004, Utz et al. 2000). There are high numbers of segregating alleles for a complex trait in advanced backcross lines. Small population sizes and limited phenotypic evaluation together constitute insufficient sampling, which can cause lack of repeatability of QTL mapping results (Xu 2003). Hence, the number of advanced backcross lines should also be increased to have a high probability of recovering all favourable alleles. In order to achieve this goal, the current study contains population sizes of 223 (T84) and 176 (D84) BC_2F_4 lines.

V) An appropriate number and density of molecular markers play a pivotal role in the outcome of AB-QTL analysis. So far, only SSR markers were used in the AB-QTL anaylses in wheat. The number of polymorphic markers between the crossing parents varied from 97 markers (Naz et al. 2008) to 205 markers (Huang et al. 2003b). In this study, a total of 94 (T84) and 106 (D84) SSR markers were genotyped, respectively. However, the markers were not evenly distributed across the genome caused by sparsely polymorphism between the crossing parents of BC_2F_4 lines, multiple loci and artificial fragments, not amplified and due to markers having less than five exotic alleles in a population, which were later excluded from the QTL analysis.

VI) Number and variability of tested environments is important in terms of the reproducibility of a QTL effect. Hai et al. (2008) assumed that QTL analysis conducted with data from a single environment is likely to underestimate the number of QTL for a certain trait. Also, Bernardo (2008) mentioned that the detection of a QTL in one environment but not in others hinders the transferability of QTL mapping results. Therefore, a QTL analysis should be based on several distinct environments for QTL detection (Perretant et al. 2000). Advanced backcross populations were usually evaluated in only three (Liu et al. 2006) to ten (Naz et al. 2008) environments, thus sampling a limited set of QTL×environment interaction effects and preventing results from being applicable to a wider range of environments (Xu 2003). The number of replications of lines at a tested environment further improves the precision of a QTL experiment, for instance without (Kunert et al. 2007b, Mohamed 2007, Naz et al. 2008) and three (Narasimhamoorthy et al. 2006) replications. Further, Kumar at el. (2007) described that it is usual for QTL mapping to be measured on different sites or over different years to determine which QTLs are most robust. Accordingly, four sites and two years revealing eight different environments were used for measuring the traits of interest in the present report.

VII) A important consideration in QTL mapping and interpretation of QTL data is the threshold employed for inferring statistical significance. Because QTL mapping involves many analyses of independent genetic markers throughout a genome, there are many opportunities for false positive results to arise. Stringent significance thresholds must be employed to avoid these false positive QTLs (Rong et al. 2007, Arbelbide et al. 2006a). Also, Bernardo (2008) recommended if the eventual goal of QTL mapping is to identify candidate genes, the penalty of a false positive is severe. Therefore, the statistical stringency or threshold for declaring the presence of the QTL must be very high. Huang et al. (2004, 2003b) specified the significance threshold according to Fulton et al. (2000, 1997b) and Tanksley et al. (1996b). Regions of the genomes were identified as a QTL if the results met one or more of the following criteria: a significant effect was observed for a single marker×trait combination at a single location with $P = 0.001$, significant effects were observed in the same direction for a single marker×trait combination at two or more locations with $P = 0.01$, significant effects were observed in the same direction for a single marker×trait combination at three or more locations with $P = 0.1$. A recent study specified the threshold at $P = 0.001$ for QTL detection using a two-way ANOVA method (Pshenichnikova et al. 2008). In contrast, Narasimhamoorthy et al. (2006) used the threshold with $P = 0.05$, based on the ability to repeatedly detect the same QTL with similar effects across all environments. Arbelbide et al. (2006a) mentioned that although fewer QTLs would be published at high levels of significance, these significant markers have a much higher probability of being truly linked to a QTL. For this reason, the threshold was used at $P = 0.01$ in the present QTL mapping methods.

VIII) The statistical models exert a major impact on the results of a QTL analysis (Pillen et al. 2003). Previous AB-QTL studies used mostly one-way models (Liu et al. 2006, Narasimhamoorthy et al. 2006, Huang et al. 2004, 2003b) for QTL mapping. To further investigate the stability of a QTL effect in multiple environments, the environments and the interaction effect between marker and environment are important considerations. Thus, this study employed a three-way model with the marker genotype as fixed factor, the environment and the BC_2F_4 line nested in the marker genotype as random factors. The fixed marker effect was used for allowing the estimation of an effect for each marker allele. This method inherently identifies the favourable marker alleles and the inbreds that most likely carry favourable alleles at specific QTL (Arbelbide et al. 2006a). In addition, the factor N-supply was implemented in a four-way model. Following Pillen et al. (2003), it was expected to reduce the residual variance of the experiment by including the environment and N-supply in the statistical model and, thus, to increase the probability of detecting a QTL effect. These models enabled the integration of additional random factors, such as the interaction effect between marker×environment and marker×nitrogen.

IX) A frequently used method for QTL mapping in a plant genetic context is the ANOVA method (Stich et al. 2008). The adjusted power to detect QTL of all mapping methods increased with increasing size of the genetic effect assigned to an allele. In comparison with the other

mapping methods, the ANOVA method showed the lowest adjusted power to detect QTL for all examined sizes of genetic effects. Stich et al. (2008) assumed that this method was inappropriate for association mapping, because it resulted in a proportion of spurious marker×phenotype associations that is considerably higher than the nominal test type 1 error rate. The mixed-model association mapping methods using a kinship matrix estimated by REML are more appropriate for association mapping than recently proposed methods. Another study compared the ANOVA and REML method resulting that the REML method yielded identical results (Spilke et al. 2005). They assumed that all ANOVA estimates for variance components were positive. Otherwise, results differ, because REML variance components estimates were constrained to be positive (Spilke et al. 2005). All previously published AB-QTL studies used only the ANOVA method for detecting QTLs. Kumar at el. (2007) recommended that more than one method of QTL mapping methods should be employed. To that fact, two different QTL mapping methods, ANOVA and REML were utilised in the present report.

X) All AB-QTL studies and most of QTL analyses used single-locus methods for QTL mapping (Gupta et al. 2008). A current study described a comparison of single-locus and multi-locus methods in multiple environments (Bauer et al. 2009). They assumed that the estimated marker effects seem to be less biased if a forward selection method is computed. The computations resulted in that many significant marker×trait associations were computed using the single-locus analysis. Bauer et al. (2009) mentioned that it could be due to the consideration of only a single marker point at a time. Compared to the REML multi-locus mapping, using a REML forward selection method, fewer markers were found to be significant. Thus, as expected, the forward selection analysis seems to be more powerful for QTL mapping. Furthermore, the estimated marker effect of exotic alleles will be increased in forward selection in the same manner as the F-value decreases and the P-value of F-test increases. Similar, Cuthbert et al. (2008) used a forward stepwise regression with backward elimination to search for QTL and identify cofactors for composite interval mapping analysis. Therefore, the present study computed single-locus and multi-locus methods according Bauer et al. (2009).

4.2 Genetic constitution of BC_2F_4 populations

SSR markers were used for genotyping the advanced backcross populations including 223 (T84) and 176 (D84) BC_2F_4 lines. The polymorphism survey has been resulted 94 (T84) and 106 (D84) markers for the QTL analysis. The distribution of analysed markers was not homogeneous across the A, B and D genomes. Thus, several genomic regions covered gaps with marker intervals greater than 50 cM notably on the A genome.

The marker analysis revealed distorted segregation in 26% (T84) and 25% (D84) of the BC_2F_4 lines. While a single exotic introgression was specified in four (T84) BC_2F_4 lines. Two (D84) BC_2F_4 lines were detected with two exotic introgressions. Further, 25% (T84) and 22% (D84) of genotyped markers showed distorted segregation. Exotic alleles were present at all analysed marker loci in both populations.

Excluding from the analyses numerous marker loci revealed less than five individuals carrying the homozygous exotic alleles in both populations (data not presented).

All seven homologous groups have been involved in segregation distortion. Most of distorted segregations were identified on the B genome and the D genome ranked second in the number of segregation distortion, according to Xue et al. (2008). Segregation distortion is defined as a deviation of observed genetic ratios from the expected Mendelian ratios in a given phenotypic or genotypic class within a segregating population. Distorted segregation had frequently been found during the construction of genetic linkage maps (Lu et al. 2002, Peng et al. 2000). Numerous studies mentioned that segregation distortion has appeared in different types of mapping populations as in a double haploid population (Quarrie et al. 2005, Cadalen et al. 1997), F_2 to F_7 progeny recombinant inbred lines (Xue et al. 2008, Liu et al. 2005, Blanco et al. 2004, Paillard et al. 2003, Liu and Tsunewaki 1991), a *T. dicoccoides*×*T. durum* F_2 population (Peng et al. 2000) and a *Ae. tauschii* F_2 population (Faris et al. 1998). Besides, Singh et al. 2007) assumed that segregation distortion in favour of the female parent was observed in most previous studies. Possible causes for segregation deviation of molecular markers are androgenesis ability (Quarrie et al. 2005, Cadalen et al. 1997), gametophytic genes (Xue et al. 2008, Lu et al. 2002) and meiotic drive (Lyttle 1991). However, these factors may work simultaneously and in opposite directions, favouring the alleles of the exotic or cultivated crossing parent in different genomic regions (Peleg et al. 2008).

4.3 Phenotypic variation

The populations T84 and D84 were investigated at four different experimental locations with two different N-treatments in two successive years. The investigation of 15 quantitative traits was separated in nine agronomic traits, three quality parameter and three disease resistances. The agronomic trait brittleness was evaluated, observed to these quantitative traits as present or absent. Accenting, the phenotypic data were computed in at least two environments per trait. Predominantly, the mean of traits were higher in high N-supply compared to low N-supply in both populations and the corresponding recurrent parents. Besides, the standard deviations were higher in the populations compared to corresponding recurrent parents across all traits. Then the higher standard deviations indicated that a genetic variation in the population was present. Thus, the phenotypic variation was higher in the population than in the recurrent parents. Further, the means were predominatly different between the experimental locations and years. The highest diversity of means was measured for days until heading under low N-supply with significantly variations for each environment and population. Surprisingly, the phenotypic data for plant height were specified with no tendency for the various N-supplies across the investigated environments.

Quantitative traits were controlled by a number of genes and generally characterised by a low heritability with significantly environmental influence (Iqbal et al. 2007, Quarrie et al. 2005).

Heritability described the relative importance of the genetic versus the environmental influences on trait values in a population. In general, prevalent high estimates up to 0.91 of heritability were observed in most of the traits in both populations. Further, least heritability was ascertained for ears per square meter, which measured significant distinction between both N-levels across all tested environments for each population. Consequently, heritability changed according to the genetic and environmental variability present in the population. The weakest environmental influence was computed for days until heading, plant height and resistance to powdery mildew by up to 90% in T84. Several studies determined a high variation of heritability estimation values for yield and yield related traits, observing low heritability (Cuthbert et al. 2008, Hai et al. 2008) or high heritability (Marza et al. 2006). The increase of heritability of traits revealing QTLs with small effects can be achieved by reducing the environmental variation, by having more replicates or by combining analysis of several traits that the gene affects pleiotropically (Korol et al. 2001). Analogous, associations between yield and most of the yield components were described as highly significant, suggesting pleiotropy and/or coincidence with these QTLs (Cuthbert et al. 2008). Otherwise, no significant correlation coefficients between yield and its components were detected, indicating the complexity of the trait yield (Huang et al. 2003b). The pleiotropy might be the cause for the existence of a genetic correlation between traits in outbred populations (Schrooten and Bovenhuis 2002). In the current study yield components, brittleness, grain number per ear and harvest index, were highly significantly correlated with grain yield while plant height and thousand grain weight were not correlated with grain yield, coinciding with results by Cuthbert et al. (2008). In other studies, significant correlations and coincident QTLs were observed between grain yield and yield components (Kuchel et al. 2007, Kumar et al. 2007, Huang et al. 2006, Quarrie et al. 2005, Börner et al. 2002, Kato et al. 2000). Further, some trait correlations can be ascribed to pleiotropic or co-located QTLs. Pleiotropy describes the genetic effect of a single gene on multiple phenotypic traits. In T84, marker×trait associations at the marker locus Xgwm294 were significantly associated with five traits, brittleness, days until heading, grain test weight, thousand grain weight and sedimentation value, using the ANOVA I method. These coexistent localised traits were strongly negatively correlated except sedimentation value. Shah et al. (1999) suggested that pleiotropy, linkage or the presence of additional loci revealing yield traits may explain these correlations and the identification of a few lines having the favourable phenotype for one trait.

4.4 Comparison between QTL mapping methods

The present study utilised two different QTL mapping methods, ANOVA and REML, which provided similar results. To observe the stability of QTL detection, the results of three-way and four-way models computed through ANOVA and REML methods were compared (Table). The three-way ANOVA single-locus analysis (ANOVA I) revealed 105 (T84) and 78 (D84) QTLs. However, the three-way REML single-locus analysis (REML I) revealed ten (T84) and four (D84) common QTLs.

The main difference between the two mapping methods was that the first allowed computation of QTLs with significant marker×environment interaction effects, mostly if these QTLs did not appear as marker main effect. The REML method was more stringent than the ANOVA method, which only computed significant marker main effects.
In addition, using REML method no significant effects were ascertained for traits measured in up to three environments, because the residual effect might be estimated to high. To that fact, the power of QTL detection could be increased by enhancing the number of tested environments. Moreover, the ANOVA method led to a considerable decrease in genetic variance and thus to the detection of minor QTLs. Using the ANOVA analysis significant marker main effects with highest F-values, especially in marker clusters associated with single QTLs, were revealing marker main effects detected by the REML analysis. QTLs with low F-values and low explained genotypic variances in the ANOVA method were not significantly validated using the REML method.
By the REML method revealed QTLs were most computed with significances less than $P = 0.001$ and explained more than 10% of the genetic variances in the ANOVA method. It might be postulated that the other QTL regions were either false positive or small QTLs that were not robust enough through the REML method.
The REML multi-locus method resulted in fewer QTLs than detected by the REML single-locus method (Table). However, three (T84) and two (D84) common QTLs were stable detected across all QTL mapping methods. Consequently, the more stringent QTLs identified by the REML methods were used for the following discussion.

4.5 Marker×environment interaction

Breeders have often developed cultivars with superior adaptation to their target environment without a detailed knowledge of the underlying physiological mechanisms. Unfortunately, field measurements and particularly those for grain yield, are subject to significant extraneous error, which in turn reduces the effectiveness of phenotypic selection. In addition, the major stresses present in a particular year and at any particular site, may not provide the optimum environment for selecting long-term, overall, genetic performance (Kuchel et al. 2007). Genotypes grown in multi-environment trials reacted differently to environmental changes such as maximum and minimum temperature, radiation, soil characteristics and precipitation. This differential response of genotypes from one environment to another was called genotype×environment interaction (Crossa et al. 1999).
The change of the effect of the exotic allele between environments is referred to as crossover interaction. Crossover interaction can result from artefacts, like a wrong measurement of one or more lines. Another reason could be an environmental factor, drought, which displays a rather good performance of a genetic factor in an environment without drought stress and a worse performance of the same genetic factor compared to others in an environment with drought stress (Li et al. 2003).

In mapping QTLs, suitable genetic populations were grown in different environments which caused QTL×environment interactions at which QTLs with large effects in some environments and no effects in others were commonly found (Li et al. 2003, Crossa et al. 1999). The extent of QTL×environment interactions is often unknown because the QTL mapping studies have been limited to few years (replications) or locations (Collard and Mackill 2008a).

Privous AB-QTL studies did not calculate (Huang et al. 2003b), found no significant (Kunert et al. 2007b, Liu et al. 2006) or detect only few environment interaction effects (Naz et al. 2008, Narasimhamoorthy et al. 2006, Huang et al. 2004). Narasimhamoorthy et al. (2006) mentioned that QTL×environment interaction effects were seen for few QTLs, but the explained variation was swamped by environmental variation. Then, the majority of the marker×environment interaction effects were due to changes in the effect of the exotic alleles and were not useful for marker-assisted selection across environments.

The current report revealed no significant marker×environment interactions using the more stringent three-way REML mapping method. However, by using the three-way ANOVA method 48 and 30 QTLs as marker×environment interaction effects were identified in T84 and D84, respectively. At these loci, crossover interactions were obviously revealing favourable effects from exotic alleles in some environments, but unfavourable effects in others. However, 11 (T84) and 13 (D84) QTLs as marker×environment interaction effects were corresponded to marker main effects or were only due to changes in the magnitude of the effects. These QTLs may still be providing the targets for crop genetic improvement via marker-assisted selection across environments according to Quarrie et al. (2005).

4.6 Marker×nitrogen interaction

Due to economic and ecological factors, European agricultural practices are likely to go towards extensive systems with lower inputs of nitrogen (N) fertilisers. Van Sanford and MacKown (1987) reviewed that the efficient use of nitrogen in wheat depends on inorganic N-uptake, assimilation and on the successful remobilisation and partitioning of organic nitrogen.

Previous AB-QTL studies used a single N-treatment, except from Kunert (2007a). This report conducted a four-way ANOVA to reveal QTL effects in combination with N-response. The analysis revealed altogether eight (Batis×Syn-22) and four (Zentos×Syn-86) QTLs as significant marker×nitrogen interaction effects. At four (Batis×Syn-22) and two (Zentos×Syn-86) QTLs the synthetic wheat alleles improved the trait performance in low N-treatment. Another recent QTL analysis compared three methods to studying QTL×nitrogen interaction effects (Laperche et al. 2007). This study was performed on a mapping population of doubled haploid lines, obtained from the cross between an N-stress tolerant variety and an N-stress sensitive variety. The first was to compare two QTL sets detected under the two N-levels. The second was to consider variables such as (N+)–(N−) and (N−)/(N+), computed for each combination of location and year. Factorial regression constituted the third method.

This method was relevant to the study of QTL×nitrogen interaction effects insofar as interactive regions revealed by the first method were validated and new interactive loci were detected on 2D, 5A and 7B.

The current report revealed no significant marker×nitrogen interaction effects using the more stringent four-way REML mapping method. However, 11 (T84) and 13 (D84) QTLs with marker×nitrogen interaction effects were identified for nine traits, by using the four-way ANOVA method. On chromosome 7A, an N-responsive QTL for lodging at harvest was influenced by the synthetic wheat alleles, which improved the lodging in low N-level in T84. Also in D84, a N-responsive QTL was detected with favourable exotic alleles for improving grain test weight on chromosome 5A. The new interactive loci, detected by Laperche et al. (2007) could be validated for grain yield in T84 (2D, 5A, 7B) and D84 (2D, 7B), respectively. The published and current marker×nitrogen interaction loci were mapped in the identical marker region, closely linked less than 20 cM. As the marker×nitrogen interactions for yield were significant in the present study, BC_2F_4 lines behaved differently according to the N-level. Thus, genetic variability concerning nitrogen availability could be shown. Hence, improvement of nitrogen efficiency in spring wheat should be possible.

Following Baresel et al. (2008), high N-uptake capability during grain filling stage is an advantage in environments, where N-supply is high also in the later growth stages (N+), but less valuable in environments with lower N-availability, where N-supply in the later growth stages is often limiting (N-). Then, an ideal nitrogen use efficient wheat would aquire nitrogen from soil efficiently to produce biomass and/or grain yield, mentioned by An et al. (2006). To these facts, the BC_2F_4 lines, where exotic alleles improved the trait performance under low N-level, may have a high N-uptake capability in earlier growth stages and N-translocation efficiency. Hence, the results of the present study have shown that exotic alleles are a useful source for the improvement of agronomic traits in elite wheat varieties under different N-treatments.

4.7 Comparison of QTLs detected in T84 and D84

Relatively fewer markers were genotyped in T84 than in D84. Despite that, notable fewer QTLs were identified in D84 (5) than in T84 (12) using three-way and four-way REML mapping methods. Comparing, five QTLs might be validated with marker×trait associations at identical marker loci and same exotic allele's effects detected in the other population. At these common QTLs for plant height (*QHei.D84-2A*), thousand grain weight (*QTgw.T84-6B*), grain yield (*QYld.T84-3A*, *QYld.T84.3B*) and powdery mildew (*QPm.T84.7D*), significances for marker×trait associations ranged between 0.012 and 0.037.

A stable marker locus associated with common QTLs might suggest that synthetic wheat introgressions at this locus may be advantageous to indivergent genetic backgrounds and growing conditions. Then, the corresponding location of a QTL in independent populations confirms that a chromosomal region might be important for the expression of the trait under investigation, indicating a similar genetic control in different populations.

Beyond, the synthetic wheat alleles (Syn-84) were similar in their effects and clearly different from the recurrent alleles (Triso and Devon). The effectiveness of exotic alleles in the different genetic backgrounds revealed a first indication that alleles from this synthetic wheat donor might not yet be present in elite genotypes. Further six QTLs could be validated in corresponding regions in the other population. Still, the results indicate that this synthetic wheat derived from wild emmer wheat×*Ae. tauschii* carries favourable QTL alleles for agronomic traits and resistance to powdery mildew, which might be useful for breeding improved wheat varieties by marker-assisted selection. Further six QTLs were validated at marker loci in close vicinity to QTLs for days until heading (*QHea.T84-4A, QHea.T84-5A*), plant height (*QHei.T84-4Ab, QHei.D84-5A*), thousand grain weight (*QTgw.T84-2Ab*) and powdery mildew (*QPm.T84-7Bb*) with significances for marker×trait associations ranged between 0.013 and 0.045, respectively. The remaining six QTLs were not validated because no marker×trait association was detected in the other population. These QTLs indicated a disappearing in the validation population.
Simultaneously, the majority of studies investigated QTLs for agronomic traits with inconsistent QTL detection across different experiments, environments and populations (Campbell et al. 2004). Several reports assumed reasons for disappearing QTLs between mapping populations.

I) Studies revealing a strong association at a particular locus with an important trait in one population, but could not be validated in another population. They assumed that such disappearing genes occur far too frequently to be explained multiple false positives.

II) Another explanation might be that non-validated QTLs are cross-specific, subject to genotype×environment interaction effects or illusory. Illusory QTLs may also be artefacts of small mapping populations, error in the phenotyping experiments or reflect fundamental limitations to QTL analysis methods (Langridge et al. 2001). Besides, inconsistent QTL detection across environments was also a result of QTL×environment interactions, which presumably represent the genetic factors underlying the genotype×environment interaction. QTL×environment interaction analyses indicated that some QTLs were sensitive to different environmental conditions, displaying interactions caused by either changes in magnitude of the QTL effect and crossover interactions (Campbell et al. 2003).

III) It has been observed that QTLs identified in a particular mapping population may not be effective in different backgrounds (Pillen et al. 2004, Liao et al. 2001). In some cases, this is due to the small effect of an allele transferred into elite varieties (Blanc et al. 2006).

IV) Disappearing in QTL validation between the both advanced backcross populations might be the genetic variation between the elite parents and difference in population size, with a smaller population (D84) exhibiting less statistical power for QTL detection.

V) In addition, Bernrado (2008) mentioned that the estimated effects of QTLs are often inconsistent in complex traits. Reasons for the inconsistency of estimated QTL effects include different QTL segregating in different mapping populations and QTL×genetic background interaction.

VI) For complex traits, which are controlled by many minor QTLs (rather than by few major QTLs), the inconsistency of estimated QTL effects has important implications for plant breeders (Xu 2003). Estimated QTL effects for traits such as grain yield or plant height have limited transferability across populations, QTL mapping for such traits will likely have to be repeated for each breeding population. Complex traits controlled by many QTLs are likely subject to genotype×environment interaction, QTL mapping for the same population will have to be performed for each target set of environments. As the effects of sampling errors are large, population sizes of 500 to 1000 progenies are recommended, if the objective is QTL mapping for highly complex traits.

VII) In other studies, the distribution of the estimated genetic effects of individual QTL has been consistent with a quantitative trait being controlled by few QTLs with large effects and many QTLs with small effects (Bernardo 2008). Small QTLs with opposite phenotypic effects might occasionally be closely linked in coupling in early generations and separated only in advanced generations after addional recombination (Rong et al. 2007).

VIII) Often for QTL mapping experiments, parents are selected which represent the extreme ends of a trait phenotype. This increases the chance of detecting QTLs because QTL mapping is based on statistically different means of marker groups. The main disadvantage of this method is that one (or even both) parent(s) may possess QTL alleles that are similar or even identical to the elite germplasm used in breeding programmes. In this case, the effect of a QTL may be insignificant when used for introgression into elite varieties. In other cases, the effect of a QTL may differ in different genetic backgrounds due to interactions with other loci or epistasis (Holland 2001). Following Asins (2002), a F_2-progeny is better than a backcross since QTL with recessive alleles in a recurrent parent could not be detected and when dominance is present backcrosses give biased estimates of the effects because additive and dominant effects are completely confounded in this design. In contrast, traditionally breeding high yielding spring wheat cultivars has been accomplished by making direct selections for grain yield. Early generation selection has generally not been effective and breeders usually maintain large breeding populations for a number of generations before selecting for grain yield (Cuthbert et al. 2008).

IX) Epistasis provides a straight forward explanation for this phenomenon, when different populations have different allele frequencies at epistatic loci (Templeton 2000). Two genes interact and together give a large effect on the trait performance, while the indiviual effects of the genes are small. Even when favourable QTL alleles come from a particular donor parent, the effect of the introgressed QTL alleles may vary because of a general form of epistasis that is known as QTL×genetic background interaction (Blanc et al. 2006). In the present report the effects of QTLs showed no evidence of epistasis as interaction between a pair of QTLs (data not presented) corresponding to the study of Shah et al. (1999).

According to Tanksley and Nelson (1996a), epistatic interaction of QTLs from a donor parent is considered to be difficult to detect, especially in advanced backcross generations, since every backcross generation greatly reduces the number of genotypic combinations because the donor genotype is being recovered.

4.8 Comparison between QTLs with QTLs and candidate genes in other studies

The knowledge of the approximate locations of QTLs has been used for studying candidate genes that are close to the identified QTL and that may be the actual genes that affect the quantitative trait (Bernardo 2008). Therefore, the results of the present AB-QTL analysis using REML methods were compared with several QTL analyses and studies of candidate genes in wheat, in particular to seven advanced backcross QTL analyses of wheat published by Kunert (2007a, 2007b), Mohamed (2007), Naz et al. (2008), Liu et al. (2006), Narasimhamoorthy et al. (2006) and Huang et al. (2003b, 2004). The highest numbers of common QTLs coinciding with QTLs published in other QTL studies were detected for days to heading (18 QTLs on 5A), plant height (14 QTLs on 5A), thousand grain weight (14 QTLs on 2D) and grain yield (14 QTLs on 3B), listed in Appendix 16. These common QTLs might be located in gene-rich regions, where more than 85% of wheat genes were presented. The gene-rich regions were strongly associated with a high recombination rate in wheat and are predominantly located on chromosome arms, reviewed by Peleg et al. (2008).
However, no corresponding QTLs were detected in AB-QTL studies published by Naz et al. (2008), Kunert et al. (2007b), Narasimhamoorthy et al. (2006) and Liu et al. (2006). In the following, the comparison between QTLs with other studies resulting QTLs and candidate genes is separately described for each common QTL and an overview is given in Figure 6 to Figure 17 and Appendix 16.

Agronomic traits

Grain yield and its component traits, such as tillers per square meter, days until heading, plant height, thousand grain weight and yield, are generally controlled by a number of QTLs in wheat. The REML method for QTL mapping was more stringent than the ANOVA method. Hence, the agronomic traits, brittleness, grain number per ear, harvest index, grain test weight and lodging at harvest measured only in few environments were possibly not robust enough for detecting significant marker×trait associations or were identified as false positive effects. Below, all significant marker loci associated with traits of interest which mapped to corresponding loci and/or regions previously published for these traits are discussed.

Tillers per square meter

Tillers per square meter is a quantitative trait and a yield component, with its expression revealed by environment, soil fertility and sowing date. Therefore, yield usually has a low heritability (Quarrie et al. 2005).

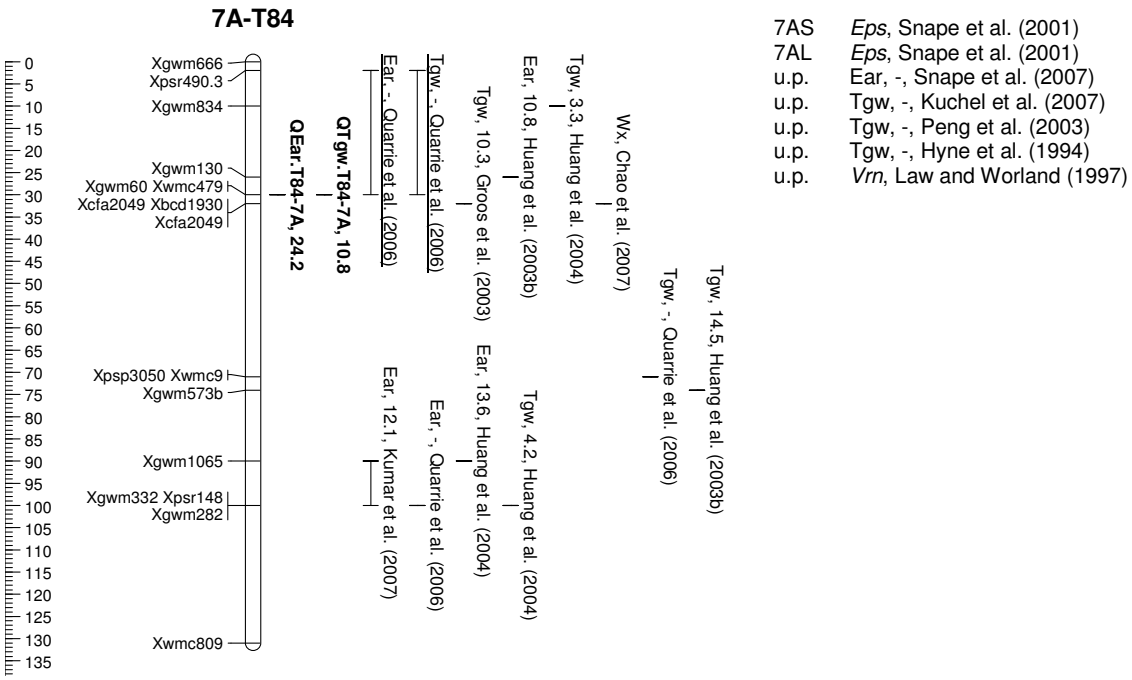

Figure 6: Localisation of current QTLs, *QEar.T84-7A* and *QTgw.T84-7A*, in T84, published QTLs and genes associated with tillers per square meter and thousand grain weight on chromosome 7A.

This graphical map was computed using MapChart (Voorrips 2002) with genetic map positions according Somers et al. (2004). The ruler (in cM) and mapped markers were indicated on the left. QTL confidence interval was indicated by a vertical bar. Bold QTLs were significant marker main effects detected by REML methods. Not bold QTLs and genes were published in other studies. Underlined QTLs and genes were detected at the identical significant marker locus as the current QTL. QTL description: Ear (Tillers per square meter), Tgw (Thousand grain weight), number (R^2 as explained genetic variance in %) and reference (study, where the common QTL was published). On the right, QTLs and genes are listed, where the position was on the short arm (S), long arm (L) or unknown (u.p.).

In the present study, the heritability ranged from 0.28 to 0.36 in both populations. Thus, the low heritability of yield related trait would allow the presence of a QTL to be identified which was environmentally stable.

In this study, a single QTL, *QEar.T84-7A*, for tillers per square meter was detected on the short arm of chromosome 7A in high N-level in population T84 (Figure 6). The Syn-84 alleles were associated with a decrease in the tiller number and explained 24.2% of the genetic variance.

Snape et al. (2001) mentioned that a gene for earliness per se (*Eps*) was located on chromosome arm 7AS. The *Eps* genes might promote yield potential by optimising the reproductive stage of development (Slafer and Rawson 1994).

Ten studies on the identification of QTLs for tiller number were published. Six QTLs could be detected on chromosome 7A. One QTL was localised at the identical marker position, published by Quarrie et al. (2006). They referred to the QTL cluster, *Qyld.csdh. 7AS1*, which was associated with tillers per plant, thousand grain weight and grain yield. This cluster was identified using the Chinese Spring×SQ1 doubled haploid population. A second QTL cluster, *Qyld.csdh. 7AL*, for tillers per square meter was localised on chromosome arm 7AL (Quarrie et al. 2006).

Huang et al. (2003b) detected the QTL, *QTn.ipk-7A*, 4 cM distant to *QEar.T84-7A*, with a reduced tiller number revealed from the W-7984 alleles, by using the Prinz×synthetic wheat M6 advanced backcross population. Another advanced backcross population from the cross Flair×synthetic wheat XX86, revealed the QTL, *QTn.ipk-7A*, explaining 13.9% of the phenotypic variance (Huang et al. 2004). This QTL revealed an increasing effect from the synthetic wheat, which alleles were located in the similar region. Further two QTLs were localised not closely linked to *QEar.T84-7A* (Snape et al. 2007, Kumar et al. 2007). The remaining four studies were not able to detect QTLs for tillers per square meter on chromosome 7A.

Days until heading

The plant life cycle includes three basic growth stages: germination, vegetative growth and reproductive growth. Flowering is a key component of the reproductive stage and is important for continual cropping and adaption to target environments. Days until heading is critical for adaption of wheat varieties to different growing areas and cropping systems, since synchronisation of flowering with optimal temperature and moisture conditions is essential to yield. Probably all of the wheat homologous groups carry genes involved in the control of flowering time.

Three classes of genes are known responsible for days to heading (Snape et al. 2001): vernalisation response (*Vrn*), photoperiod response (*Ppd*) and earliness per se (developmental rate, *Eps*) genes.

Vernalisation response is mostly controlled by the homoeoloci *Vrn-A1*, *Vrn-B1* and *Vrn-D1* mapped on the long arm of chromosomes 5A, 5B and 5D (Shindo et al. 2003, Leonova et al. 2003, Sarma et al. 1998). According to requirements for vernalisation, wheat cultivars can be divided into winter, semi-winter and spring types. Vernalisation is necessary for winter wheat and accelerates development of semi-winter types to initiate reproductive growth (Cockram et al. 2007). Besides vernalisation, photoperid is also required to regulate the phase change of plant growth. The major genes revealing photoperiod response in wheat, *Ppd-A1*, *Ppd-B1* and *Ppd-D1*, were mapped to the homologous positions on the short arms of group 2 chromosomes (Mohler et al. 2004, Law et al. 1978). Earliness per se genes have been detected on almost all homologous groups of wheat (Snape et al. 2001). These genes influence flowering time independently of environmental conditions and are usually responsible for fine-tuning flowering time (Lin et al. 2008). An *Eps* gene in a diploid wheat showed significant epistatic interactions with photoperiod and vernalisation treatments, suggesting that the different classes of genes revealing heading date interact as part of a complex network (Bullrich et al. 2002). Also, Miura and Worland (1994) found that *Eps* genes have striking effects on ear emergence time by reducing the number of days to heading independently of environmental stimuli. Already, Hoogendoorn et al. (1985) published loci associated with earliness per se on chromosome 4A.

In the present study, two QTLs, *QHea.T84-4A* and *QHea.T84-5A*, associated with days to heading were mapped in population T84. Though, Triso and Syn-84 are spring wheat types and vernalisation is not the major factor causing the flowering time differences between them.
Across eight environments, the QTL analysis revealed two QTLs for days to heading, which were previously published. At the significant marker loci the Syn-84 alleles determined earlier flowering in T84. Early maturity has been an important objective in wheat breeding.

Days until heading was analysed across 26 studies on chromosome 4A. *QHea.T84-4A* was validated in one QTL on chromosome arm 4AS (Figure 7). The current marker locus at Xwmc468 was significant for heading time under high N-supply and both N-levels. *QHea.T84-4A* was corresponding with flowering time in Nanda2419× Wangshuibai recombinant inbred lines (Lin et al. 2008). Lin et al. (2008) detected two flowering time QTLs on chromosome 4A. *QFlt.nau-4A.1* was localised at the identical marker locus, explaining 10% of the phenotypic variance. The second QTL, *QFlt.nau-4A.2*, explained 19% of the phenotypic variance and could be related to photoperiod sensitivity.
A QTL meta-analysis was carried out by Hanocq et al. (2007) to examine the replicability of QTLs for heading time across 13 independent studies. This method increased the power of QTL detection when their positions were similar in different populations. The QTL meta-analysis revealed on chromosome 4A, four QTLs originating from four studies, which were included in the QTL cluster, named as *MQTL 7*. This QTL cluster, *MQTL 7*, was mapped 19 cM distant to *QHea.T84-4A*. At *MQTL 7*, wheat alleles explained a mean of 8.1% of the phenotypic variance and appeared to be reliable. Consequently, *QHea.T84-4A* could be a serious candidate for marker-assisted selection.
Further four heading QTLs were mapped above 20 cM distant to *QHea.T84-4A* on chromosme arm 4AL. In Chinese Spring×Chinese Spring Kanto107 recombinant substitution lines, *QEet.ocs-4A.1* associated with the *Wx-B1* locus (Araki et al. 1999). The region adjacent to the *Wx-B1* locus was also associated with plant height.
Using the ITMI population, Opata85×W-7984, the QTL, *QDh.ccsu-4A.1*, corresponding with days to heading and explained 7.7% of the phenotypic variance (Kulwal et al. 2003). Börner et al. (2002) also mapped a QTL, *QEet.ipk-4A*, with minor effects in the ITMI population, which may also be related to the *Wx-B1* locus. In addition, they identified QTLs controlling ear length, grain number, grain weight per ear, height and waxiness in this region. The identical QTL, *QEet.ipk-4A*, was detected in the BC_2F_1 population derived from the cross Flair×synthetic wheat XX86 (Huang et al. 2004). Synthetic wheat alleles explained 22.8% of the phenotypic variance and were favourable for the trait performance. In the RL4452×AC Domain doubled haploid population the *Wx-B1* locus may not have a direct effect on ear emergence time or time to maturity (McCartney et al. 2005). Even though, the QTL, *QMat.crc-4A*, associated with time for maturity was mapped to the *Wx-B1* locus. McCartney et al. (2005) also located an increasing yield QTL on chromosome arm 4AS with 10 cM distant to Xwmc468, although about 40 cM distant to *QMat.crc-4A* and *Wx-B1*.

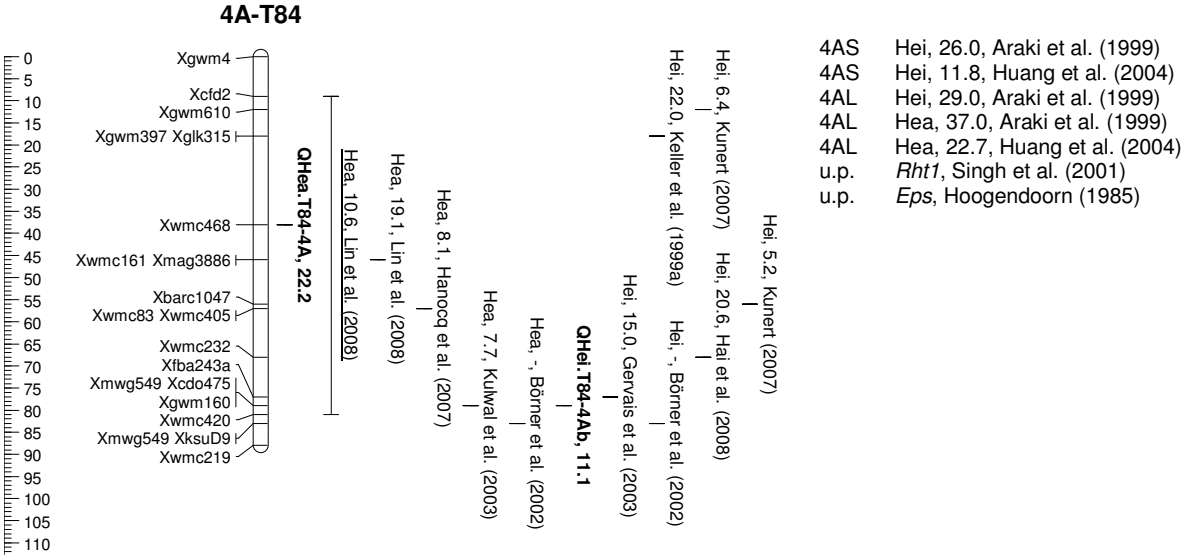

Figure 7: Localisation of current QTLs, *QHea.T84-4A* and *QHei.T84-4Ab*, in T84, published QTLs and genes associated with days until heading and plant height on chromosome 4A.

This graphical map was computed using MapChart (Voorrips 2002) with genetic map positions according Somers et al. (2004). Mapped markers were indicated on the right and their corresponding genetic distances (cM) were indicated on the left. QTL confidence interval was indicated by a vertical bar. Bold QTLs were significant marker main effects detected by the REML methods. Not bold QTLs and genes were published in other studies. Underlined QTLs and genes were detected at the identical significant marker locus as the current QTL. QTL description: Hea (Days until heading), Hei (Plant height), number (R^2 as explained genetic variance in %) and reference (study, where the common QTL was published). On the right, QTLs and genes are listed, where the position was on the short arm (S), long arm (L) or unknown (u.p.).

The present QTL *QHea.T84-4A* mapped on the short arm of chromosome 4A might not be related to known wheat vernalisation and photoperiod response or earliness per se genes. Another study used Thatcher 4A substitution lines, for analysing genes controlling heading date and found that chromosome 4A was not involved in control heading (Ahmed and Aksel 1972).

In contrast, chromosome 5A is known to carry a number of major genes revealing productivity and adaptability. Several QTL studies have published the most repeatable heading QTL, located on chromosome arm 5AL in similar position to grain yield QTLs (Cuthbert et al. 2008, Marza et al. 2006, Quarrie et al. 2005, Huang et al. 2004, Kato et al. 2000). The second QTL, *QHea.T84-5A*, identified in the population T84 on the long arm of chromosome 5A was detected under high N-supply. *QHea.T84-5A* located in close vicinity to the vernalisation requirement gene *Vrn-A1*, with 6 cM distance, according to the comparative map Wheat-Composite 2004, which pooled eleven mapping studies (GrainGenes 2008, Figure 8).

Days until heading was analysed across 32 studies on chromosome 5A. Eighteen QTLs associated with heading time were previously published. Two common QTLs were localised at the identical maker locus (Mohamed 2007, Peng et al. 2003). Further seven QTLs were found at the *Vrn-A1* locus or closely linked to them. Convincingly, Peng et al. (2003) analysed the cross between wild emmer wheat (*T. dicoccoides*, a donor of exotic alleles in Syn-84 in the current study) and a durum wheat cultivar.

Thus, they found two QTL clusters, *DSF6* and *DSF7*, involving heading date inside domestication syndrome factor (DSF) regions. In contrast, *T. dicoccoides* alleles increased the value of heading date and were responsible for late flowering of the *T. dicoccoides* parent.

Further, *QHea.T84-5A* coincided with QTLs for ear emergence time mapped in different advanced backcross populations published by Kunert (2007a), Mohamed (2007) and Huang et al. (2003b). Firstly, Mohamed (2007) found a QTL, *QHea.T84-5A.a*, at the identical marker locus using the identical population T84. Synthetic wheat alleles improved heading under both well-watered and drought-stress treatments. Secondly, a remote QTL, *QHea.Z86-5A.a*, on chromosome arm 5AS was identified by Kunert (2007a), where synthetic wheat alleles revealed a reduction in days until heading. Thirdly, Huang et al. (2003b) detected the QTL, *QEet.ipk-5A*, at which synthetic wheat alleles explained 9% of the phenotypic variance. Exotic alleles revealed an increase of ear emergence time on chromosome arm 5AL.

Hanocq et al. (2004) published a QTL with 5 cM distant close to *QHea.T84-5A.a*, which was in close vicinity to *Vrn-A1* and *Fr-A1*, explaining up to 40% of the phenotypic variation. This QTL was detected in recombinant inbred lines derived from a cross between two French wheat varieties Renan and Récital. Kato et al. (1999a) located the significant locus *QEet.ocs-5A.1* in an equal position using single chromosome recombinant lines developed from a cross between Chinese Spring derived lines Cappelle-Desprez 5A and *T. spelta* 5A. This QTL was in close vicinity to the morphological *Q* gene. Then, Kato et al. (1999a) assumed that the gene for vernalisation requirement *Vrn-A1* and *QEet.ocs-5A.1* were major determinants of genetic variation for ear emergence time. Chu et al. (2008) identified the QTL *QEet.fcu-5A* near the *Vrn-A1* region using a doubled haploid population developed from the cross between durum derived synthetic hexaploid wheat accession TA4152-60 and hard red spring wheat line ND495. The QTL *QEet.fcu-5A* explained 41% of the phenotypic variance and reduced heading date under green house and growth chamber conditions.

Further, the Trident×Molineux doubled haploid population revealed a QTL for heading was detected, which was in close vicinity to *Vrn-A1* (Kuchel et al. 2007). In addition, Klahr et al. (2007) detected the QTL, *QEet.whs-5A*, stable across environments using Cansas×Ritmo recombinant inbred lines. This genomic region was found to harbour the gene *Vrn-A1*. On this map segment also a QTL associated with resistance against *Fusarium* head blight was ascertained. Another study used the QTL meta-analysis containing five QTLs on chromosome arm 5AL originating from several studies (Hanocq et al. 2007). This analysis revealed the QTL cluster, *MQTL 10*, associated with vernalisation requirement and heading date. The phenotypic *Vrn-A1* marker was mapped inside *MQTL 10*. Shindo et al. (2002) analysed diploid *T. monococcum* and localised also QTLs for heading time corresponding to vernalisation requirement (*Vrn-A^{m}1*) and narrow-sense earliness (*Nse-5A^m*) on chromosome 5A^m. The map position in other cereals revealed that *Vrn-A^{m}1* is orthologous to *Vrn-A1, Vrn-B1 and Vrn-D1* in hexaploid wheat (Korzun et al. 1997).

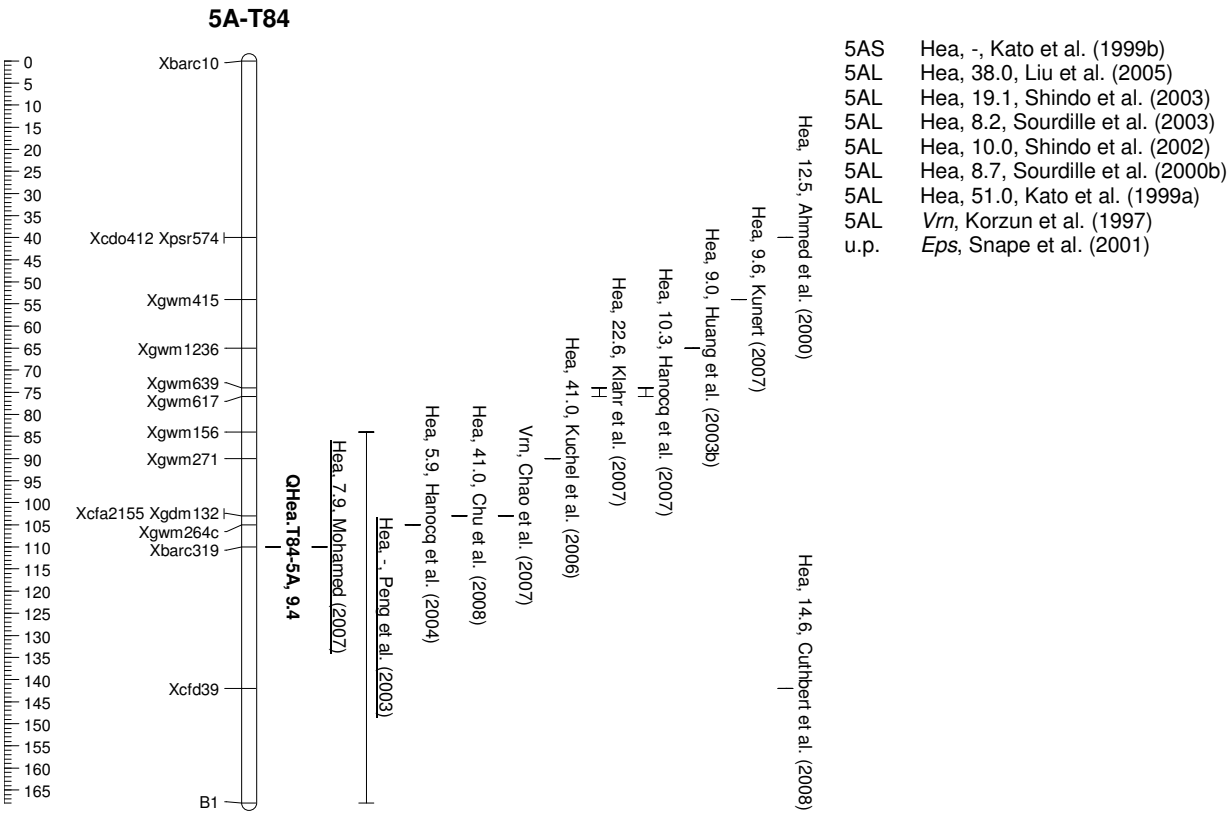

Figure 8: Localisation of the current QTL, *QHea.T84-5A*, in T84, published QTLs and genes associated with days until heading on chromosome 5A.

This graphical map was computed using MapChart (Voorrips 2002) with genetic map positions according Somers et al. (2004). Mapped markers were indicated on the right and their corresponding genetic distances (cM) were indicated on the left. QTL confidence interval was indicated by a vertical bar. Bold QTLs were significant marker main effects detected by the REML methods. Not bold QTLs and genes were published in other studies. Underlined QTLs and genes were detected at the identical significant marker locus as the current QTL. QTL description: Hea (Days until heading), number (R^2 as explained genetic variance in %) and reference (study, where the common QTL was published). On the right, QTLs and genes are listed, where the position was on the short arm (S), long arm (L) or unknown (u.p.).

In accordance with Sarma et al. (1998) the effects of spring alleles of the *Vrn-1* genes from the B and D genomes are weaker. Spring alleles of *Vrn-1* are dominant and reduce the requirement for vernalisation. Spring alleles of the *Vrn-1* gene on the A genome, *Vrn-A1*, have the strongest effect on flowering time and plants with the *Vrn-A1* spring allele do not require any vernalisation (Trevaskis et al. 2003).

Confirming, the major significant QTL effect on the A genome was validated in the present study. Fifteen other studies validated this heading QTL at or near the *Vrn-A1* locus. An explanation for this effect could be the reduced recombination in a region of the *Vrn-A1* gene, published by Chao et al. (2007). The described linkage disequilibrium among United States of America wheat germplasm was not significant in the flanking regions of genes determining the spring and winter growth habit. Hence, Chao et al. (2007) mentioned that the spring growth habit conferred independently by mutations in any of the three copies of the *Vrn-1* gene relaxing the selection pressure. The genes controlling marker classes may have been fixed in the ancestral lines many generations ago.

Consequently, these genes and their surrounding regions have been subjected to little or no selection pressure during the breeding process and recombination showed eroded linkage disequilibrium (Chao et al. 2007).

Besides, Snape et al. (2001) described according to mapping data in barley the existence of the gene *Eps-5A* at a homologous position. These genes are considered to be important in determining heading date when vernalisation is incomplete. Also, Kato et al. (2003) supposed that in the target region of *QEet.ocs-5A.1* earliness per se locus was detected in the Cappelle-Desprez 5A×*T. spelta* 5A near-isogenic line. The chromosomal segment from *T. spelta* including *QEet.ocs-5A.1* reduced days to flowering. A second QTL, *QEet.ocs-5A.2*, identified in the identical population described by Kato et al. (1999b) was possibly influenced by an earliness per se gene. Kato et al. (1999b) assumed that *QEet.ocs-5A.2* and *eps4L* in barley may be homologous loci proving high correspondence among QTLs for similar traits in crop plants. Also, in Chinese Spring×*T. spelta* ssp. *duhamelianum* recombinant inbred lines a QTL for heading was detected (Ahmed et al. 2000). Ahmed et al. (2000) indicated that the QTL was related to earliness per se. Sourdille et al. (2003, 2000b) identified in the similar position a QTL for heading time using the Courtot×Chinese Spring doubled haploid population. They also published a QTL associated with photoperiod response under long-day conditions.

Confirming, Shindo et al. (2003) detected alleles near the centromere, which caused early heading under vernalisation and short day condition. They found a QTL associated with photoperiod sensitivity in Chinese Spring×*T. spelta* ssp. *duhameliamum* recombinant inbred lines. Liu et al. (2005) anaylsed the Grandin×BR34 population and revealed the QTL, *QEet.fcu-5AL*. At this locus, Grandin alleles explained 38% of the phenotypic variance. *QEet.fcu-5AL* was also in close vicinity to the morphological gene *Q*. This QTL may be the *Q* gene or a closely linked gene responsible for governing ear emergence time. They assumed that BR34 alleles also possesses a gene for earliness that went undetected, possibly due to a lack of markers in a particular genomic region harbouring the QTL.

Moreover, a QTL, *QHdg.crc-5A*, was analysed over nine environments with increasing days to heading, using the Superb×BW278 doubled haploid population (Cuthbert et al. 2008). This QTL was linked with the morphological gene *B1*, responsible for the presence and absence of awns, mapped by Kato et al. (1999a). Accessory, a significant locus for grain filling time, *QGrf.ipk-5A*, was located on chromosome arm 5AL using various wheat cultivars obtained from the Australian Winter Cereal Collection (Börner et al. 2002). Beside flowering time, the time for grain filling influenced the time of harvest and, to some extent, the final grain yield. Plants having a lengthened grain-filling time may have higher grain weights.

Further, the QTL, *QHea.T84-5A*, was in the similar position that corresponded to a major QTL revealing drought-induced abscisic acid accumulation (Quarrie et al. 1994). This locus was tightly linked to dehydrin genes, suggesting a genetic linkage between abscisic acid accumulation and tolerance to drought stress via early flowering date (Mohamed 2007, Quarrie et al. 1994).

In addition, Galiba et al. (1995) found the frost resistance gene *Fr-A1* besides the *Vrn-A1* locus. Keller et al. (1999a) found a negative correlation between days to flowering and lodging thus, late genotypes were more lodging resistant. These findings are in agreement with the current study. In T84 and D84, days until heading and lodging at harvest revealed slightly negative correlation. Indeed, associations for lodging were analysed for lodging on chromosomes 4A (P = 0.04) and 5A (P = 0.03) in T84.

Plant height

Plant height is an important trait for wheat cultivars. A reduction in plant height can improve lodging resistance and partitioning of assimilates to the developing grain (Börner et al. 1996). Genetic studies indicated that the genetic control of plant height in bread wheat is complex and most chromosomes harbour factors that can affect it. Dwarfing or reduced height *Rht* genes have been associated with large increases in the yield potential of cereals and have been a key component of the Green Revolution since they were introduced in wheat and rice breeding programmes (Peng et al. 1999a). Singh et al. 2001) mentioned that dwarf bread wheat had significantly better harvest index, spikes per square meter, kernels per spike and kernels per square meter. To date, more than 20 genes with major effects on plant height have been identified (McIntosh et al. 2008).

Gibberellic acid insensitive and sensitive genes are responsible for plant height (Cadalen et al. 1998, Worland et al. 1998). The major semi-dwarfing genes, *Rht-B1* and *Rht-D1*, derived from the Japanese wheat variety Norin 10, has gibberellic acid insensitive alleles that are introgressed into the majority of wheat varieties grown today (Ellis et al. 2005). By conferring insensitivity to gibberellic acid, these genes have pleiotropic effects on plant growth, causing reductions in coleoptile length and seedling leaf area (Börner et al. 2002). Other dwarfing genes that do not confer gibberellic acid insensitivity may therefore be more suitable in reducing final plant height without compromising early plant growth. The gibberellic acid responsive dwarfing genes, *Rht8* and *Rht9*, were introduced from the Japanese landrace Akagomugi into southern European varieties, which do not affect coleoptile length or seedling vigour (Rebetzke et al. 1999).

In the present report, three plant height QTLs were detected in T84 (*QHei.T84-4Ab)* and in D84 (*QHei.D84-2A*, *QHei.D84-5A*), which were previously published in other studies.

Population D84 revealed the QTL, QHei.D84-2A, on chromosome arm 2AL under high N-supply and both N-levels (Figure 9). At this locus, synthetic wheat alleles revealed an increasing effect on plant height. This genomic region was possibly influenced by the dwarfing gene Rht7 (Worland et al. 1980). Worland et al. (1980) observed a positive relationship between height and yield and some of its components. Thus, *Rht7* reduced the height by about 30%. This indicated that *Rht7* unlike *Rht1* and *Rht2* would probably be of little use in breeding programmes seeking high yielding short-strawed wheat. In addition, genes for photoperiod sensitivity and earliness per se, *Ppd-A1* and *Eps-2AS*, were located on chromosome arm 2AS (Snape et al. 2001, Mohler et al. 2004).

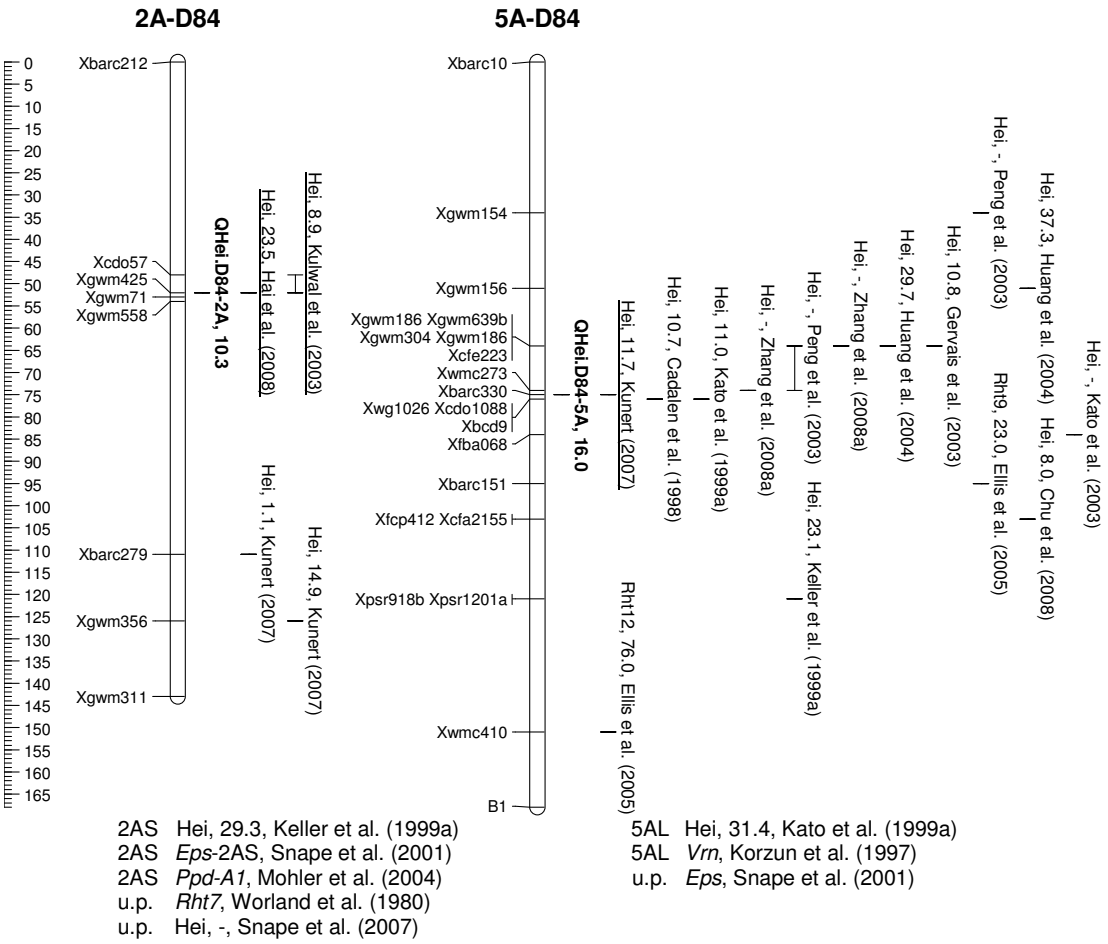

Figure 9: Localisation of current QTLs, *QHei.D84-2A* and *QHei.D84-5A*, in D84, published QTLs and genes associated with plant height on chromosomes 2A and 5A.

This graphical map was computed using MapChart (Voorrips 2002) with genetic map positions according Somers et al. (2004). Mapped markers were indicated on the right and their corresponding genetic distances (cM) were indicated on the left. QTL confidence interval was indicated by a vertical bar. Bold QTLs were significant marker main effects detected by the REML methods. Not bold QTLs and genes were published in other studies. Underlined QTLs and genes were detected at the identical significant marker locus as the current QTL. QTL description: Hei (Plant height), number (R^2 as explained genetic variance in %) and reference (study, where the common QTL was published). Below, QTLs and genes are listed, where the position was on the short arm (S), long arm (L) or unknown (u.p.).

Twenty-five QTL studies analysed plant height on chromosome 2A. Two published QTLs for plant height closely linked with 1 cM (Kulwal et al. 2003) and 2 cM (Hai et al. 2008) distant to *QHei.D84-2A*. Kulwal et al. (2003) detected a QTL explaining 8.9% of the phenotypic variance. Hai et al. (2008) identified a stable plant height QTL explaining 23.5% of the phenotypic variation using doubled haploid lines of bread wheat derived from the cross CA9613×H1488.

Besides, *QHei.D84-2A* was located in the same deletion bin position as two stable increasing plant height QTLs (Kunert 2007a). In the similar genomic region, Snape et al. (2007) found also one significant QTL for plant height on chromosome 2A.

In addition, Börner et al. (2002) and Ahmed et al. (2000) mentioned that alleles for early heading reduced plant height, while alleles which led to late heading, increased plant height. They considered that their findings account for the fact that plant height showed a highly significant positive correlation with the heading date.

Therefore, they suggested these QTLs exert pleiotropic effects on heading and plant height. This fact was validated in the current study on chromosome 2A with an association (P = 0.03) for reduced days until heading with a major gene conferring photoperiod intensitivity (*Ppd-A1*) segregated in D84, which can be a pleiotropic effect of the plant height QTL in the deletion bin C-2AL1-0.85. In T84, two associations for increased plant height (P = 0.03) and reduced heading time (P = 0.03) were also analysed. However, plant height and days until heading were not or slightly positive correlated.

In addition, Keller et al. (1999a) identified three consistent QTLs for reduced lodging on chromosomes 2A, 4A and 5A, accounting for 29.3%, 22.5% and 31.4% of the phenotypic variance, respectively. These QTLs were evaluated using recombinant inbred lines originating from the cross between Swiss winter wheat Forno and spelt Oberkulmer. They mentioned that lodging QTLs were linked with shortened plant height and later ear emergence QTLs at identical loci. Confirming, at chromosome arm 4AL, the present marker locus Xgwm160 was significant for the QTL *QHei.T84-4Ab* associated with shortened plant height and reduced lodging at harvest (P = 0.04) in T84 in high N-level.

In T84, the QTL, *QHei.T84-4Ab*, was detected in high N-level on chromosome arm 4AL. In comparison with 26 QTL studies on chromosome 4A, the present QTL could be validated in three QTLs closely linked and six QTLs located more than 20 cM distant to *QHei.T84-4Ab* (Figure 7). Previous studies mentioned that dwarfing gene *Rht1* and earliness per se gene were located on chromosome 4A (Singh et al. 2001, Hoogendoorn 1985).

Gervais et al. (2003) and Börner et al. (2002) localised plant height QTLs in close vicinity to *QHei.T84-4Ab* on chromosome arm 4AL. The QTL, *QPht.nfcri-4A*, revealed extended plant height in the same deletion bin (Hai et al. 2008). Araki et al. (1999) mapped two QTLs for shortened plant height on chromosome arms 4AL and 4AS.

In addition, two QTLs for increasing plant height were described by Kunert (2007a) and Huang et al. (2004), on chromosome arm 4AS. A QTL associated with reduced plant height were published by Keller et al. (1999a), which coincided with lodging QTLs on chromosome arm 4AS.

In D84, the second plant height QTL, *QHei.D84-5A*, was identified with increasing effect on chromosome arm 5AL in high N-level and both N-treatments (Figure 9), respectively. *QHei.D84-5A* was in close vicinity to the dwarfing gene *Rht9* mapped by Ellis et al. (2005). They confirmed the influence of different gibberellic acid responsive *Rht* genes on height reduction, which were repeated across a broad range of environments. Therefore, they deduced that selection of these genes for reducing plant height is likely to be useful in breeding wheat across a range of environments. Moreover, Korzun et al. (1997) tightly linked gene *Rht12* to the isozyme locus ß-*amy-A1*. In addition, gene *Rht12* was co-segregated with the *B1* locus and delayed ear emergence (Worland 1986). A second gibberellic acid responsive gene *Rht12* was located on chromosome arm 5AL mentioned by Ellis et al. (2005).

The QTL, *QHei.D84-5A*, was validated in one QTL at the identical marker locus and eight QTLs on similar positions analysed by 29 studies for plant height on chromosome 5A. At the identical marker locus, by using the Batis×Syn22 advanced backcross population, exotic alleles revealed also an increased plant height by 6.3 cm explaining 11.7% of the genetic variance (Kunert 2007a).

In addition, four QTLs associated with increasing effect for plant height were mentioned by Zhang et al. (2008a), Huang et al. (2004), Gervais et al. (2003) and Cadalen et al. (1998). These QTLs were mapped in the same deletion bin region as *QHei.D84-5A*. Zhang et al. (2008a) studied plant height using the Huapei3×Yumai57 doubled haploid population. They detected two QTLs, *Qph5A-1* and *Qph5A-2*, analysed in three environments. Further, Huang et al. (2004) analysed the Flair×XX86 advanced backcross population. They have found two QTLs, *QHt.ipk-5A.1* and *QHt.ipk-5A.2*, detected in four environments. At these loci, XX86 alleles led an increased plant height explaining the phenotypic variance by up to 37.3%. Gervais et al. (2003) found an increased plant height QTL, *QHt.inra-5A*, which was overlapped with a QTL, *QFhs.inra-5a2*, associated with *Fusarium* head blight resistance using the Renan×Récital population. In addition, Cadalen et al. (1998) mapped a QTL with an increasing effect on plant height in the Courtot×Chinese Spring doubled haploid population. This locus was only detected in one environment. Hence, they assumed that this may be explained either by genotype×environment interactions or by statistical artefacts.

However, other QTLs with shortened effects on plant height were published by Chu et al. (2008), Kato et al. (2003, 1999a), Peng et al. (2003) and Keller et al. (1999a). Peng et al. (2003) analysed the wild emmer wheat×durum population. They localised QTLs for plant height in a domestication syndrome factor region *DSF6*, which was closely linked with 11 cM distant to *QHei.D84-5A*.

Chu et al. (2008) analysed plant height using the doubled haploid population developed from the cross between durum derived synthetic hexaploid wheat accession TA4152-60 and spring wheat line ND495. They found a minor QTL only detected in green house, which was located in close vicinity to the gene *Vrn-A1*. This QTL, *QHt.fcu-5A*, revealed a reduction of plant height by 7.2 cm. Previously, Kato et al. (1999a) detected the QTL, *Qt.ocs-5A.1*, with plant height reduction, which was possibly influenced by the *Vrn-A1* locus. Consequently, Chu et al. (2008) suggested that the gene *Vrn-A1* may be a candidate gene for *QHt.fcu-5A*. Later, Kato et al. (2003) mentioned that the genetic effect on reducing the elongation of the lower internodes and the differentiation of the internodes was associated with the *Q* locus. In addition, a gene for earliness per se was mentioned to be located on chromosome 5A (Snape et al. 2001).

In addition, Keller et al. (1999a) detected a shortened plant height QTL, which coincided with QTLs for reduced lodging, increased culm stiffness, reduced leaf width, more erect growth habit, later ear emergence and increased culm thickness on chromosome 5AL. Confirming these results, *QHei.D84-5A* was mapped in the identical position as a association for increased lodging at harvest ($P = 0.03$) in the present study.

As described above for the trait days until heading, Quarrie et al. (1994) found a QTL on chromosome arm 5AL, which was likely to regulate expression of the abscisic acid under abiotic stresses. Quarrie et al. (1994) resumed that hormone was responsible for regulating many processes of growth and development. They referred that increased tissue hormone concentrations make the plant better adapted to withstand the effects of water shortage. In the similar sense, another study described significantly decreased stem height induced by an exogenous abscisic acid application (Zhang et al. 2005).

Thousand grain weight

Among the various grain related traits, grain weight is one of the phenotypically most stable components of grain yield. Grain weight has been shown to be controlled by a number of QTLs located on different chromosomes. Unfortunately, an improvement in grain weight through plant breeding has generally been found to be of no consequence, since an increase in grain weight is known to be associated with a reduction in grain number per spike, thus neutralising the benefit derived from the increased grain weight (Blanco et al. 2006, Varshney et al. 2000). Agreeing, in the present study the traits thousand grain weight and grain number per ear were negatively correlated in both advanced backcross populations. Therefore, Blanco et al. (2006) meant that the components of grain yield, number of kernels per spike and the kernel weight should not be considered separately for detecting grain yield QTLs.

In the present report, altogether four QTLs were associated with thousand grain weight in T84 (*QTgw.T84-2Ab*, *QTgw.T84-6B*, *QTgw.T84-7A*) and in D84 (*QTgw.D84-2D*).
In T84, the QTL, *QTgw.T84-2Ab*, was detected in high N-level. At the closet marker Xgwm294, synthetic wheat alleles improved the thousand grain weight. Sixteen other studies analysed grain weight on chromosome 2A. The QTL, *QTgw.T84-2Ab*, was validated in three grain weight QTLs at the consistent marker locus Xgwm294 on chromosome arm 2AL (Mohamed 2007, McCartney et al. 2005, Peng et al. 2003, Figure 10).
Mohamed (2007) found the QTL, *QTgw.T84-2A.a*, by using the identical population T84, where exotic alleles increased the grain weight. Besides, McCartney et al. (2005) detected the QTL, *QGwt.crc-2A*, in the RL4452×AC Domain doubled haploid population. The AC Domain alleles decreased thousand grain weight at *QGwt.crc-2A*, which overlapped with the grain yield QTL *QYld.crc-2A*. Completing, Peng et al. (2003) detected a major hundred grain weight QTL in the domestication syndrome factor region *DSF4* in the wild emmer wheat×durum population.
Kunert (2007a) identified two QTLs, *QTgw.Z86-2A.a* and *QTgw.N-Z86-2A*, by using Zentos×Syn-86 advanced backcross population. Further, Verma et al. (2005) found a seed weight QTL by using the Milan×Catbird doubled haploid population.
In addition, on chromosome arm 2AS, QTLs associated with grain weight were detected with contrasting effects revealed by exotic alleles in two advanced backcross populations (Huang et al. 2004, 2003b), the ITMI population (Kumar et al. 2007) and the Spark×Rialto doubled haploid population (Snape et al. 2007).

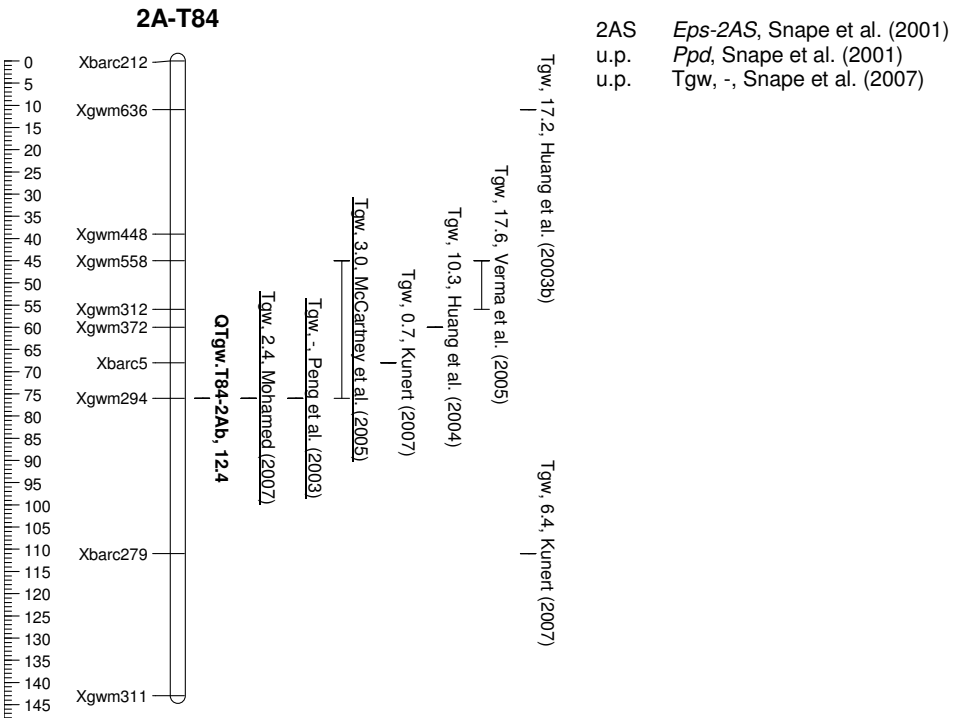

Figure 10: Localisation of the current QTL, *QTgw.T84-2Ab*, in T84, published QTLs and genes associated with thousand grain weight on chromosome 2A.

This graphical map was computed using MapChart (Voorrips 2002) with genetic map positions according Somers et al. (2004). Mapped markers were indicated on the right and their corresponding genetic distances (cM) were indicated on the left. QTL confidence interval was indicated by a vertical bar. Bold QTLs were significant marker main effects detected by the REML methods. Not bold QTLs and genes were published in other studies. Underlined QTLs and genes were detected at the identical significant marker locus as the current QTL. QTL description: Tgw (Thousand grain weight), number (R^2 as explained genetic variance in %) and reference (study, where the common QTL was published). On the right, QTLs and genes are listed, where the position was on the short arm (S), long arm (L) or unknown (u.p.).

Interestingly, Snape et al. (2001) mentioned that an earliness per se gene *Eps-2AS* was mapped on chromosome arm 2AS. Validating, Kuchel et al. (2007) found a QTL, *QEps.agt-2AS*, associated with decreasing grain yield in a multi-environmental trial. However, eight other studies could not identify associations for grain weight on chromosome 2A.

Interestingly, Worland et al. (1998a) mentioned that dominant *Ppd* alleles greatly reduce sensitivity to photoperiod and confer an early flowering phenotype, resulting in yield benefits under certain agro-environments. These major *Ppd* loci have been mapped to collinear positions on the short arms of the group 2 chromosomes in wheat (Snape et al. 2001).

Exciting, in *T. monococcum sinskajae*, the soft glume character is controlled by a single gene *Sog*, which was mapped by Taenzler et al. (2002). They mentioned that the locations of *Tg*, *Tg2* and *Sog* are in homologous chromosomes of hexaploid, tetraploid and diploid wheat, respectively. Further, as in the case of *Tg*, *Tg2*, *Q* and *Q2*, the *sog* allele is tightly associated with very compact ears.

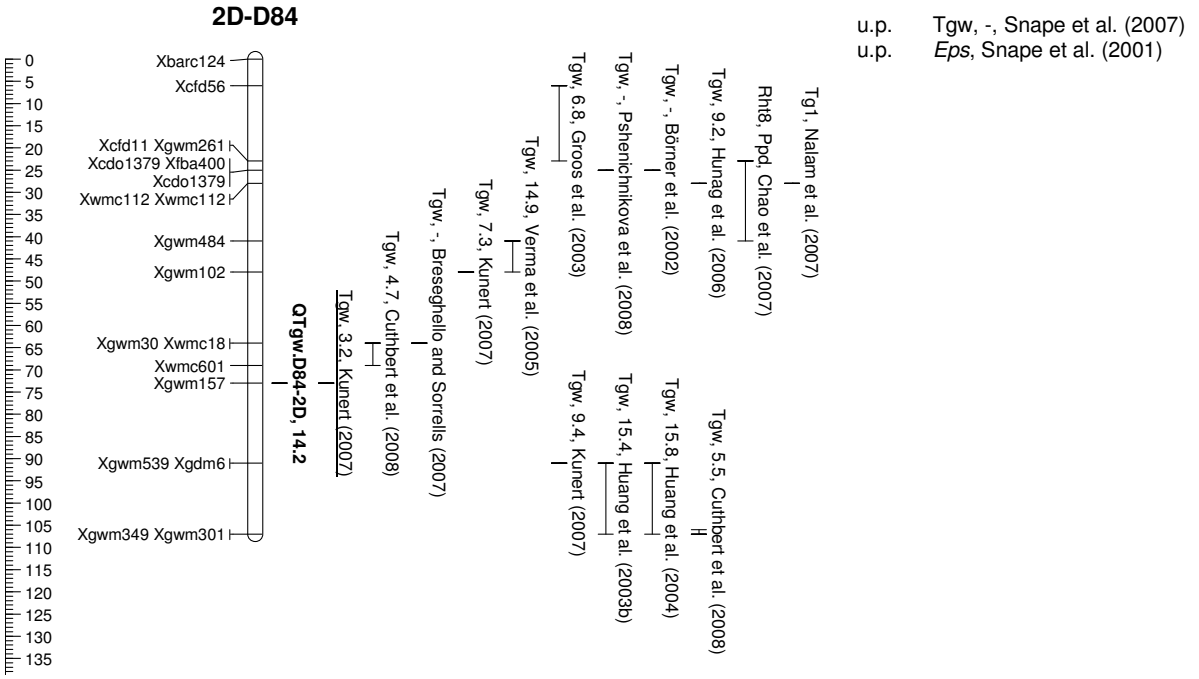

Figure 11: Localisation of the current QTL, *QTgw.D84-2D*, in D84, published QTLs and genes associated with thousand grain weight on chromosome 2D.

This graphical map was computed using MapChart (Voorrips 2002) with genetic map positions according Somers et al. (2004). Mapped markers were indicated on the right and their corresponding genetic distances (cM) were indicated on the left. QTL confidence interval was indicated by a vertical bar. Bold QTLs were significant marker main effects detected by the REML methods. Not bold QTLs and genes were published in other studies. Underlined QTLs and genes were detected at the identical significant marker locus as the current QTL. QTL description: Tgw (Thousand grain weight), number (R^2 as explained genetic variance in %) and reference (study, where the common QTL was published). On the right, QTLs and genes are listed, where the position was on the short arm (S), long arm (L) or unknown (u.p.).

In D84, the QTL, *QTgw.D84-2D*, was detected with exotic alleles revealingcreased grain weight under high N-supply and both N-levels, respectively. Twenty QTL mapping studies were published for thousand grain weight on chromosome 2D. Thereof, one QTL was detected at the identical marker locus, identified by Kunert (2007a). This common QTL also revealed favourable exotic alleles. Further six grain weight QTLs coincided with *QTgw.D84-2D*, which revealed an improving effect of thousand grain weight on chromosome arm 2DL (Figure 11).

Other two advanced backcross populations revealed QTLs closely linked to *QTgw.D84-2D*, described by Huang et al. (2004, 2003b). At *QTgw.ipk-2D*, synthetic wheat alleles increased grain weight. Besides, Cuthbert et al. (2008) detected two QTLs associated with increasing grain weight on chromosme arm 2DL in a spring wheat doubled haploid population across nine environments. Completing, Breseghello and Sorrells (2007) analysed the AC Reed×Grandin doubled haploid population. They detected a QTL consistent across two environments at a marker locus 9 cM distant to *QTgw.D84-2D*, according to the comparative map Wheat-Composite 2004 (GrainGenes 2008).

In addition, seven studies located grain weight QTLs on chromosome arm 2DS, revealing contrasting effects on the trait performance (Pshenichnikova et al. 2008, Kunert 2007, Snape et al. 2007, Huang et al. 2006, Verma et al. 2005, Groos et al. 2003, Börner et al. 2002).

These QTLs were probably caused by pleiotropy of dwarfing gene *Rht8*, photoperiod response gene *Ppd-D1*, earliness per se gene *Eps-2DLS* and tenacious glumes gene *Tg1* (Chao et al. 2007, Nalam et al. 2007, Ellis et al. 2005, Börner et al. 2002, Snape et al. 2001, Worland et al. 1998b). Besides, a study detected major QTLs for increased yield and late flag leaf senescence on chromosome arm 2DL using the Beaver×Soissons doubled haploid population (Verma et al. 2004). Further six studies analysed yield related traits on chromosome 2D, but they detected not any QTL associated with grain weight.

In T84, the second QTL, *QTgw.T84-6B*, associated with thousand grain weight was detected in both N-levels. The closet marker Xgwm626 mapped on chromosome arm 6BL, even so assigned to the deletion bin C-6BS5-0.76 on chromosome arm 6BS, as computed by Sourdille et al. (2004). *QTgw.T84-6B* was possibly in close vicinity to earliness per se genes, *Eps-6BL.1* and *Eps-6BL.2*, and photoperiod sensitive gene *Ppd-B3* (Snape et al. 2001, Hoogendoorn 1985), respectively. Cockram et al. 2007) mentioned that loci controlling the vernalisation response have been found on the group 6 chromosomes.

Indeed, a total of 18 studies analysed thousand grain weight on chromosome 6B. Thereof, one QTL, which validated *QTgw.T84-6B* at the identical marker locus was found (Quarrie et al. 2005, Figure 12). Further, 1 cM distant to *QTgw.T84-6B*, a QTL associated with reduced thousand grain weight was mapped in the same deletion bin 6BL5-0.40-1.00 (Kunert 2007a). Mohamed (2007) published the QTL, *QTgw.D84-6B.a*, at which exotic alleles reduced the trait of interest under both well-watered and drought-stress treatments. *QTgw.D84-6B.a* was mapped in the same deletion bin as the current QTL, *QTgw.T84-6B.* Thus, using the identical population T84 two QTLs were localised revealing an unfavourable reduction of grain weight, which were detected in well-watered and drought-stress treatments (Mohamed 2007).

Beyond, Elouafi and Nachit (2004) identified two QTLs associated with thousand kernel weight by using the durum wheat×*T. dicoccoides* backcross population across 18 environments. These QTLs were mapped 4 cM and 9 cM distant to *QTgw.T84-6B*. Börner et al. (2002) also published two QTLs for grain weight, one was mapped closely to the centromere and the second was located on the chromsome arm 6BL.

In T84, the third QTL, *QTgw.T84-7A*, for improved thousand grain weight was detected in high N-level on chromosome arm 7AS. Eighteen studies analysed thousand grain weight in wheat on chromosome 7A (Figure 6). One QTL was localised at the identical marker locus (Quarrie et al. 2006) and one QTL was 2 cM distant to *QTgw.T84-7A* (Groos et al. 2003). The Chinese Spring×SQ1 doubled haploid population revealed the QTL cluster, *Qyld.csdh. 7AS1,* associated with ears per plant, thousand grain weight and grain yield (Quarrie et al. 2006).

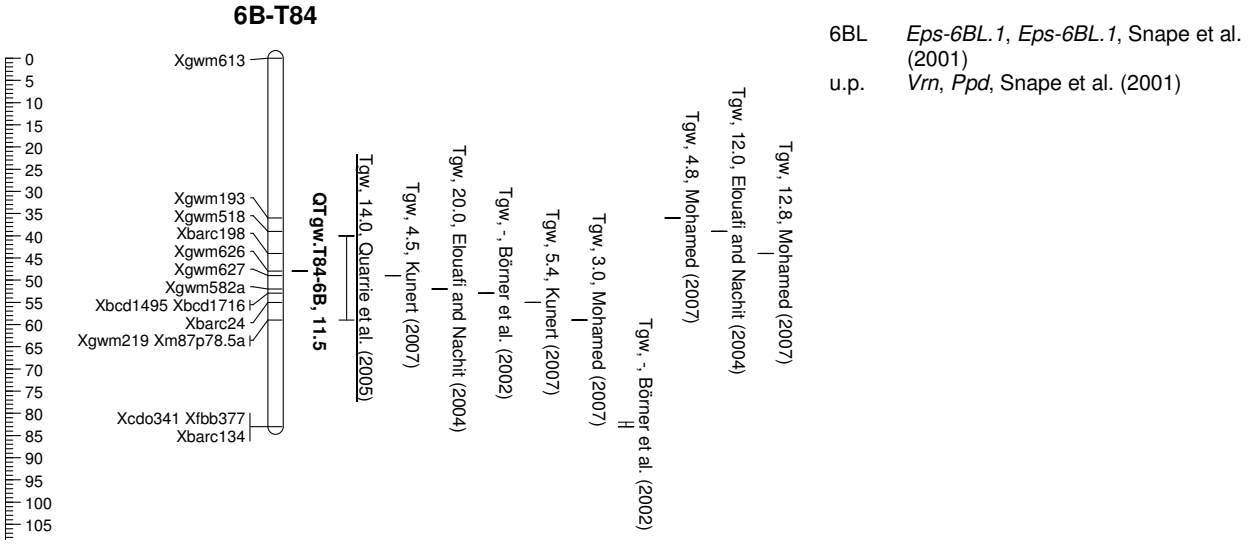

Figure 12: Localisation of the current QTL, *QTgw.T84-6B*, in T84, published QTLs and genes associated with thousand grain weight on chromosome 6B.

This graphical map was computed using MapChart (Voorrips 2002) with genetic map positions according Somers et al. (2004). Mapped markers were indicated on the right and their corresponding genetic distances (cM) were indicated on the left. QTL confidence interval was indicated by a vertical bar. Bold QTLs were significant marker main effects detected by the REML methods. Not bold QTLs and genes were published in other studies. Underlined QTLs and genes were detected at the identical significant marker locus as the current QTL. QTL description: Tgw (Thousand grain weight), number (R^2 as explained genetic variance in %) and reference (study, where the common QTL was published). On the right, QTLs and genes are listed, where the position was on the short arm (S), long arm (L) or unknown (u.p.).

Quarrie et al. (2006) recommended that QTLs for yield and yield related traits might be influenced by pleiotropic effects. The identical effect was found in the present study that QTLs for tillers per square meter and thousand grain weight were localised at the identical marker locus. Groos et al. (2003) detected a QTL for kernel weight in Renan×Récital recombinant inbred lines, designated as *QGw1.inra-7A* (McIntosh et al. 2008). They presumed that a vernalisation response gene possibly controlled the kernel weight loci on chromosome arm 7AS. The wild emmer wheat×durum population revealed a QTL associated with hundred grain weight (Peng et al. 2003). At this QTL, *T. dicoccoides* alleles influenced the trait performance in agreement with the present result. Further QTLs linked more than 20 cM distant to *QTgw.T84-7A*, were published by Huang et al. (2004, 2003b) and Hyne et al. (1994). Huang et al. (2004, 2003b) detected three QTLs by using advanced backcross populations, where synthetic wheat alleles increased the trait of interest. Furthermore, Hyne et al. (1994) identified a fifty grain weight QTL in doubled haploid lines derived from a cross between intervarietal chromosome substitution lines of Chinese Spring varieties Sicco 5B and Highbury 5B.

Remaining nine studies found no QTLs for thousand grain weight on chromosome 7A. In addition, genes for earliness per se, photoperiod sensitivity, vernalisation requirement and starch composition were mapped on chromosome arm 7AS (Chao et al. 2007, Kuchel et al. 2007, Snape et al. 2001, Law and Worland 1997), which were possibly linked with *QTgw.T84-7A*. Kuchel et al. (2007) found a photoperiod sensitive locus equal on chromosome arm 7AL, identified in the Trident×Molineux doubled haploid population. They demonstrated a decrease in grain yield associated with photoperiod insensitivity conferred by *QPpd.agt-7A*.

Grain yield

Grain yield is a particularly complex trait, being the end product of many processes in the plant and, in consequence, is very environmentally dependent (Quarrie et al . 2005, Araki et al. 1999). Therefore, they assumed that yield usually has a low heritability. In the present study, the heritability for yield in both populations was high by up to 0.84. This result supposes that grain yield was not strongly influenced by environment and/or could be resulted by the high phenotypic variance in the population revealed by the synthetic wheat parent. Further, grain yield QTLs could be possibly found for a complex trait but not for its components, when effects on QTLs are small on individual components, but aggregate to be sufficiently significant for the complex trait. In addition, tiller number can increase yield directly by increasing the number of ears. But late-developing tillers often fail to produce ears and compete with ear-bearing tillers for resources and thus reduce yield indirectly (Bezant et al. 1997).

Numerous studies mentioned genes for earliness per se, photoperiod insensitivity, semi-dwarf plant height and vernalisation, which are associated with grain yield (Ellis et al. 2005, van Beem et al. 2005, Worland et al. 1998a, Worland 1996).

In previous studies, grain yield QTLs are published on all chromosomes with the exception of chromosomes 3D and 5D (Cuthbert et al. 2008, Kuchel et al. 2007, Kumar et al. 2007, Huang et al. 2006, 2004, 2003b, Marza et al. 2005, McCartney et al. 2005, Quarrie et al. 2005, Börner et al. 2002). Most of these studies have identified a large number of grain yield QTLs. However, the majority of these QTLs were only detected in a single environment. When a QTL was detected in more than one environment, variation in the magnitude of its effects was typically observed (Kuchel et al. 2007, Kumar et al. 2007, Huang et al. 2004, 2003b).

In the present study, five QTLs associated with grain yield were detected in T84 (*QYld.T84-3A*, *QYld.T84.3B*, *QYld.T84.5Ba*) and in D84 (*QYld.D84.3Ba*, *QYld.D84.6B*). At these QTLs, synthetic wheat alleles reduced grain yield.

In T84, the QTL, *QYld.T84-3A*, was localised at the marker locus, Xgwm5, in the deletion bin C-3AL3-0.42 under high N-supply and both N-levels. A total of 24 studies analysed grain yield on chromosome 3A. *QYld.T84-3A* was validated in two QTLs at the identical marker locus (Crossa et al. 2007, Kunert 2007a, Figure 13). Even the Zentos×Syn-86 advanced backcross population revealed the QTL, *QYld.Z86-3A.a*, with reduced grain yield (Kunert 2007a). Crossa et al. (2007) described a QTL cluster associated with yield and yield related traits.

Further, Peng et al. (2003) localised QTLs for domestication related traits as grain yield, yield components, brittle rachis, heading date, plant height and grain size, conducted by *T. dicoccoides* alleles. They detected the QTL cluster, *DSF5*, influencing all traits in the same deletion bin region as *QYld.T84-3A*.

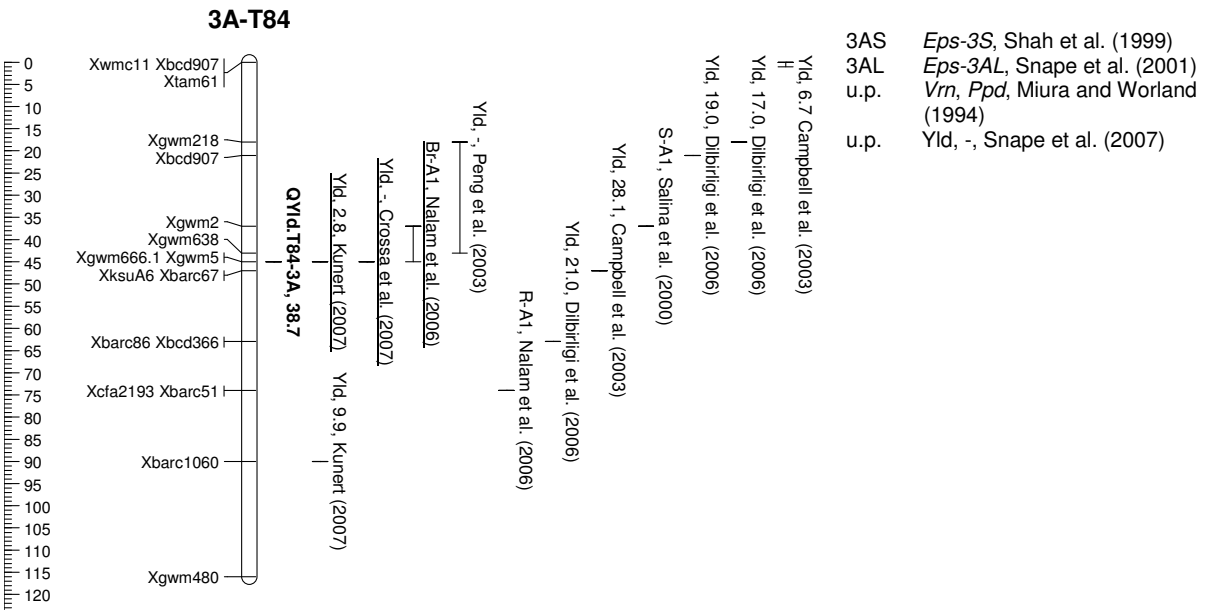

Figure 13: Localisation of the current QTL, *QYld.T84-3A*, in T84, published QTLs and genes associated with grain yield on chromosome 3A.

This graphical map was computed using MapChart (Voorrips 2002) with genetic map positions according Somers et al. (2004). Mapped markers were indicated on the right and their corresponding genetic distances (cM) were indicated on the left. QTL confidence interval was indicated by a vertical bar. Bold QTLs were significant marker main effects detected by the REML methods. Not bold QTLs and genes were published in other studies. Underlined QTLs and genes were detected at the identical significant marker locus as the current QTL. QTL description: Yld (Grain yield), number (R^2 as explained genetic variance in %) and reference (study, where the common QTL was published). On the right, QTLs and genes are listed, where the position was on the short arm (S), long arm (L) or unknown (u.p.).

Campbell et al. (2003) described the QTL, *QGyld.unl-3A.2*, 2 cM distant to *QYld.T84-3A*. This QTL explained 28.1% of the phenotypic variation and increased grain yield, which coincided with a QTL for kernel number per square meter. Besides, six QTLs were mapped more than 20 cM distant to *QYld.T84-3A* (Kunert 2007a, Dilbirligi et al. 2006, Campbell et al. 2003). Dilbirligi et al. (2006) identified three QTLs in Cheyenne×Cheyenne/Wichita 3A recombinant inbred lines. Shah et al. 1999) used the same mapping population to detect QTLs for grain yield and yield related traits. They detected grain yield QTLs only in individual environments and assumed that a small population size, few replications within each environment and large genotype interaction, might limit the detection of grain yield QTLs. Still, they detected a locus for earliness per se on chromosome arm 3AS, which influenced plant height, thousand kernel weight and kernel number per spike, respectively.

In addition, Snape et al. (2007) identified a single QTL for adjusted plot yield in the Spark×Rialto doubled haploid population. However, 16 other studies analysed grain yield on chromosome 3A, which were unable to identify yield QTLs.

Previous studies mentioned that a region associated with earliness per se was located on chromosome 3A (Miura and Worland 1994, Hoogendoorn et al. 1985). Corresponding, Snape et al. (2001) assumed that earliness per se gene, *Eps-3AL*, might be located on chromosome arm 3AL, according to comparative analysis of barley.

Besides, Miura and Worland 1994 found a multiple allelic series at new *Vrn* and *Ppd* loci on group 3 chromosomes that would be expected to contribute to the fine-tuning for both macro and micro environmental differences.

In addition, grain colour gene *R-A1* (Sherman et al. 2008, Bassoi and Flintham 2005), *sphaerococcum* spike characteristic gene *S-A1* (Salina et al. 2000) and rachis brittleness gene *Br-A1* (Nalam et al. 2006) were mapped in close vicinity to *QYld.T84-3A*.

The brittle rachis character, which causes spontaneous spike shattering, is an adaptive character in wild grass species (Watanabe et al. 2006). Effectively, *QYld.T84-3A* is associated with brittleness and exotic alleles explained 33.6% of the genetic variance by increasing brittleness up to 69.8% (see chapter 3.7.1). Confirming, the traits grain yield and brittleness were strongly negative correlated in T84 and D84 (Table 11, Table 12). Wheat has the genotype *brbrtgtgQQ*, where the *Br* gene controls rachis brittleness, *Tg* gene controls glume toughness and *Q* gene controls seed threshability. In wild ancestral wheat, shattering is caused by a brittle rachis, which is conferred by dominant *Br* allele. A recessive *br* allele at this locus produced a non brittle spike (Li and Gill 2006). Comparative mapping analysis of *Br* loci suggested the homologous origin of these major loci for brittle rachis inside wheat (Watanabe et al. 2006) and between wheat and barley (Nalam et al. 2006).

The current study revealed two grain yield QTLs in T84 (*QYld.T84.3B*) and in D84 (*QYld.D84.3Ba*) under both N-treatments. These QTLs were localised on chromosome arm 3BS in different deletion bins (Sourdille et al. 2004, Figure 14). Previously 18 studies analysed grain yield on chromosome 3B.

As described for chromosome 3A, homologous genes possibly revealed the trait performance of grain yield were located on chromosome 3B. The genes *Vrn* and/or *Ppd* (Miura and Worland 1994), *Eps* (Snape et al. 2001, Hoogendoorn et al. 1985), *Br-B1* (Nalam et al. 2006), *S-B1* (Salina et al. 2000) and *R-B1* (Bassoi and Flintham 2005) were identified on chromosome 3B.

In T84, the second grain yield QTL, *QYld.T84.3B*, was validated at the identical marker locus in two QTLs (Mohamed 2007, Cuthbert et al. 2008). Reconfirming, Mohamed (2007) detected the QTL, *QYld.T84-3B.a*, in the identical population T84 in well-watered and drought-stress treatments. Cuthbert et al. (2008) detected across five environments the QTL, *QYld.crc-3B*, revealing an increased yield, which was also associated with yield related traits.

In addition, three yield QTLs were mapped 1 cM distant to *QYld.T84.3B* (Li et al. 2007a, Kunert 2007a). Two QTLs were mapped in the same deletion bin in the Batis×Syn-22 advanced backcross population (Kunert 2007a). Li et al. (2007a) described the QTL, *QGy.sdau-3B.e3*, with an increasing effect on yield using Chuang35050×Shannong483 recombinant inbred lines.

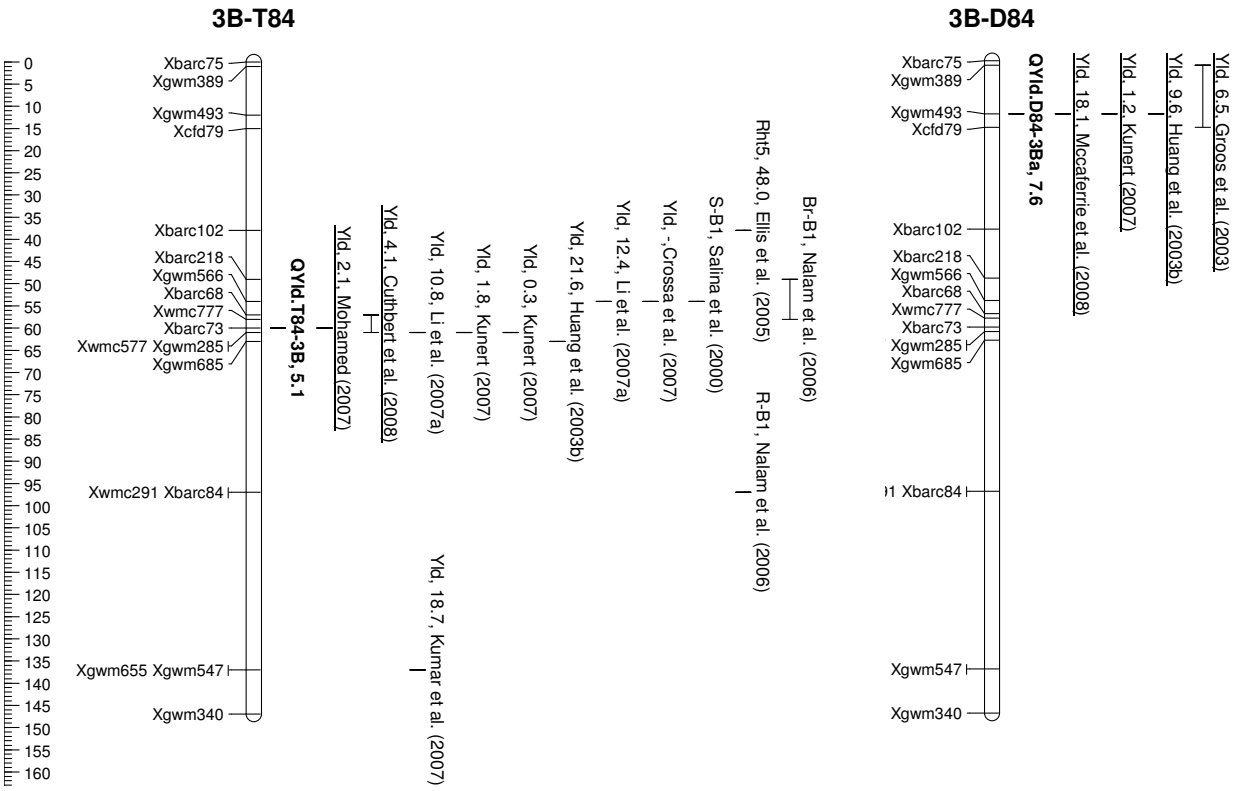

Figure 14: Localisation of current QTLs, *QYld.T84-3B* and *QYld.D84-3Ba*, in T84 and D84, published QTLs and genes associated with grain yield on chromosome 3B.

This graphical map was computed using MapChart (Voorrips 2002) with genetic map positions according Somers et al. (2004). Mapped markers were indicated on the right and their corresponding genetic distances (cM) were indicated on the left. QTL confidence interval was indicated by a vertical bar. Bold QTLs were significant marker main effects detected by the REML methods. Not bold QTLs and genes were published in other studies. Underlined QTLs and genes were detected at the identical significant marker locus as the current QTL. QTL description: Yld (Grain yield), number (R^2 as explained genetic variance in %) and reference (study, where the common QTL was published).

Three further grain yield QTLs were mapped up to 6 cM distant to *QYld.T84.3B* (Huang et al. 2003b, Crossa et al. 2007, Li et al. 2007a). Huang et al. (2003b) found a QTL in the Prinz×W-7984 advanced backcross population, at which synthetic wheat alleles reduced grain yield.

Snape et al. (2007) located a QTL for adjusted plot yield stable across four environments. A remote yield QTL on the long arm was mapped by Kumar et al. (2007). In addition, yield related traits such as grain test weight and grain weight per ear were detected in close vicinity to *QYld.T84.3B* (McCartney et al. 2005, Huang et al. 2004).

In D84, *QYld.D84.3Ba* was validated in four QTLs, which were mapped at the consistent marker locus, Xgwm493 (Figure 14). Interestingly, the deletion bin harbouring *QYld.D84.3Ba* was published to contain the dwarfing gene *Rht5*, which might be responsible for the effect on yield (Ellis et al. 2005). Two other advanced backcross populations revealed reduced grain yield conducted by synthetic wheat alleles (Kunert 2007a, Huang et al. 2003b).

Across seven environments the yield QTL, *QYld.idw-3B*, explained 18.1% of the phenotypic variance and was detected in Kofa×Svevo recombinant inbred lines (Maccaferri et al. 2008). Groos et al. (2003) localised also a yield QTL at Xgwm493.

In T84, the third grain yield QTL, *QYld.T84.5Ba*, was identified in high N-level on chromosome 5B. Twenty-one studies investigated grain yield on chromosome 5B. Two QTLs were localised at the identical marker locus (Mohamed 2007, Huang et al. 2003b) and two QTLs were closely linked with up to 11 cM distances (Crossa et al. 2007, Marza et al. 2006, Figure 15).

Mohamed (2007) detected the same QTL *QYld.T84-5B.a* in the identical population T84. Though, synthetic wheat alleles revealed a marker×environment interaction effect, improving grain yield in the drought-stress treatment. Another yield QTL revealed favourable alleles contributed by the synthetic wheat W-7984 in the advanced backcross population (Huang et al. 2003b).

Crossa et al. (2007) localised a grain yield QTL with 2 cM distant to *QYld.T84.5Ba*. Marza et al. (2006) used the population of recombinant inbred lines derived from the cross between Chinese wheat and Amercian wheat, Ning7840×Clark, and detected a yield QTL.

Besides, seven QTLs were mapped with more than 20 cM distant to *QYld.T84.5Ba.* Kunert (2007a) analysed two other advanced backcross populations revealing two grain yield QTLs. These QTLs were identified with variations in the magnitude of its effects across environments. Quarrie et al. (2005) found a QTL across eight environments with increasing yield effects corresponding with QTLs for grains per ear and thousand grain weight. Moreover, on the long arm, four yield QTLs were detected (Crossa et al. 2007, Gonzalez-Hernandez et al. 2004, Huang et al. 2004, Groos et al. 2003). Gonzalez-Hernandez et al. 2004) used *T. turgidum* ssp. *dicoccoides* recombinant inbred lines to identify the QTL, *QGy.ndsu-5B*, where alleles explained 34% of the genetic variation.

In addition, a QTL effect on the abscisic acid accumulation was localised on chromosome arm 5BL that regulate many processes of growth and development (Quarrie et al. 1994).

Furthermore, chromosome 5B was mentioned to contain genes for earliness per se (Snape et al. 2001) and vernalisation response (Chao et al. 2007, Crossa et al. 2007, Hoogendoorn et al. 1985), which possibly influence the trait performance of grain yield.

The remaining 12 analyses on grain yield found no QTLs on chromosome 5B.

In D84, the second grain yield QTL, *QYld.D84.6B*, was located on chromosome arm 6B in high N-level (Figure 16). At this locus, synthetic wheat alleles reduced grain yield and explained 16.6% of the genetic variance. *QYld.D84.6B* coincided with associations for reduced thousand grain weight ($P = 0.01$) and increased lodging at harvest ($P = 0.02$), where exotic alleles explained 10.3% and 12.9% of the genetic variation, respectively. Accordingly, grain yield and lodging at harvest were significantly correlated (-0.34), whereas yield and thousand grain weight were not significantly correlated.

Several studies assumed that genes on chromosome 6B have been implicated in determining photoperiod response (Lin et al. 2008, Snape et al. 2001, Worland et al. 1998a) and earliness per se (Snape et al. 2001, Hoogendoorn et al. 1985) contingently influencing the effects of yield.

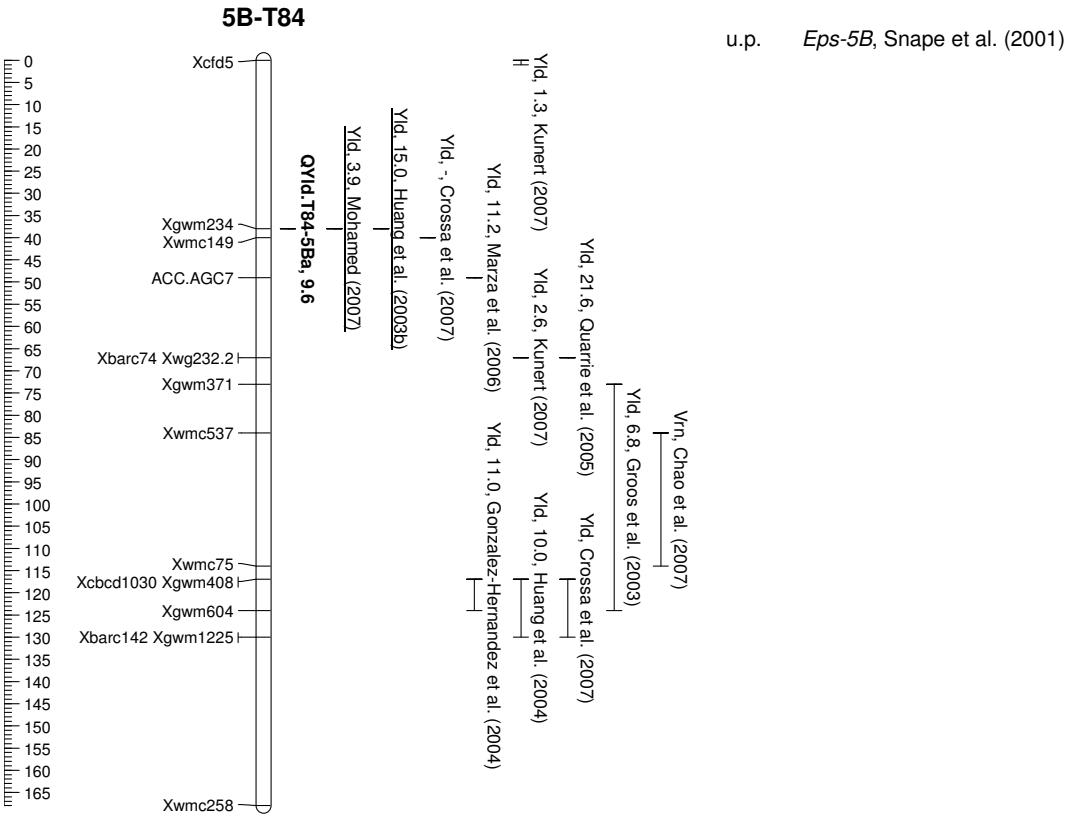

Figure 15: Localisation of the current QTL, *QYld.T84-5Ba*, in T84, published QTLs and genes associated with grain yield on chromosome 5B.

This graphical map was computed using MapChart (Voorrips 2002) with genetic map positions according Somers et al. (2004). Mapped markers were indicated on the right and their corresponding genetic distances (cM) were indicated on the left. QTL confidence interval was indicated by a vertical bar. Bold QTLs were significant marker main effects detected by the REML methods. Not bold QTLs and genes were published in other studies. Underlined QTLs and genes were detected at the identical significant marker locus as the current QTL. QTL description: Yld (Grain yield), number (R^2 as explained genetic variance in %) and reference (study, where the common QTL was published). On the right, gene is listed, where the position was unknown (u.p.).

A total of 23 studies analysed grain yield on chromosome 6B. Still, four QTLs associated with grain yield were published in close vicinity to *QYld.D84-6B*. Mohamed (2007) localised a QTL, 8 cM distant to *QYld.D84-6B*, in the identical Devon×Syn-84 advanced backcross population. Another advanced backcross population, Flair×XX86, revealed an unfavourable yield QTL, where synthetic XX86 alleles explained 11.8% of the phenotypic variance (Huang et al. 2004). One QTL was detected in the centromeric region of chromosome 6B in the ITMI population (Ayala et al. 2002). Marza et al. (2006) identified a favourable QTL increasing grain yield in a population derived from wheat cultivars.

In addition, Crossa et al. (2007) found two QTL clusters associated with grain yield on chromosome arm 6BL and 6BS, which were due largely to variation in thousand grain weight. The 16 remaining studies found no QTLs associated with yield on chromosome 6B.

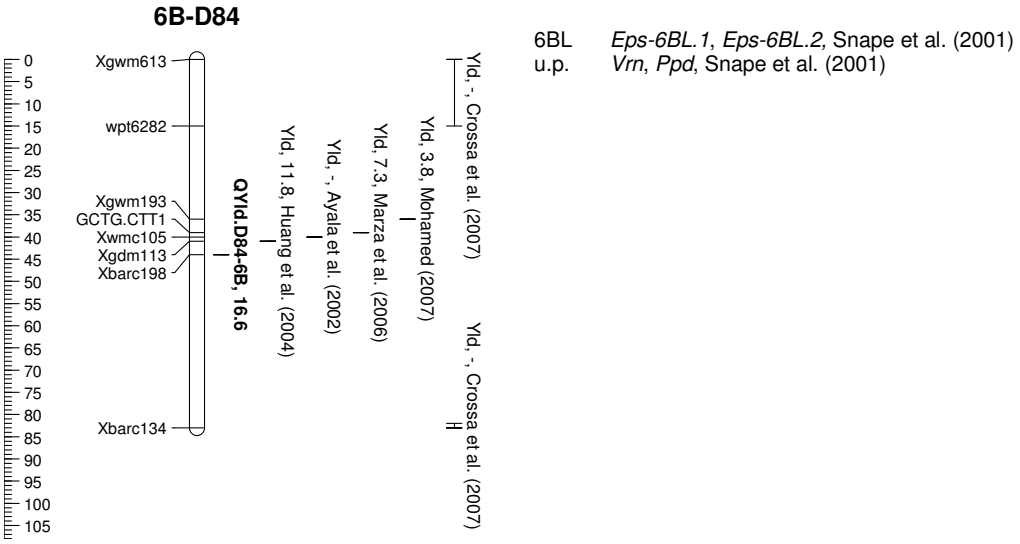

Figure 16: Localisation of the current QTL, *QYld.D84-6B*, in D84, published QTLs and genes associated with grain yield on chromosome 6B.

This graphical map was computed using MapChart (Voorrips 2002) with genetic map positions according Somers et al. (2004). Mapped markers were indicated on the right and their corresponding genetic distances (cM) were indicated on the left. QTL confidence interval was indicated by a vertical bar. Bold QTLs were significant marker main effects detected by the REML methods. Not bold QTLs and genes were published in other studies. Underlined QTLs and genes were detected at the identical significant marker locus as the current QTL. QTL description: Yld (Grain yield), number (R^2 as explained genetic variance in %) and reference (study, where the common QTL was published). On the right, genes are listed, where the position was on long arm (L) or unknown (u.p.).

Quality parameters

The REML mapping method revealed no significant marker×trait associations for quality traits, grain protein content, sedimentation value and grain hardness, as above mentioned in chapter 4.5. Although not significant ($P = 0.036$) at the marker locus, Xbarc130, one association for grain hardness as marker main effect was observed on chromosome arm 5DS in population T84. Chromosome arm 5DS is known to be associated with grain hardness and genes influenced puroindoline-a content (*Pina-D1*) and puroindoline-b content (*Pinb-D1*), which are apparently required for the expression of grain softness (Pshenichnikova et al. 2008, Kunert et al. 2007, Narasimhamoorthy et al. 2006, Crepieux et al. 2005, Igrejas et al. 2002, Perretant et al. 2000, Giroux and Morris 1998, Sourdille et al. 1996).

The texture of the endosperm results mostly from the expression of a major gene designated hardness (*Ha/ha*) located at marker loci, Xmta9 and Xtma10, on chromosome arm 5DS (Igrejas et al. 2002). The gene *Ha* is located only on chromosome 5D because the copies on chromosomes 5A and 5B were eliminated after polyploidisation (Gautier et al. 2000).

In the present study, Xbarc130 was mapped at the same marker locus as Xtam10 and the puroindoline-a gene *Pina-D1* (Wheat-MacGene, GrainGenes 2008). Synthetic wheat alleles explained 71.5% of the genetic variance and caused softer grains by 15.6%. This marker main effect associated with grain hardness confirmed the marker locus Xtma10 that was published to account for up to 71% of the phenotypic variability in grain hardness (Igrejas et al. 2002).

Further, advanced backcross populations revealed synthetic wheat alleles led to softer grains in close vicinity to the marker locus, Xbarc130 (Kunert et al. 2007, Narasimhamoorthy et al. 2006). Four other studies located QTLs closely linked at the *Ha* locus at the same region on chromosome arm 5DS, which have been frequently identified to be associated with grain hardness (Pshenichnikova et al. 2008, Igrejas et al. 2002, Perretant et al. 2000, Sourdille et al. 1996).

Disease resistances

The disease resistances, leaf rust and *Septoria* leaf blotch were only investigated in a few environments under natural field conditions. As mentioned above, for these traits no significant marker×trait associations were identified. In contrast, powdery mildew was measured across eight environments and revealed significant QTL effects. The wheat powdery mildew, caused by the pathogen *Blumeria graminis* f. ssp. *tritici*, is a very destructive leaf disease, which causes great yield losses in many wheat production areas of the world, especially in the regions with high rainfall and with temperate and maritime climates (Bennett 1984).

Race-specific resistance to wheat powdery mildew is controlled by the *Pm* genes. So far, 31 *Pm* genes were designated for resistance according to McIntosh et al. (2008). Concluding, the latest study detected the gene *Pm39* (Lillemo et al. 2008).

Some of the *Pm* genes were introgressed from wheat relatives. Interestingly, wild emmer wheat *T. turgidum* ssp. *dicoccoides* was found to be polymorphic for resistances to several pathogens (Peng et al. 1999b, Reader and Miller 1991). Besides, *Ae. tauschii* was also published as a potential donor of numerous beneficial genes for disease resistances to wheat cultivars (Lutz et al. 1995).

In the current study, both the diploid and tetraploid wheat donors were used for hybridisation to produce the synthetic hexaploid wheat accession, Syn-84, as donor for exotic alleles in advanced backcross populations, T84 and D84. Effectively, two QTLs, *QPm.T84-7Bb* and *QPm.T84-7D*, associated with effects on powdery mildew were detected in population T84.

The QTL, *QPm.T84-7Bb*, synthetic wheat alleles increased sensitivity to powdery mildew, introgressed by *T. dicoccoides* and explained 7.2% of the genetic variance. Previously, chromosome 7B was identified to contain several *Pm* genes influencing resistance against powdery mildew, designated as *Pm5* (Keller et al. 1999b), *Pm5a*, *Pm5b*, *Pm5c*, *Pm5d* (Hsam et al. 2001) and *Pm5e* (Huang et al. 2003a), respectively. *QPm.T84-7Bb* was located at the identical marker locus, Xgwm577, as the resistance gene *Pm5d*, mapped on chromosome arm 7BL (Nematollahi et al. 2008, Figure 17).

Hence, the common marker locus, Xgwm577, may be very useful for developing a diagnostic marker to select the favourable resistance genes against powdery mildew for wheat resistance breeding.

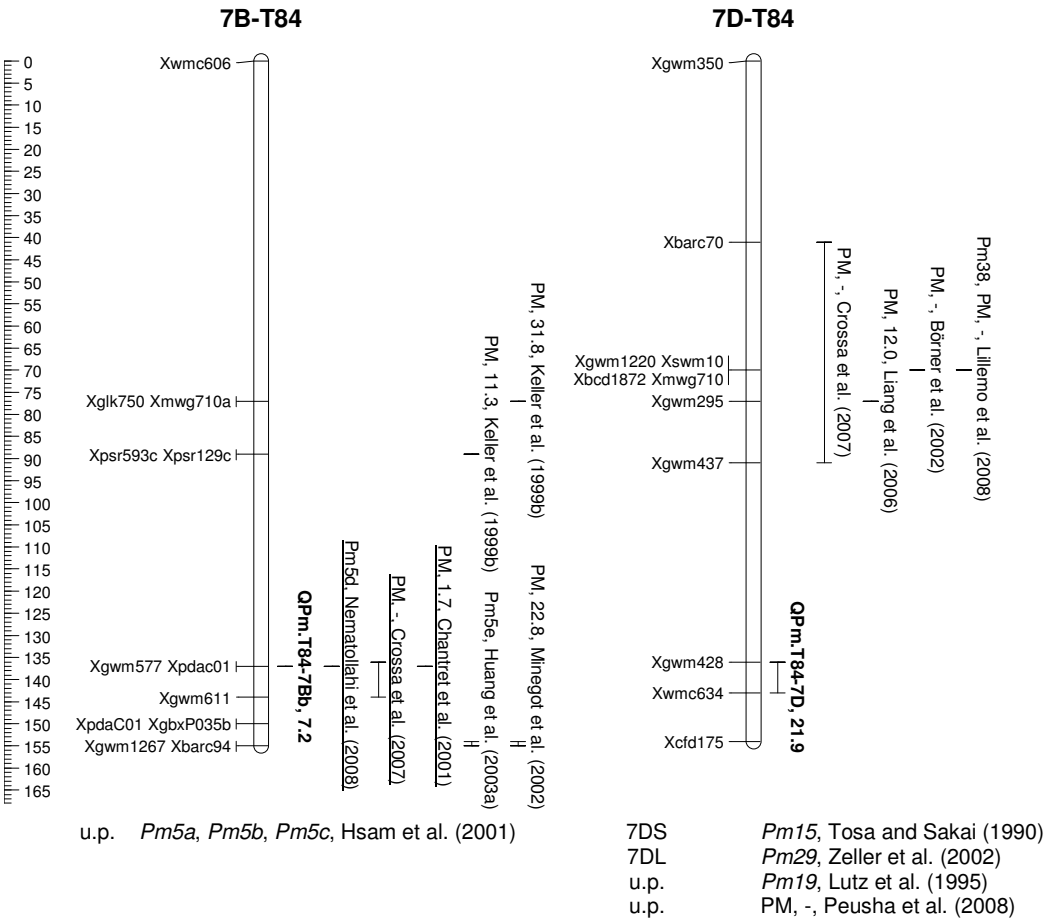

Figure 17: Localisation of current QTLs, *QPm.T84-7Bb* and *QPm.T84-7D*, in T84, published QTLs and genes associated with powdery mildew on chromosomes 7B and 7D.

This graphical map was computed using MapChart (Voorrips 2002) with genetic map positions according Somers et al. (2004). Mapped markers were indicated on the right and their corresponding genetic distances (cM) were indicated on the left. QTL confidence interval was indicated by a vertical bar. Bold QTLs were significant marker main effects detected by the REML methods. Not bold QTLs and genes were published in other studies. Underlined QTLs and genes were detected at the identical significant marker locus as the current QTL. QTL description: PM (Powdery mildew), number (R^2 as explained genetic variance in %) and reference (study, where the common QTL was published). Under chromosomes, QTLs and genes are listed, where the position was on short arm (7DS), long arm (7DL) or unknown (u.p.).

A total of 16 studies revealed two QTLs associated with resistance to powdery mildew at the identical marker locus, which were validated by using the CIMMYT elite spring wheat set (Crossa et al. 2007) and the RE714×Hardi population (Chantret et al. 2001).

Moreover, Mingeot et al. 2002) found a QTL with 13 cM distant to *QPm.T84-7Bb* in the RE714×Festin double haploid population. Keller et al. 1999b) analysed Forno×Oberkulmer recombinant inbred lines across four environments and detected two QTLs explaining up to 31.8% of the phenotypic variance. They proved the residual effects of *Pm5* to one QTL on chromosome arm 7BL.

Besides, closely linked resistance genes were clustered in the region of chromosome arm 7BL, where genes for catalase, chitinase, thaumatins and an ion channel regulator were located (Faris et al. 1999, Li et al. 1999).

The second QTL for powdery mildew, *QPm.T84-7D*, was identified on chromosome arm 7DL coinciding with the resistance gene *Pm29*, previously mapped on chromosome arm 7DL in the resistant wheat line Pova conducted by *T. aestivum*×*Ae. ovata* (Zeller et al. 2002, Figure 17). Another resistance gene *Pm19* was localised in the synthetic hexaploid wheat XX186 derived from *T. durum*×*Ae. tauschii* (Lutz et al. 1995).

QPm.T84-7D was mapped at the marker locus, Xwmc634, where exotic alleles caused a decrease of sensitivity for powdery mildew with 34.7% and explained 21.9% of the genetic variation. The high heritability (0.91) for powdery mildew resistance suggested that the environmental influence did not affect the resistance phenotype to a great extent in accordance with findings of Keller et al. (1999b). *QPm.T84-7D* was validated in population D84 with the identical allele's effect (P = 0.037) at the same marker locus Xwmc634. Exotic alleles reduced the sensitivity for powdery mildew with 27.5% and explained 8.8% of the genetic variance.

Fifteen other studies identified six QTLs, which mapped to chromosome arm 7DS (Lillemo et al. 2008, Crossa et al. 2007, Liang et al. 2006, Börner et al. 2002) and with unknown position (Peusha et al. 2008). Three QTLs were coinciding with the powdery mildew resistance gene *Pm38* (Lillemo et al. 2008, Crossa et al. 2007, Liang et al. 2006) and one QTL was corresponding with the *Pm15* gene (Börner et al. 2002). Börner et al. (2002) detected the QTL, *QPm.ipk-7D*, across three environments, at which favourable alleles were introgressed by the synthetic wheat W-7984 into the ITMI population. Previously, Tosa and Sakai (1990) published this genomic region for harbouring the gene *Pm15*. In addition, Peusha et al. (2008) localised in the cultivar, Vinjett, a QTL associated with a defence to powdery mildew on chromosome 7D presumably responsible for the high resistance in this cultivar.

Further, Liang et al. 2006 analysed Saar×Avocet recombinant inbred lines. They found a powdery mildew QTL linked with the powdery mildew resistance gene *Pm38* and the leaf rust resistance genes *Lr34/Yr18* on chromosome arm 7DS. At this QTL, Saar alleles explained up to 56.5% of the phenotypic variance. Liang et al. (2006) assumed the co-location of genes for partial and non-race specific resistance to three biotrophic pathogens at this region analysed in the Fukuho-komugi×Oligoculm doubled haploid population.

In addition, Zeller and Hsam (1996) mentioned that suppressor genes for *Pm8* and *Pm17* were localised on chromosome 7D by using the monosomic set of the wheat cultivar Caribo. They assumed that the expression of resistance to fungal diseases is often reduced when genes are transferred from related species, particularly from lower level to a higher level of ploidy.

Besides, Chantret (2001) confirmed that quantitative resistance might be resulted from a complex of polygene-for-polygene interactions and resistance to different populations of powdery mildew might involve a different number of genes according to the complexity of the populations.

So far, no QTL was published in close vicinity to *QPm.T84-7D*. This locus associated with increased resistance to powdery mildew may be a new resistance locus introgressed by *Ae. tauschii* in Syn-84.

4.9 Conclusions

Tanksley and Nelson (1996a) proposed the AB-QTL strategy to discover and transfer favourable QTL alleles from exotic donor lines into elite breeding lines. So far, seven studies used the AB-QTL analysis for detecting QTLs in wheat.

The present study of advanced backcross QTL analysis was aimed to use exotic alleles conducted by one synthetic hexaploid wheat accession, Syn-84, to improve agronomic traits, quality parameters, disease resistances and enriching genetic diversity in two different genetic backgrounds of elite wheat cultivars, Triso and Devon, simultaneously. These diverse and differentiated parents from different genetic germplasms, which represent the extreme ends of a trait phenotype are selected. Thus, the chance increases to indentify QTLs because of statistically different means of marker groups. Then, in order to have durable effects a more advanced generation, BC_2F_4, was used to detect favourable QTL effects of synthetic wheat alleles. The revealing populations with 223 (T84) und 176 (D84) BC_2F_4 lines, might increase the power to detect and correctly estimate the location and magnitude of QTL effects compared to small populations like 50 lines. Both populations, T84 and D84, were phenotyped in field plots at eight environments in two different N-treatments, high and low N-supplies, to increase the reproducibility of a QTL effect. In addition, the populations were genotyped with 94 (T84) and 106 (D84) SSR markers to homogeneously distribute the wheat genomes. Even so, several genomic regions covered gaps with marker intervals greater than 50 cM notably on the A genome caused by the low marker density because of sparsely polymorphism between parents of advanced backcross populations.

Multi-environmental QTL mapping was carried out using different QTL mapping methods with a stringent significance threshold of $P = 0.01$ to avoid false positive QTLs. The QTL models included marker as fixed effect, the environment, line nested in marker genotype and the marker interaction effects as random effects to reduce the residual variance of the experiment and, thus, to increase the probability of detecting a QTL effect. The QTL models were considered in three-way (high N-level) and four-way (high and low N-levels) models determined through ANOVA single-locus, REML single-locus and REML multi-locus methods in SAS programme (SAS Institute 2003). Thus, the three-way models allowed differentiating 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 marker×environment interaction effect where the effect is considered to depend on a particular environment. In addition, four-way models allowed detecting a QTL significant as a marker×nitrogen interaction effect where the effect is considered to depend on an N-supply as an N-responsive QTL effect.

A comparison between QTL mapping methods revealed that REML single-locus methods validated QTLs with highest F-value computed by ANOVA single-locus methods. The REML methods computed only significant marker main effects and may be more stringent than the ANOVA methods. Thus, non validated QTLs using the REML methods were either false positive or small QTLs that were not robust enough through the stringent REML methods.

By using three-way QTL mapping models in high N-level, 105 (T84) and 78 (D84) QTLs were detected as marker main effects and marker×environment interaction effects using the ANOVA single-locus method. Despite less marker density across the genomes but large population sizes, up to eight tested environments and the statistical design may be responsible for the high number of QTLs detected using the ANOVA single-locus method.

Favourable loci represented QTLs with low F-value resulting from the long size of introgressions like marker cluster associated with one QTL. On the same chromosomal segment, favourable alleles of the synthetic wheat could be still masked by many deleterious alleles. Then, the development of nearly-isogenic lines (NILs) could reveal beneficial QTLs with stronger effects on the traits.

Through the three-way REML single-locus method ten (T84) and four (D84) QTLs as marker main effects were identified. Further, the REML multi-locus method resulted in fewer QTLs than detected by the REML single-locus method. The stringet statistical design of the REML methods may be responsible for the low number of QTLs.

By using four-way QTL mapping models in high and low N-levels, 11 (T84) and 13 (D84) marker×nitrogen interaction effects as N-responsive QTLs were ascertained using the ANOVA single-locus method. The ANOVA single-locus method revealed only a few minor N-responsive QTLs. The detection of minor N-responsive QTLs suggests that introgressions of *T. dicoccoides* and *Ae. tauschii* germplasm into elite wheat genomes may have small effects on trait performance in relation to N-response, considering the extreme phenotypic difference between the two germplasm. By using the REML single-locus method, 12 associations as marker×nitrogen interaction effects were detected, thus, no N-responsive QTLs were significant. To that fact, the intensive field experiment did not come up to expectations. Hence, a replication of the populations in each environment could increase the power of QTL detection.

Altogether, 17 QTLs were detected for agronomic traits and powdery mildew resistance across multiple environments using the REML methods. Thus, it is necessary to saturate the target genomic regions by additional molecular markers for further clarifying pleiotropic or close linkage effects of improved traits. However, in T84 (6) and D84 (1) exotic alleles improved the trait performance. Therefore, it might be suggested that wild relatives of modern crop species as synthetic wheat provide a valuable resource of favourable alleles for the trait improvement and widening genetic diversity to elite wheat cultivars. Resulting from the current study the wild emmer alleles improved agronomic traits as days until heading, plant height and thousand grain weight. The *Ae. tauschii* alleles increased thousand grain weight and improved the resistance against powdery mildew. One genomic region of special interest was associated with a favourable QTL effect originating from *Ae. tauschii* alleles on chromosome arm 7DL, which contributed to resistance against powdery mildew. So far, this QTL was not yet published in several studies of powdery mildew. The QTL for powdery mildew resistance might be new exotic alleles.

In future, BC_2F_4 lines of population T84, which possess exotic resistance QTL alleles on chromosome 7D can be utilised to generate QTL bearing NILs. These NILs contain a single donor segment in the background of the recipient genome (Pillen et al. 2004) and can be derived from advanced backcross populations in one or two additional generations for further genetic characterisation of improved traits (Huang et al. 2003b). These NILs may be used to validate QTL effects in new field experiments. Then, validated NILs can be directly used both for development of improved varieties and for map-based cloning of the QTL underlying resistance genes (Naz et al. 2008).

According to Huang et al. (2004) the favourable QTL effects need to be confirmed in a large BC_3 population. Further, the development of a large BC_3 population can be revealing more favourable QTLs rather than in a BC_2 population (Fulton et al. 1997a).

Consequential, a marker-assisted selection on this QTL of interest should be accompanied by the monitoring of the fixation of the elite genetic background to minimizing linkage drag (Somers et al. 2005).

In the present study, the comparison of QTLs with QTLs and candidate genes published in other QTL studies was complicated because of numerous chromosome maps, revealed from several mapping populations. In addition, designed populations as advanced backcross populations represent a rather narrow germplasm base and mapping results may not apply to other genetic backgrounds (Parisseaux and Bernardo 2004). Then, the marker position sometimes varied considerably. For instance, the marker Xgwm234 was localised at 0.0 cM up to 91.6 cM on chromosome 5B. However, most markers were not identical in mapping populations because of the polymorphism between cross parents. Furthermore, numerous studies mentioned a QTL of interest, but they gave no information to the marker position and QTL effect.

The current study demonstrates that QTLs with exotic alleles can improve quantitative traits as agronomic traits and the resistance against powdery mildew validated across multiple environments. Thus, there should be refined strategies, which efficiently characterise and use the valuable exotic germplasm resources. The detection of QTLs associated with favourable exotic alleles mainly depend on complex strategies, which focus on the structure and size of mapping populations, total number and density of markers, accurate methods of phenotyping and finally an efficient statistical model to dissect the variance caused by exotic alleles. Hence, a successful QTL detection by using the AB-QTL analysis is a sophisticated choice for the direct and specific utilisation of exotic germplasm.

5 Summary

The objective of the present study was to use exotic germplasm derived from synthetic hexaploid wheat for identifying favourable alleles. These exotic alleles should improve 16 quantitative agronomic traits, quality parameters and disease resistances in elite wheat varieties. According to Tanksley and Nelson (1996a), the advanced backcross breeding strategy (AB-QTL) was applied for the simultaneous identification and introgression of favourable quantitative trait loci (QTLs) alleles from synthetic wheat into elite wheat varieties.

Therefore, two advanced backcross populations in generation BC_2F_4 were derived from crosses of two German spring wheat varieties (Triso and Devon) and one synthetic hexaploid wheat accession (Syn-84). The synthetic wheat Syn-84 is a non-adapted exotic wheat germplasm and was hybridised from *T. turgidum* ssp. *dicoccoides* (wild emmer wheat) and *Ae. tauschii*. Two revealing advanced backcross populations reffered to as T84 and D84 counted 223 and 176 BC_2F_4 lines, respectively.

BC_2F_4 lines were phenotyped in field plots at four different locations in Germany under two different nitrogen (N) supplies (high and low N-level) in seasons 2004 and 2005. In addition, the populations were genotyped with 94 and 106 SSR markers in populations T84 and D84, respectively.

Phenotype and genotype data were merged to different QTL mapping methods with a significance threshold of $P = 0.01$. Thus, it was expected to reduce the residual variance of the experiment by including the environment and N-supply in the statistical model and, thus, to increase the probability of detecting a QTL effect. Multi-environmental QTL detections were considered in three-way (high N-level) and four-way (high and low N-levels) models including marker as fixed effect, the environment, line nested in marker genotype, marker×environment and marker×nitrogen interaction effects as random effects. QTL analyses were determined through ANOVA single-locus and REML single-locus methods as well as REML multi-locus methods in SAS programme (SAS Institute 2003).

By using three-way QTL mapping methods under high N-level, 105 and 78 QTLs were detected as marker main effects and marker×environment interaction effects using the ANOVA single-locus method in populations T84 and D84, respectively. Altogether, 24 (T84) and 11 (D84) QTLs showed favourable effects derived from the presence of exotic alleles. Through the REML single-locus method, ten (T84) and four (D84) QTLs were identified as marker main effects. Thus, no significant marker×environment interaction effects were detected. Altogether, seven QTLs were associated with improved trait performance conducted by the exotic genotype in populations T84 and D84. The REML multi-locus method revealed seven and two QTLs as marker main effects in populations T84 and D84, respectively.

By using four-way QTL mapping methods under high and low N-levels, 11 and 13 marker×nitrogen interaction effects as N-responsive QTLs as well as 48 and 48 QTLs as marker main effects were ascertained using the ANOVA single-locus method in populations T84 and D84, respectively.

Altogether, six (T84) and four (D84) N-responsive QTLs showed favourable effects derived from the presence of exotic alleles under low N-supply. Through the REML single-locus method, five (T84) and four (D84) QTLs as marker main effects were detected. Twelve associations as marker×nitrogen interaction effects were identified. Hence, no N-responsive QTLs were ascertained. The REML multi-locus method revealed four and three QTLs as marker main effects in populations T84 and D84, respectively.

A comparison between QTL mapping methods revealed that REML single-locus methods validated QTLs with highest F-value computed by ANOVA single-locus methods. Thus, by the REML single-locus methods common QTLs were computed with significances less than $P = 0.001$ and explained more than 10% of the genetic variances in the ANOVA method. Further, the REML multi-locus method resulted in fewer QTLs than detected by the REML single-locus method. Moreover, no significant interaction effects were permitted using REML methods. Hence, it might be postulated that non validated QTLs were either false positive or small QTLs that were not robust enough through the stringent REML methods. Consequently, the more stringent QTLs identified by REML methods were used for the discussion. However, three and two common QTLs were stably detected across all QTL mapping methods in populations T84 and D84, respectively.

The stringent REML single-locus methods computed with three-way and four-way models revealed six (T84) and one (D84) QTLs associated with exotic alleles improving traits of interest in regard to breeding efforts. Exotic alleles reduced, for example, sensitivity to powdery mildew by 34.7% at QTL *QPm.T84-7D*, on chromosome arm 7DL in population T84. So far, this locus associated with resistance to powdery mildew was not published in other QTL studies. *QPm.T84-7D* may be associated with a new resistance to powdery mildew conducted by *Aegilops tauschii*. The second population D84 validated the new QTL, *QPm.T84-7D*, where identical exotic alleles reduced sensitivity to powdery mildew by 27.5% ($P = 0.037$).

At the new QTL, *QPm.T84-7D*, synthetic wheat alleles (Syn-84) were similar in their effects and clearly different from the recurrent alleles, Triso and Devon. Thus, the effectiveness of exotic alleles in these different genetic backgrounds revealed a first indication that alleles from this synthetic wheat donor might not yet be present in elite wheat varieties.

In population T84, BC_2F_4 lines were selected, which carried favourable exotic QTL alleles in at least one introgression. For days until heading, plant height and thousand grain weight eight, one and four BC_2F_4 lines were selected, which improved the trait performance significantly compared to the recurrent parent Triso. Following QTL mapping, favourable QTLs may be targeted for development on nearly-isogenic lines (NILs) for development of improved varieties and for map-based cloning of the QTL underlying resistance genes.

The results of the current study confirms that wild relatives of modern crop species as synthetic hexaploid wheat provide a valuable resource of favourable alleles for improving quantitative traits, as agronomic traits and disease resistances, and widening genetic diversity in elite wheat varieties.

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7 Abbreviations

Abbreviation	Explanation
AA	genotype: homozygous elite alleles
Aa	genotype: heterozygous alleles
aa	genotype: homozygous exotic alleles
AB	advanced backcrossing
AB-QTL	advanced backcross quantitativ trait locus analysis
Acc-1	gene associated with plastid acetyl-carboxylase
Ae.	*Aegilops*
ANOVA	analysis of variance
APS	ammoniumperoxodisulfat
BARC	label for SSR markers provided by United States Wheat and Barley Scab Initiative
BC	backcross and generation
Bg	gene associated with black color glume
bp	base pairs
Br, br	gene associated with brittle rachis
BRT	brittleness
B04, B05	Boldebuck in season 2004 and 2005
ºC	degree Celsius
C, *c*	gene associated with club spike shape
cDNA	complementary DNA
CFA	label for SSR markers provided by INRA
CFD	label for SSR markers provided by INRA
CGIAR	Consultative Group on International Agricultural Research
Chr.	chromosome
CIMMYT	Centro Internacional de Mejoramiento de Maiz y Trigo
cM	centi-Morgan
cQTL	common QTL
CTAB	cetyl trimethylammonium bromide
ddH_2O	redistilled water
DH	double haploid
DNA	desoxyribonucleic acid
dNTPs	desoxynucleotid triphosphate
DS	distorted segregation
DSV	Deutsche Saatveredlung Lippstadt – Bremen GmbH
D84	advanced backcross population derived from Devon×Syn-84
D04, D05	Dikopshof in season 2004 and 2005
EAR	tillers per square meter
EDTA	ethylendiamintetraacetat
eQTLs	expression QTLs
EST	expressed sequence tag
et al.	et alii, and others
EWDB	European Wheat Database
FAO	Food and Agriculture Organization
F_2 to F_t	generation
F04, F05	Feldkirchen in season 2004 and 2005
GABI	Genomanalyse im biologischen System Pflanze
GFD	grain-filling duration
GDM	label for SSR markers provided by IPK
GH	grain hardness
GmbH	Gesellschaft mit beschränkter Haftung
GNE	grain number per ear
GPC	grain protein content
Gpc-B1	gene associated with seed size
GS	gene associated with glutamine synthetase
GWM	label for SSR markers provided by IPK
Ha	gene associated with grain hardness
HCL	hydrochloric acid
HEA	days until heading

Abbreviation	Explanation
HEI	plant height
HI	harvest index
HLW	grain test weight
Hz	hertz
H04, H05	Hovedissen in season 2004 and 2005
ICARDA	International Center for Agricultural Research in the Dry Areas
INRA	Institut National de la Recherche Agronomique
INRES	Institute of Crop Science and Resource Conservation
IPK	Leibniz Institute of Plant Genetics and Crop Plant Research
IRD	infrared
ITMI	International Triticeae Mapping Initiative
IWGSC	International Wheat Genome Sequencing Consortium
LAH	Lodging at harvest
LR	leaf rust
Lr	gene associated with leaf rust
Lrk	gene associated with receptor-like kinase associated with *Lr* locus
LS-means	least squares means
KCL	potassium chloride
M	marker main effect
M×E	marker×environment interaction effect
M×N	marker×nitrogen interaction effect
MAS	marker-assisted selection
Mb	mega base paires
mg	milligram
$MgCL_2$	magnesium chloride
min.	minute
ml	millilitre
µl	microlitre
mM	millimolar
N	nitrogen
N+	high nitrogen supply
N-	low nitrogen supply
n	number
NaCL	sodium chloride
ng	nanogram
NIL	Nearly-isogenic line
n.k.	not known
n.s.	not significant
n.sp.	not specified
PCR	polymerase chain reaction
Pgk-1	gene associated with plastid 3-phosphoglycerate kinase
pH	pH-value
Ph1	gene associated with pairing genes (Khlestkina et al. 2006) and gene *Pm*
Phs	gene associated with preharvest sprouting
PM	Powdery mildew
Pm	gene associated with powdery mildew
Pos.	position
Ppd	gene associated with adaption to photoperiod
PPO	polyphenol oxidase
Q, *q*	gene associated with threshability
QTL	quantitative trait locus
Ref.	references
REML	restricted maximum likelihood
RFLP	restriction fragment length polymorphism
Rg	gene associated with red color glume
Rht	gene associated with semi-dwarf
RNA	ribonucleic acid
Rnase	ribonuclease
rpm	random per minute
R^2	coefficient of determination

Abbreviation	Explanation
SAS	Statistical Analysis System software
SDS	sodiumdodecylsulfat
SED	sedimentation value
SEP	*Septoria* leaf bloth
SINGER	Systemwide Information Network for Genetic Resources
SNP	single nucleotide polymorphism
ssp.	subspecies
SSR	simple sequence repeat
S-1, *s-1*	gene associated with *sphaerococcum* factor
T.	*Triticum*
TAE	Tris-Acetat-EDTA
TBE	Tris-Boric acid-EDTA
TE	Tris-EDTA
TEMED	tetramethylethylendiamin
TILLING	targeting induced local lesions in genomics
Tg, *tg*	gene associated with tenacious glumes
TGW	thousand grain weight
Tris	tris (hydroxymethyl) aminomethan
T84	advanced backcross population derived from Triso×Syn-84
u.p.	unknown posotion
V	volt
VIR	Vavilov Institute
Vol	volume
Vrn	gene associated with vernalisation requirement
WGGRC	Wheat Genetic and Genomic Resources Center
WMC	Wheat Microsatellite Consortium
YLD	grain yield
2n = 4x = 28	

8 Table index

9 Figure index

10 Appendix

Appendix 1: Family structure and distribution of genotypes in T84, determined of 94 markers for 223 BC_2F_4 lines.

BC_2F_4 line	BC_1F_1 plant	BC_2F_1 plant	n [AA]	n [Aa]	n [aa]	[aa] (%)	Ambiguous genotype (%)	DS
Tri 001	1	1	65	5	8	13.5	17.0	n.s.
Tri 002	1	1	71	1	11	13.9	11.7	n.s.
Tri 003	1	2	68	5	10	15.1	11.7	n.s.
Tri 004	1	2	62	3	15	20.6	14.9	*
Tri 005	1	3	72	5	7	11.3	10.6	n.s.
Tri 006	1	3	69	6	9	14.3	10.6	n.s.
Tri 007	1	4	62	4	6	11.1	23.4	n.s.
Tri 008	1	5	70	4	10	14.3	10.6	n.s.
Tri 009	1	5	73	1	7	9.3	13.8	n.s.
Tri 010	1	6	65	0	15	18.8	14.9	*
Tri 011	1	6	70	3	8	11.7	13.8	n.s.
Tri 012	2	7	65	4	15	20.2	10.6	*
Tri 013	2	8	74	5	4	7.8	11.7	*
Tri 014	2	8	78	4	1	3.6	11.7	**
Tri 015	2	8	62	2	9	13.7	22.3	n.s.
Tri 016	2	8	77	0	8	9.4	9.6	n.s.
Tri 017	2	9	63	2	18	22.9	11.7	**
Tri 018	2	10	71	2	10	13.3	11.7	n.s.
Tri 019	2	10	68	9	3	9.4	14.9	**
Tri 020	2	11	72	4	5	8.6	13.8	n.s.
Tri 021	2	11	62	1	11	15.5	21.3	n.s.
Tri 022	2	12	64	2	14	18.8	14.9	n.s.
Tri 023	2	13	76	2	7	9.4	9.6	n.s.
Tri 024	2	13	73	1	9	11.4	11.7	n.s.
Tri 025	2	14	68	9	4	10.5	13.8	**
Tri 026	2	14	70	1	12	15.1	11.7	n.s.
Tri 027	2	15	69	2	11	14.6	12.8	n.s.
Tri 028	3	16	68	1	11	14.4	14.9	n.s.
Tri 029	3	17	62	6	8	14.5	19.1	*
Tri 030	3	18	74	2	7	9.6	11.7	n.s.
Tri 031	3	19	79	0	5	6.0	10.6	*
Tri 032	3	20	70	4	8	12.2	12.8	n.s.
Tri 033	3	20	72	2	5	7.6	16.0	n.s.
Tri 034	3	20	69	4	8	12.3	13.8	n.s.
Tri 035	3	21	61	4	10	16.0	20.2	n.s.
Tri 036	3	22	71	2	9	12.2	12.8	n.s.
Tri 037	3	22	63	2	17	22.0	12.8	**
Tri 038	3	23	71	5	9	13.5	9.6	n.s.
Tri 039	3	23	71	6	7	11.9	10.6	n.s.
Tri 040	3	24	60	7	15	22.6	12.8	**
Tri 041	3	25	59	11	4	12.8	21.3	**
Tri 042	3	25	77	1	7	8.8	9.6	n.s.
Tri 043	3	26	68	5	12	17.1	9.6	n.s.
Tri 044	3	27	73	3	8	11.3	10.6	n.s.
Tri 045	3	27	79	2	3	4.8	10.6	n.s.
Tri 046	3	28	43	5	12	24.2	36.2	**
Tri 047	4	29	73	3	8	11.3	10.6	n.s.
Tri 048	4	29	69	3	3	6.0	20.2	n.s.
Tri 049	4	30	78	1	6	7.6	9.6	n.s.
Tri 050	4	31	36	6	4	15.2	50.5	**
Tri 051	4	31	68	10	5	12.0	11.7	**
Tri 052	4	32	66	7	12	18.2	9.6	**
Tri 053	4	32	75	3	7	10.0	9.6	n.s.
Tri 054	4	33	60	3	13	19.1	19.1	n.s.
Tri 055	4	33	68	2	13	16.9	11.7	n.s.
Tri 056	4	34	72	2	10	13.1	10.6	n.s.
Tri 057	4	34	68	4	10	14.6	12.8	n.s.
Tri 058	4	35	76	3	3	5.5	12.8	n.s.
Tri 059	4	35	72	4	9	12.9	9.6	n.s.

BC_2F_4 line	BC_1F_1 plant	BC_2F_1 plant	n [AA]	n [Aa]	n [aa]	[aa] (%)	Ambiguous genotype (%)	DS
Tri 060	4	36	76	1	8	10.0	9.6	n.s.
Tri 061	4	37	69	9	4	10.4	12.8	**
Tri 062	4	38	72	4	8	11.9	10.6	n.s.
Tri 063	4	38	74	5	6	10.0	9.6	n.s.
Tri 064	4	38	71	4	10	14.1	9.6	n.s.
Tri 065	4	39	74	1	10	12.4	9.6	n.s.
Tri 066	4	40	69	4	13	17.4	8.5	n.s.
Tri 067	4	40	69	3	13	17.1	9.6	n.s.
Tri 068	4	41	71	1	14	16.9	8.5	n.s.
Tri 069	4	41	77	1	6	7.7	10.6	n.s.
Tri 070	4	41	69	3	13	17.1	9.6	n.s.
Tri 071	4	42	75	2	8	10.6	9.6	n.s.
Tri 072	4	42	75	1	9	11.2	9.6	n.s.
Tri 073	5	43	65	16	3	13.1	10.6	**
Tri 074	5	43	69	12	4	11.8	9.6	**
Tri 075	5	44	78	3	3	5.4	10.6	n.s.
Tri 076	5	44	74	1	10	12.4	9.6	n.s.
Tri 077	5	45	72	5	9	13.4	8.5	n.s.
Tri 078	5	46	62	4	20	25.6	8.5	**
Tri 079	5	46	61	3	12	17.8	19.1	n.s.
Tri 080	5	47	74	4	5	8.4	11.7	n.s.
Tri 081	5	48	76	0	9	10.6	9.6	n.s.
Tri 082	5	49	72	5	7	11.3	10.6	n.s.
Tri 083	5	49	65	4	8	13.0	18.1	n.s.
Tri 084	5	50	64	6	10	16.3	14.9	*
Tri 085	5	51	77	7	2	6.4	8.5	**
Tri 086	6	52	64	2	18	22.6	10.6	**
Tri 087	6	52	68	1	14	17.5	11.7	n.s.
Tri 088	6	53	69	12	4	11.8	9.6	**
Tri 089	6	54	72	1	9	11.6	12.8	n.s.
Tri 090	6	55	74	0	7	8.6	13.8	n.s.
Tri 091	6	55	76	3	6	8.8	9.6	n.s.
Tri 092	6	56	71	5	5	9.3	13.8	n.s.
Tri 093	7	57	65	2	11	15.4	17.0	n.s.
Tri 094	7	57	76	3	7	9.9	8.5	n.s.
Tri 095	7	58	73	2	8	10.8	11.7	n.s.
Tri 096	7	58	77	5	3	6.5	9.6	*
Tri 097	7	58	72	3	8	11.4	11.7	n.s.
Tri 098	7	59	72	4	9	12.9	9.6	n.s.
Tri 099	7	59	68	2	6	9.2	19.1	n.s.
Tri 100	7	59	75	0	10	11.8	9.6	n.s.
Tri 101	7	60	75	2	8	10.6	9.6	n.s.
Tri 102	7	60	76	1	7	8.9	10.6	n.s.
Tri 103	7	60	68	2	9	12.7	16.0	n.s.
Tri 104	7	60	67	3	4	7.4	21.3	n.s.
Tri 105	7	61	76	1	5	6.7	12.8	n.s.
Tri 106	7	62	67	3	4	7.4	21.3	n.s.
Tri 107	7	63	73	2	6	8.6	12.9	n.s.
Tri 108	7	64	66	2	10	14.1	17.0	n.s.
Tri 109	7	65	68	4	7	11.4	16.0	n.s.
Tri 110	8	66	71	1	10	12.8	12.8	n.s.
Tri 111	8	67	72	2	5	7.6	16.0	n.s.
Tri 112	8	67	66	2	6	9.5	21.3	n.s.
Tri 113	8	68	51	3	6	12.5	36.2	n.s.
Tri 114	8	69	52	3	22	30.5	18.1	**
Tri 115	8	69	50	2	13	21.5	30.9	*
Tri 116	8	69	63	4	12	17.7	16.0	n.s.
Tri 117	8	70	68	3	11	15.2	12.8	n.s.
Tri 118	8	70	66	3	13	17.7	12.8	n.s.
Tri 119	8	71	64	2	12	16.7	17.0	n.s.
Tri 120	8	72	66	1	9	12.5	19.1	n.s.
Tri 121	8	72	69	4	4	7.8	18.1	n.s.
Tri 122	8	73	59	4	15	21.8	17.0	*
Tri 123	8	73	64	2	14	18.8	14.9	n.s.
Tri 124	9	74	56	13	8	18.8	18.1	**

BC_2F_4 line	BC_1F_1 plant	BC_2F_1 plant	n [AA]	n [Aa]	n [aa]	[aa] (%)	Ambiguous genotype (%)	DS
Tri 125	9	75	59	5	7	13.4	24.5	n.s.
Tri 126	9	76	72	3	6	9.3	13.8	n.s.
Tri 127	9	77	67	3	11	15.4	13.8	n.s.
Tri 128	9	77	66	10	4	11.3	14.9	**
Tri 129	9	78	64	7	11	17.7	12.8	**
Tri 130	10	79	75	5	1	4.3	13.8	**
Tri 131	10	80	66	2	11	15.2	16.0	n.s.
Tri 132	10	81	77	1	4	5.5	12.8	n.s.
Tri 133	10	82	61	4	18	24.1	11.7	**
Tri 134	10	83	63	2	16	21.0	13.8	*
Tri 135	10	84	67	4	7	11.5	17.0	n.s.
Tri 136	10	85	63	1	17	21.6	13.8	**
Tri 137	10	85	63	4	10	15.6	18.1	n.s.
Tri 138	10	86	67	3	10	14.4	14.9	n.s.
Tri 139	10	87	66	5	10	15.4	13.8	n.s.
Tri 140	10	88	65	2	10	14.3	18.1	n.s.
Tri 141	10	89	68	4	10	14.6	12.8	n.s.
Tri 142	10	89	71	3	8	11.6	12.8	n.s.
Tri 143	10	90	66	5	10	15.4	13.8	n.s.
Tri 144	11	91	72	3	6	9.3	13.8	n.s.
Tri 145	11	91	71	3	6	9.4	14.9	n.s.
Tri 146	11	91	57	8	8	16.4	22.3	**
Tri 147	11	92	70	1	9	11.9	14.9	n.s.
Tri 148	11	92	69	0	11	13.8	14.9	n.s.
Tri 149	11	92	65	2	8	12.0	20.2	n.s.
Tri 150	11	92	71	3	6	9.4	14.9	n.s.
Tri 151	11	93	77	3	3	5.4	11.7	n.s.
Tri 152	12	94	68	6	8	13.4	12.8	n.s.
Tri 153	12	95	67	2	9	12.8	17.0	n.s.
Tri 154	12	96	67	1	10	13.5	17.0	n.s.
Tri 155	12	96	73	2	3	5.1	17.0	n.s.
Tri 156	12	97	70	1	5	7.2	19.1	n.s.
Tri 157	12	98	70	1	9	11.9	14.9	n.s.
Tri 158	13	99	53	9	3	11.5	30.9	**
Tri 159	13	99	66	2	8	11.8	19.1	n.s.
Tri 160	13	100	59	3	11	17.1	22.3	n.s.
Tri 161	13	100	67	2	10	13.9	16.0	n.s.
Tri 162	13	101	72	1	9	11.6	12.8	n.s.
Tri 163	13	102	72	1	5	7.1	17.0	n.s.
Tri 164	13	103	64	7	7	13.5	17.0	**
Tri 165	13	103	67	1	13	16.7	13.8	n.s.
Tri 166	13	104	63	2	9	13.5	21.3	n.s.
Tri 167	13	105	74	3	6	9.0	11.7	n.s.
Tri 168	14	106	71	5	5	9.3	13.8	n.s.
Tri 169	14	106	69	3	9	13.0	13.8	n.s.
Tri 170	14	106	69	6	7	12.2	12.8	*
Tri 171	14	107	58	4	21	27.7	11.7	**
Tri 172	14	107	65	2	12	16.5	16.0	n.s.
Tri 173	14	107	66	5	11	16.5	12.8	n.s.
Tri 174	14	108	76	0	4	5.0	14.9	*
Tri 175	14	108	66	2	13	17.3	13.8	n.s.
Tri 176	14	108	60	3	17	23.1	14.9	**
Tri 177	14	109	57	5	16	23.7	17.0	**
Tri 178	15	110	76	1	4	5.6	13.8	n.s.
Tri 179	15	111	72	3	6	9.3	13.8	n.s.
Tri 180	15	111	64	2	12	16.7	17.0	n.s.
Tri 181	15	111	64	3	12	17.1	16.0	n.s.
Tri 182	15	112	76	1	6	7.8	11.7	n.s.
Tri 183	15	112	75	1	7	9.0	11.7	n.s.
Tri 184	15	112	73	3	4	6.9	14.9	n.s.
Tri 185	15	112	74	7	2	6.6	11.7	**
Tri 186	15	113	71	2	8	11.1	13.8	n.s.
Tri 187	15	114	67	3	10	14.4	14.9	n.s.
Tri 188	15	114	66	10	6	13.4	12.8	**
Tri 189	15	115	71	4	6	9.9	13.8	n.s.

BC_2F_4 line	BC_1F_1 plant	BC_2F_1 plant	n [AA]	n [Aa]	n [aa]	[aa] (%)	Ambiguous genotype (%)	DS
Tri 190	15	116	72	1	7	9.4	14.9	n.s.
Tri 191	15	116	72	2	8	11.0	12.8	n.s.
Tri 192	15	117	71	2	7	10.0	14.9	n.s.
Tri 193	15	117	67	2	6	9.3	20.2	n.s.
Tri 194	15	117	69	6	5	10.0	14.9	*
Tri 195	15	118	69	0	8	10.4	18.1	n.s.
Tri 196	15	118	70	2	4	6.6	19.1	n.s.
Tri 197	16	119	59	2	14	20.0	20.2	*
Tri 198	16	119	57	2	12	18.3	23.7	n.s.
Tri 199	16	119	53	6	9	17.6	27.7	**
Tri 200	16	120	68	3	8	12.0	16.0	n.s.
Tri 201	16	120	67	3	9	13.3	16.0	n.s.
Tri 202	16	120	63	2	6	9.9	24.5	n.s.
Tri 203	16	121	64	4	8	13.2	18.3	n.s.
Tri 204	16	122	74	3	2	4.4	16.0	*
Tri 205	16	123	61	1	1	2.4	33.0	**
Tri 206	17	124	65	2	10	14.3	18.1	n.s.
Tri 207	17	125	71	1	8	10.6	14.9	n.s.
Tri 208	17	125	67	1	4	6.3	23.4	n.s.
Tri 209	17	126	69	1	9	12.0	16.0	n.s.
Tri 210	17	126	68	3	3	6.1	21.3	n.s.
Tri 211	17	127	64	12	3	11.4	16.0	**
Tri 212	17	128	65	2	9	13.2	19.1	n.s.
Tri 213	17	128	75	2	1	2.6	17.0	**
Tri 214	17	129	73	0	4	5.2	18.1	*
Tri 215	17	129	75	3	2	4.4	14.9	*
Tri 216	17	130	69	2	6	9.1	18.1	n.s.
Tri 217	17	131	71	0	9	11.3	14.9	n.s.
Tri 218	17	131	74	1	4	5.7	16.0	n.s.
Tri 219	18	132	65	2	10	14.3	18.1	n.s.
Tri 220	18	133	62	2	13	18.2	18.1	n.s.
Tri 221	18	134	63	5	7	12.7	20.2	n.s.
Tri 222	18	134	62	9	5	12.5	19.1	**
Tri 223	18	135	66	4	6	10.5	19.1	n.s.
Sum	18	135	15,201	741	1,872			56
Mean			68.2	3.3	8.4	12.6	15.0	

BC_2F_4 line: Advanced backcross line in BC_2F_4 generation. BC_1F_1, BC_2F_1 plant: Number of backcrossed plants for development the advanced backcross populations. n [AA]: Number of markers showing the cultivar genotype (Triso). n [Aa]: Number of markers showing the heterozygous genotype. n [aa]: Number of markers showing the exotic genotype (Syn-84). [aa] (%): Proportion of exotic genotype in every BC_2F_4 line. Ambiguous genotype (%): Proportion of ambiguous genotyped alleles. DS: Distorted segregation specified the deviation from the expected genotype distribution of cultivar (86%) to heterozygous (3%) to exotic (11%) genotypes were computed with Chi-square test (** P = 0.01, * P = 0.05, n.s. P > 0.01).

Appendix 2: Family structure and distribution of genotypes in D84, determined of 106 markers for 176 BC_2F_4 lines.

BC_2F_4 line	BC_1F_1 plant	BC_2F_1 plant	n [AA]	n [Aa]	n [aa]	[aa] (%)	Ambiguous genotype (%)	DS
Dev 001	1	1	84	6	7	10.3	8.5	n.s.
Dev 002	1	1	74	6	19	22.2	6.6	**
Dev 003	1	2	78	4	18	20.0	5.7	n.s.
Dev 004	1	3	76	4	19	21.2	6.6	*
Dev 005	2	4	87	1	10	10.7	7.5	n.s.
Dev 006	2	5	78	2	17	18.6	8.5	n.s.
Dev 007	2	5	74	1	21	22.4	9.4	**
Dev 008	2	6	62	22	10	22.3	11.3	**
Dev 009	2	7	73	7	15	19.5	10.4	*
Dev 010	2	8	66	8	25	29.3	6.6	**
Dev 011	3	9	85	4	12	13.9	4.7	n.s.
Dev 012	3	10	81	4	13	15.3	7.5	n.s.
Dev 013	3	11	88	5	4	6.7	8.5	n.s.
Dev 014	3	12	77	10	11	16.3	7.5	**
Dev 015	3	12	67	3	18	22.2	17.0	**
Dev 016	3	12	79	2	13	14.9	11.3	n.s.
Dev 017	3	12	80	7	13	16.5	5.7	n.s.

BC_2F_4 line	BC_1F_1 plant	BC_2F_1 plant	n [AA]	n [Aa]	n [aa]	[aa] (%)	Ambiguous genotype (%)	DS
Dev 018	3	13	87	4	7	9.2	7.5	n.s.
Dev 019	3	13	92	4	4	6.0	5.7	n.s.
Dev 020	3	14	92	3	5	6.5	5.7	n.s.
Dev 021	4	15	84	4	12	14.0	5.7	n.s.
Dev 022	4	16	85	3	11	12.6	6.6	n.s.
Dev 023	4	17	81	3	14	15.8	7.5	n.s.
Dev 024	4	17	84	4	9	11.3	8.5	n.s.
Dev 025	5	18	83	12	3	9.2	7.5	**
Dev 026	5	19	85	2	10	11.3	8.5	n.s.
Dev 027	5	20	69	6	16	20.9	14.2	*
Dev 028	5	20	75	5	9	12.9	16.0	n.s.
Dev 029	5	21	80	8	8	12.5	9.4	**
Dev 030	5	21	76	3	8	10.9	17.9	n.s.
Dev 031	5	22	65	4	20	24.7	16.0	*
Dev 032	5	23	81	5	10	13.0	9.4	n.s.
Dev 033	5	23	74	5	11	15.0	15.1	n.s.
Dev 035	6	24	85	5	9	11.6	6.6	n.s.
Dev 036	6	25	90	3	4	5.7	8.5	n.s.
Dev 034	6	26	76	12	12	18.0	5.7	*
Dev 037	7	27	78	4	15	17.5	8.5	n.s.
Dev 039	7	28	83	8	6	17.7	9.4	n.s.
Dev 040	7	28	77	4	15	9.6	6.6	n.s.
Dev 041	7	29	88	3	8	7.5	5.7	n.s.
Dev 042	7	30	90	5	5	24.0	7.5	*
Dev 043	8	31	72	5	21	23.0	7.5	*
Dev 044	8	31	70	11	17	22.5	5.7	*
Dev 045	8	31	74	7	19	15.2	6.6	n.s.
Dev 046	8	32	82	4	13	14.1	9.4	n.s.
Dev 047	8	33	79	7	10	11.3	8.5	n.s.
Dev 048	8	34	84	4	9	8.5	5.7	*
Dev 049	8	34	88	7	5	14.9	8.5	n.s.
Dev 050	8	34	79	7	11	14.7	19.8	n.s.
Dev 051	8	35	70	5	10	14.0	22.6	n.s.
Dev 052	8	36	70	1	11	14.7	10.4	n.s.
Dev 053	8	36	78	6	11	4.6	8.5	*
Dev 054	9	37	92	1	4	6.3	32.1	n.s.
Dev 055	9	38	67	1	4	7.8	9.4	n.s.
Dev 056	9	39	87	3	6	15.3	10.4	n.s.
Dev 057	9	40	79	3	13	10.8	12.3	n.s.
Dev 058	9	40	82	2	9	6.7	8.5	n.s.
Dev 038	9	41	90	1	6	10.3	8.5	*
Dev 059	9	42	96	1	2	2.5	6.6	*
Dev 061	10	44	74	5	12	15.9	14.2	n.s.
Dev 062	10	44	89	2	8	9.1	6.6	n.s.
Dev 063	10	45	91	3	6	7.5	5.7	n.s.
Dev 064	10	46	84	2	8	9.6	11.3	n.s.
Dev 065	10	46	78	6	10	13.8	11.3	n.s.
Dev 066	10	46	85	5	11	13.4	4.7	n.s.
Dev 067	10	47	86	5	6	8.8	8.5	n.s.
Dev 060	10	43	80	2	14	15.6	9.4	n.s.
Dev 068	10	47	72	7	11	16.1	15.1	*
Dev 069	10	48	90	2	6	7.1	7.5	n.s.
Dev 070	10	48	83	1	14	14.8	7.5	n.s.
Dev 071	10	48	81	1	6	7.4	17.0	n.s.
Dev 072	11	49	78	11	8	13.9	8.5	*
Dev 073	11	50	86	4	7	9.3	8.5	n.s.
Dev 074	11	51	83	3	10	12.0	9.4	n.s.
Dev 075	11	52	76	7	13	17.2	9.4	*
Dev 076	11	53	76	3	18	20.1	8.5	n.s.
Dev 077	12	54	85	5	9	11.6	6.6	n.s.
Dev 078	12	55	85	2	6	7.5	12.3	n.s.
Dev 079	12	55	83	2	7	8.7	13.2	n.s.
Dev 080	12	56	84	2	11	12.4	8.5	n.s.
Dev 081	12	57	83	5	9	11.9	8.5	n.s.
Dev 082	13	58	84	5	9	11.7	7.5	n.s.

BC_2F_4 line	BC_1F_1 plant	BC_2F_1 plant	n [AA]	n [Aa]	n [aa]	[aa] (%)	Ambiguous genotype (%)	DS
Dev 083	13	59	88	4	6	8.2	7.5	n.s.
Dev 084	14	60	86	0	10	10.4	9.4	n.s.
Dev 085	14	60	80	11	4	10.0	10.4	*
Dev 086	14	61	83	2	13	14.3	7.5	n.s.
Dev 087	14	62	82	5	11	13.8	7.5	n.s.
Dev 088	14	63	89	5	3	5.7	8.5	*
Dev 089	14	64	79	0	11	12.2	15.1	n.s.
Dev 090	14	64	82	2	13	14.4	8.5	n.s.
Dev 103	15	65	77	4	9	17.2	12.3	n.s.
Dev 093	15	65	84	4	5	16.2	6.6	n.s.
Dev 094	15	66	82	2	15	13.9	8.5	n.s.
Dev 095	15	66	81	5	11	14.8	7.5	n.s.
Dev 096	15	67	80	7	11	16.5	17.0	n.s.
Dev 097	15	67	73	1	14	20.2	16.0	*
Dev 098	15	67	70	2	17	19.5	22.6	n.s.
Dev 099	15	68	64	4	14	11.3	24.5	n.s.
Dev 100	15	68	70	2	8	10.3	40.6	n.s.
Dev 101	15	69	55	3	5	21.7	15.1	*
Dev 102	16	70	68	5	17	19.9	17.0	n.s.
Dev 091	16	71	69	3	16	12.2	15.1	n.s.
Dev 104	16	71	75	4	14	12.0	21.7	n.s.
Dev 105	16	72	72	2	9	14.5	12.3	n.s.
Dev 106	16	72	79	1	13	22.0	12.3	*
Dev 108	16	73	71	3	19	21.9	16.0	*
Dev 092	16	74	68	3	18	7.5	12.3	n.s.
Dev 109	17	76	74	2	16	12.8	18.9	n.s.
Dev 111	17	75	72	6	8	18.1	11.3	n.s.
Dev 112	18	77	76	2	16	12.9	12.3	n.s.
Dev 113	18	78	78	6	9	11.8	12.3	n.s.
Dev 114	18	79	79	6	8	11.7	15.1	n.s.
Dev 115	19	80	77	5	8	7.7	14.2	n.s.
Dev 116	19	81	83	2	6	10.6	19.8	*
Dev 110	19	82	70	12	3	18.5	13.2	n.s.
Dev 117	19	83	81	1	10	11.4	13.2	n.s.
Dev 118	19	83	78	1	8	9.8	17.9	n.s.
Dev 119	19	84	79	3	8	10.6	15.1	n.s.
Dev 120	19	85	54	3	4	9.0	42.5	n.s.
Dev 122	19	86	77	4	11	16.1	15.1	n.s.
Dev 123	20	87	73	5	12	21.4	14.2	*
Dev 124	20	88	70	3	18	21.1	15.1	*
Dev 125	20	88	69	4	17	23.9	13.2	*
Dev 126	20	88	69	2	21	10.9	13.2	n.s.
Dev 127	20	89	81	2	9	16.9	16.0	*
Dev 128	20	90	74	0	15	18.8	12.3	n.s.
Dev 129	20	90	74	3	16	5.4	13.2	n.s.
Dev 130	20	91	86	2	4	17.0	11.3	n.s.
Dev 121	20	92	75	6	13	14.1	13.2	n.s.
Dev 131	20	93	80	3	10	12.4	12.3	n.s.
Dev 132	20	93	66	7	20	25.3	12.3	*
Dev 133	20	94	40	2	10	21.2	50.9	*
Dev 134	20	94	80	2	9	11.0	14.2	n.s.
Dev 135	20	94	77	2	12	14.3	14.2	n.s.
Dev 136	20	94	81	3	10	12.2	11.3	n.s.
Dev 137	21	95	79	4	11	13.8	11.3	n.s.
Dev 138	21	95	73	3	14	17.2	15.1	n.s.
Dev 139	21	96	75	3	5	7.8	21.7	n.s.
Dev 140	21	96	84	3	7	9.0	11.3	n.s.
Dev 141	21	97	88	2	4	5.3	11.3	n.s.
Dev 142	22	98	79	1	11	12.6	14.2	n.s.
Dev 143	22	99	74	3	11	14.2	17.0	n.s.
Dev 144	22	100	71	6	17	21.3	11.3	*
Dev 145	22	100	80	3	8	10.4	14.2	n.s.
Dev 146	23	101	75	7	11	15.6	12.3	*
Dev 147	23	101	56	1	14	20.4	33.0	*
Dev 148	23	102	68	3	13	17.3	20.8	n.s.

BC_2F_4 line	BC_1F_1 plant	BC_2F_1 plant	n [AA]	n [Aa]	n [aa]	[aa] (%)	Ambiguous genotype (%)	DS
Dev 149	23	102	79	2	6	8.0	17.9	n.s.
Dev 150	23	103	79	6	6	9.9	14.2	n.s.
Dev 151	23	104	79	0	13	14.1	13.2	n.s.
Dev 152	23	105	70	5	19	22.9	11.3	*
Dev 153	23	106	77	4	8	11.2	16.0	n.s.
Dev 157	24	109	85	3	5	7.0	12.3	n.s.
Dev 158	24	109	65	2	7	10.8	30.2	n.s.
Dev 159	24	110	77	4	13	16.0	11.3	n.s.
Dev 160	24	111	72	5	9	13.4	18.9	n.s.
Dev 154	24	107	68	3	7	10.9	26.4	n.s.
Dev 155	24	108	78	2	8	10.2	17.0	n.s.
Dev 161	24	112	71	4	12	16.1	17.9	n.s.
Dev 156	24	108	74	6	9	13.5	16.0	n.s.
Dev 162	25	113	71	7	13	18.1	14.2	*
Dev 163	25	113	63	3	13	18.4	25.5	n.s.
Dev 164	25	114	83	2	7	8.7	13.2	n.s.
Dev 165	25	114	72	0	6	7.7	26.4	n.s.
Dev 166	25	115	76	1	17	18.6	11.3	*
Dev 167	25	116	85	1	7	8.1	12.3	n.s.
Dev 168	25	117	81	2	8	9.9	14.2	n.s.
Dev 169	25	117	84	3	2	3.9	16.0	*
Dev 170	26	118	88	1	3	3.8	13.2	*
Dev 171	27	119	81	2	7	8.9	15.1	n.s.
Dev 172	27	119	70	3	8	11.7	23.6	n.s.
Dev 173	27	120	84	2	7	8.6	12.3	n.s.
Dev 174	27	121	76	2	16	18.1	11.3	n.s.
Dev 175	27	121	79	1	11	12.6	14.2	n.s.
Dev 176	27	122	75	4	11	14.4	15.1	n.s.
Dev 177	27	123	74	4	6	9.5	20.8	n.s.
Sum	27	123	13,702	687	1,863			44
Mean			77.9	3.9	10.6	13.6	12.9	

Gloss based on Appendix 1.

Appendix 3: Summary of 451 markers evaluated in polymorphic between the cross parents (Triso, Devon, Syn-84) of populations T84 and D84, arranged according to chromosome position.

Marker	Reference	Chr.	Pos. (cM)	Specification	Genotyped	For analysis
Xgwm136	Röder et al. (1998)	1A	12	Artificial fragments		
Xcfa2226	Sourdille et al. (2001)	1A	24	Not amplified		
Xgwm33	Röder et al. (1998)	1A	27	Multiple loci		
Xbarc263	Song et al. (2005)	1A	29	Artificial fragments		
Xgwm357	Röder et al. (1998)	1A	52	Polymorphic	x	x
Xgwm164	Röder et al. (1998)	1A	56	Polymorphic	x	x
Xbarc148	Song et al. (2005)	1A	57	Multiple loci	x	
Xgwm135	Röder et al. (1998)	1A	61	Artificial fragments		
Xwmc312	Gupta et al. (2002)	1A	69	Without exotic fragment		
Xgwm497	Röder et al. (1998)	1A	86	Multiple loci		
Xwmc716	Gupta et al. (2002)	1A	91	Artificial fragments	x	
Xbarc158	Song et al. (2005)	1A	114	Artificial fragments		
Xbarc145	Song et al. (2005)	1A	116	Multiple loci	x	
Xbarc213	Song et al. (2005)	1A	125	Monomorphic		
Xgwm99	Röder et al. (1998)	1A	126	Polymorphic	x	x
Xbarc194	Song et al. (2005)	1B	8	Polymorphic	x	x
Xgwm608	Röder et al. (1998)	1B	12	Multiple loci		
Xgwm550	Röder et al. (1998)	1B	14	Artificial fragments		
Xbarc128	Song et al. (2005)	1B	20	Multiple loci	x	
Xgwm264	Röder et al. (1998)	1B	21	Multiple loci		
Xbarc8	Song et al. (2005)	1B	25	Monomorphic		
Xgwm413	Röder et al. (1998)	1B	26	Polymorphic	x	x
Xgwm133	Röder et al. (1998)	1B	28	Multiple loci		
Xgwm494	Röder et al. (1998)	1B	30	Multiple loci		
Xgwm131	Röder et al. (1998)	1B	31	Multiple loci		

Marker	Reference	Chr.	Pos. (cM)	Specification	Genotyped	For analysis
Xgwm498	Röder et al. (1998)	1B	31	Polymorphic	x	x
Xgwm273	Röder et al. (1998)	1B	33	Multiple loci		
Xgwm18	Röder et al. (1998)	1B	34	Polymorphic	x	x
Xgwm11	Röder et al. (1998)	1B	34	Multiple loci	x	
Xgwm582	Röder et al. (1998)	1B	37	Artificial fragments		
Xgwm374	Röder et al. (1998)	1B	38	Multiple loci	x	
Xwmc416	Gupta et al. (2002)	1B	44	Monomorphic		
Xwmc134	Gupta et al. (2002)	1B	47	Not amplified		
Xgwm403	Röder et al. (1998)	1B	50	Multiple loci		
Xgwm274	Röder et al. (1998)	1B	61	Multiple loci		
Xgwm153	Röder et al. (1998)	1B	61	Artificial fragments		
Xbarc81	Song et al. (2005)	1B	62	Not amplified		
Xbarc188	Song et al. (2005)	1B	63	Artificial fragments		
Xgwm268	Röder et al. (1998)	1B	64	Artificial fragments	x	
Xgwm124	Röder et al. (1998)	1B	64	Artificial fragments	x	
Xwmc44	Gupta et al. (2002)	1B	92	Polymorphic	x	x
Xwmc367	Gupta et al. (2002)	1B	103	Not amplified		
Xbarc80	Song et al. (2005)	1B	106	Not amplified		
Xgwm259	Röder et al. (1998)	1B	107	Monomorphic		
Xgwm140	Röder et al. (1998)	1B	111	Monomorphic		
Xgwm147	Röder et al. (1998)	1D	0	Monomorphic		
Xbarc149	Song et al. (2005)	1D	14	Not amplified		
Xwmc147	Gupta et al. (2002)	1D	16	Polymorphic	x	x
Xgdm126	Pestova et al. (2000)	1D	19	Without exotic fragment		
Xwmc222	Gupta et al. (2002)	1D	30	Artificial fragments	x	
Xbarc152	Song et al. (2005)	1D	32	Not amplified		
Xgwm106	Röder et al. (1998)	1D	36	Artificial fragments	x	
Xgwm191	Röder et al. (1998)	1D	45	Multiple loci		
Xgwm337	Röder et al. (1998)	1D	48	Polymorphic	x	x
Xbarc99	Song et al. (2005)	1D	51	Not amplified		
Xgwm458	Röder et al. (1998)	1D	55	Polymorphic	x	x
Xbarc169	Song et al. (2005)	1D	58	Not amplified		
Xgwm642	Röder et al. (1998)	1D	75	Polymorphic	x	x
Xcfd63	Sourdille et al. (2001)	1D	84	Monomorphic		
Xbarc66	Song et al. (2005)	1D	92	Artificial fragments		
Xbarc271	Song et al. (2005)	1D	96	Not amplified		
Xbarc346	Song et al. (2005)	1D	106	Artificial fragments		
Xgwm232	Röder et al. (1998)	1D	107	Polymorphic	x	x
Xgdm111	Pestova et al. (2000)	1D	116	Polymorphic	x	x
Xbarc62	Song et al. (2005)	1D	117	Artificial fragments		
Xbarc212	Song et al. (2005)	2A	0	Polymorphic	x	x
Xgwm614	Röder et al. (1998)	2A	10	Multiple loci		
Xgwm636	Röder et al. (1998)	2A	11	Monomorphic		
Xwmc667	Gupta et al. (2002)	2A	12	Artificial fragments		
Xgwm296	Röder et al. (1998)	2A	13	Multiple loci		
Xgwm512	Röder et al. (1998)	2A	16	Monomorphic		
Xgwm359	Röder et al. (1998)	2A	24	Artificial fragments	x	
Xwmc598	Gupta et al. (2002)	2A	29	Polymorphic		
Xgwm71	Röder et al. (1998)	2A	30	Multiple loci		
Xwmc522	Gupta et al. (2002)	2A	45	Polymorphic		
Xgwm122	Röder et al. (1998)	2A	51	Multiple loci		
Xgwm339	Röder et al. (1998)	2A	51	Monomorphic		
Xgwm515	Röder et al. (1998)	2A	52	Multiple loci		
Xgwm425	Röder et al. (1998)	2A	52	Artificial fragments		
Xgwm10	Röder et al. (1998)	2A	52	Multiple loci		
Xgwm448	Röder et al. (1998)	2A	52	Artificial fragments		
Xgwm275	Röder et al. (1998)	2A	52	Artificial fragments		
Xgwm249	Röder et al. (1998)	2A	53	Multiple loci		
Xgwm95	Röder et al. (1998)	2A	53	Polymorphic	x	x
Xgwm558	Röder et al. (1998)	2A	54	Polymorphic	x	x
Xgwm473	Röder et al. (1998)	2A	57	Multiple loci		
Xgwm328	Röder et al. (1998)	2A	58	Artificial fragments		
Xgwm372	Röder et al. (1998)	2A	60	Monomorphic		
Xbarc5	Song et al. (2005)	2A	63	Multiple loci	x	
Xgwm47	Röder et al. (1998)	2A	66	Multiple loci		

Marker	Reference	Chr.	Pos. (cM)	Specification	Genotyped	For analysis
Xgwm445	Röder et al. (1998)	2A	68	Polymorphic	x	x
Xgwm312	Röder et al. (1998)	2A	74	Monomorphic		
Xgwm294	Röder et al. (1998)	2A	76	Polymorphic	x	x
Xgwm356	Röder et al. (1998)	2A	126	Polymorphic	x	x
Xbarc76	Song et al. (2005)	2A	131	Multiple loci		
Xbarc279	Song et al. (2005)	2A	138	Polymorphic	x	x
Xwmc658	Gupta et al. (2002)	2A	140	Without exotic fragment	x	
Xgwm382	Röder et al. (1998)	2A	140	Multiple loci		
Xgwm311	Röder et al. (1998)	2A	143	Multiple loci		
Xbarc45	Song et al. (2005)	2B	4	Multiple loci		
Xwmc661	Gupta et al. (2002)	2B	5	Artificial fragments		
Xgwm210	Röder et al. (1998)	2B	6	Multiple loci		
Xbarc318	Song et al. (2005)	2B	21	Without exotic fragment		
Xwmc154	Gupta et al. (2002)	2B	29	Without exotic fragment		
Xgwm257	Röder et al. (1998)	2B	37	Artificial fragments		
Xgwm429	Röder et al. (1998)	2B	40	Artificial fragments		
Xbarc349	Song et al. (2005)	2B	42	Artificial fragments		
Xgwm148	Röder et al. (1998)	2B	47	Polymorphic	x	x
Xgwm410	Röder et al. (1998)	2B	49	Multiple loci		
Xbarc13	Song et al. (2005)	2B	50	Monomorphic		
Xbarc183	Song et al. (2005)	2B	52	Multiple loci		
Xwmc272	Gupta et al. (2002)	2B	57	Not amplified		
Xgwm630	Röder et al. (1998)	2B	58	Not amplified		
Xcfa2278	Sourdille et al. (2001)	2B	62	Monomorphic		
Xgwm132	Röder et al. (1998)	2B	63	Multiple loci		
Xgwm319	Röder et al. (1998)	2B	63	Artificial fragments		
Xwmc477	Gupta et al. (2002)	2B	63	Polymorphic		
Xgwm271	Röder et al. (1998)	2B	65	Multiple loci		
Xgwm55	Röder et al. (1998)	2B	66	Multiple loci		
Xgwm129	Röder et al. (1998)	2B	69	Multiple loci		
Xgwm388	Röder et al. (1998)	2B	72	Artificial fragments		
Xbarc101	Song et al. (2005)	2B	76	Monomorphic		
Xgwm120	Röder et al. (1998)	2B	79	Polymorphic	x	x
Xgwm16	Röder et al. (1998)	2B	83	Multiple loci		
Xgwm501	Röder et al. (1998)	2B	85	Monomorphic		
Xwmc332	Gupta et al. (2002)	2B	93	Polymorphic	x	x
Xwmc361	Gupta et al. (2002)	2B	101	Polymorphic		
Xwmc317	Gupta et al. (2002)	2B	106	Artificial fragments		
Xwmc356	Gupta et al. (2002)	2B	117	Not amplified		
Xgwm526	Röder et al. (1998)	2B	120	Artificial fragments		
Xcfd56	Sourdille et al. (2001)	2D	7	Not amplified		
Xbarc90	Song et al. (2005)	2D	10	Monomorphic		
Xwmc503	Gupta et al. (2002)	2D	21	Polymorphic	x	x
Xgwm261	Röder et al. (1998)	2D	23	Monomorphic		
Xwmc112	Gupta et al. (2002)	2D	28	Not amplified		
Xgwm455	Röder et al. (1998)	2D	32	Polymorphic	x	x
Xgwm484	Röder et al. (1998)	2D	41	Artificial fragments		
Xbarc168	Song et al. (2005)	2D	47	Artificial fragments		
Xgwm102	Röder et al. (1998)	2D	48	Polymorphic	x	x
Xwmc18	Gupta et al. (2002)	2D	64	Polymorphic	x	x
Xgwm30	Röder et al. (1998)	2D	64	Multiple loci		
Xgwm358	Röder et al. (1998)	2D	66	Multiple loci		
Xgwm157	Röder et al. (1998)	2D	73	Polymorphic	x	x
Xgwm539	Röder et al. (1998)	2D	91	Polymorphic	x	x
Xgwm349	Röder et al. (1998)	2D	93	Polymorphic	x	x
Xcfd239	Sourdille et al. (2001)	2D	94	Monomorphic		
Xbarc219	Song et al. (2005)	2D	99	Artificial fragments		
Xgwm320	Röder et al. (1998)	2D	101	Polymorphic	x	x
Xbarc59	Song et al. (2005)	2D	101	Multiple loci	x	
Xgwm301	Röder et al. (1998)	2D	107	Artificial fragments		
Xbarc57	Song et al. (2005)	3A	0	Polymorphic	x	x
Xbarc294	Song et al. (2005)	3A	10	Artificial fragments		
Xbarc12	Song et al. (2005)	3A	10	Not amplified		
Xgwm369	Röder et al. (1998)	3A	14	Artificial fragments	x	
Xbarc086	Song et al. (2005)	3A	32	Artificial fragments		

Marker	Reference	Chr.	Pos. (cM)	Specification	Genotyped	For analysis
Xgwm2	Röder et al. (1998)	3A	37	Multiple loci		
Xgwm32	Röder et al. (1998)	3A	44	Monomorphic		
Xwmc664	Gupta et al. (2002)	3A	45	Polymorphic		
Xgwm5	Röder et al. (1998)	3A	45	Polymorphic	x	x
Xgwm4	Röder et al. (1998)	3A	45	Multiple loci		
Xgwm674	Röder et al. (1998)	3A	46	Monomorphic		
Xbarc324	Song et al. (2005)	3A	46	Artificial fragments		
Xwmc428	Gupta et al. (2002)	3A	56	Without exotic fragment		
Xcfa2262	Sourdille et al. (2001)	3A	64	Polymorphic		
Xgwm162	Röder et al. (1998)	3A	67	Multiple loci	x	
Xwmc559	Gupta et al. (2002)	3A	83	Polymorphic	x	x
Xbarc1060	Song et al. (2005)	3A	85	Monomorphic		
Xgwm155	Röder et al. (1998)	3A	85	Artificial fragments	x	
Xcfa2076	Sourdille et al. (2001)	3A	98	Not amplified		
Xwmc594	Gupta et al. (2002)	3A	105	Without exotic fragment		
Xgwm480	Röder et al. (1998)	3A	116	Polymorphic	x	x
Xbarc75	Song et al. (2005)	3B	0	Polymorphic	x	x
Xbarc180	Song et al. (2005)	3B	0	Multiple loci		
Xgwm389	Röder et al. (1998)	3B	1	Artificial fragments	x	
Xgwm533	Röder et al. (1998)	3B	6	Multiple loci		
Xbarc133	Song et al. (2005)	3B	7	Polymorphic	x	x
Xgwm493	Röder et al. (1998)	3B	12	Polymorphic	x	x
Xbarc087	Song et al. (2005)	3B	14	Multiple loci		
Xbarc102	Song et al. (2005)	3B	30	Artificial fragments	x	
Xcfd28	Sourdille et al. (2001)	3B	35	Artificial fragments		
Xwmc78	Gupta et al. (2002)	3B	51	Without exotic fragment	x	
Xgwm566	Röder et al. (1998)	3B	54	Without exotic fragment	x	
Xwmc231	Gupta et al. (2002)	3B	56	Polymorphic		
Xgwm284	Röder et al. (1998)	3B	56	Not amplified		
Xgwm72	Röder et al. (1998)	3B	57	Monomorphic		
Xbarc68	Song et al. (2005)	3B	57	Multiple loci		
Xbarc73	Song et al. (2005)	3B	60	Polymorphic	x	x
Xgwm285	Röder et al. (1998)	3B	61	Monomorphic		
Xgwm644	Röder et al. (1998)	3B	63	Multiple loci		
Xgwm376	Röder et al. (1998)	3B	63	Artificial fragments		
Xgwm77	Röder et al. (1998)	3B	65	Artificial fragments		
Xbarc139	Song et al. (2005)	3B	66	Polymorphic	x	x
Xgwm107	Röder et al. (1998)	3B	68	Multiple loci	x	
Xbarc164	Song et al. (2005)	3B	70	Not amplified		
Xwmc291	Gupta et al. (2002)	3B	90	Without exotic fragment		
Xgwm108	Röder et al. (1998)	3B	94	Artificial fragments		
Xbarc84	Song et al. (2005)	3B	97	Artificial fragments		
Xbarc206	Song et al. (2005)	3B	97	Multiple loci		
Xbarc77	Song et al. (2005)	3B	111	Polymorphic	x	x
Xgwm299	Röder et al. (1998)	3B	123	Monomorphic		
Xgwm114	Röder et al. (1998)	3B	125	Multiple loci		
Xgwm547	Röder et al. (1998)	3B	138	Artificial fragments		
Xgwm181	Röder et al. (1998)	3B	139	Artificial fragments		
Xgwm247	Röder et al. (1998)	3B	142	Artificial fragments		
Xgwm340	Röder et al. (1998)	3B	148	Polymorphic	x	x
Xgwm183	Röder et al. (1998)	3D	0	Artificial fragments		
Xcfd55	Sourdille et al. (2001)	3D	8	Monomorphic		
Xgwm161	Röder et al. (1998)	3D	13	Polymorphic	x	x
Xgwm314	Röder et al. (1998)	3D	18	Monomorphic		
Xgwm383	Röder et al. (1998)	3D	20	Polymorphic	x	x
Xgwm664	Röder et al. (1998)	3D	21	Multiple loci	x	
Xbarc52	Song et al. (2005)	3D	23	Monomorphic		
Xgwm52	Röder et al. (1998)	3D	30	Polymorphic	x	x
Xgwm456	Röder et al. (1998)	3D	30	Monomorphic		
Xgwm341	Röder et al. (1998)	3D	30	Artificial fragments		
Xbarc125	Song et al. (2005)	3D	34	Polymorphic		
Xgwm645	Röder et al. (1998)	3D	35	Artificial fragments		
Xgwm3	Röder et al. (1998)	3D	43	Polymorphic	x	x
Xgdm72	Pestova et al. (2000)	3D	62	Artificial fragments		
Xbarc323	Song et al. (2005)	3D	80	Polymorphic	x	x

APPENDIX

Marker	Reference	Chr.	Pos. (cM)	Specification	Genotyped	For analysis
Xwmc516	Gupta et al. (2002)	4A	2	Polymorphic		
Xgwm165	Röder et al. (1998)	4A	2	Multiple loci		
Xgwm601	Röder et al. (1998)	4A	9	Monomorphic		
Xgwm44	Röder et al. (1998)	4A	10	Multiple loci	x	
Xgwm610	Röder et al. (1998)	4A	12	Polymorphic	x	x
Xgwm397	Röder et al. (1998)	4A	18	Polymorphic	x	x
Xbarc170	Song et al. (2005)	4A	27	Artificial fragments		
Xgwm637	Röder et al. (1998)	4A	37	Artificial fragments		
Xwmc468	Gupta et al. (2002)	4A	38	Polymorphic	x	x
Xgwm565	Röder et al. (1998)	4A	47	Multiple loci		
Xbarc1047	Song et al. (2005)	4A	56	Artificial fragments		
Xbarc70	Song et al. (2005)	4A	71	Multiple loci	x	
Xbarc78	Song et al. (2005)	4A	71	Artificial fragments		
Xgwm160	Röder et al. (1998)	4A	79	Polymorphic	x	x
Xbarc327	Song et al. (2005)	4A	80	Polymorphic	x	x
Xwmc219	Gupta et al. (2002)	4A	88	Not amplified		
Xwmc710	Gupta et al. (2002)	4B	11	Not amplified		
Xbarc20	Song et al. (2005)	4B	22	Polymorphic	x	x
Xgwm540	Röder et al. (1998)	4B	22	Multiple loci		
Xgwm368	Röder et al. (1998)	4B	22	Not amplified		
Xbarc1096	Song et al. (2005)	4B	24	Artificial fragments		
Xbarc227	Song et al. (2005)	4B	24	Polymorphic		
Xgwm113	Röder et al. (1998)	4B	25	Polymorphic	x	x
Xbarc25	Song et al. (2005)	4B	25	Not amplified		
Xgwm66	Röder et al. (1998)	4B	25	Multiple loci		
Xgwm513	Röder et al. (1998)	4B	27	Artificial fragments	x	
Xgwm112	Röder et al. (1998)	4B	28	Multiple loci		
Xgwm192	Röder et al. (1998)	4B	29	Artificial fragments		
Xgwm149	Röder et al. (1998)	4B	31	Polymorphic	x	x
Xgwm495	Röder et al. (1998)	4B	31	Monomorphic		
Xgwm251	Röder et al. (1998)	4B	36	Polymorphic	x	x
Xbarc163	Song et al. (2005)	4B	39	Artificial fragments		
Xgwm6	Röder et al. (1998)	4B	43	Artificial fragments		
Xbarc109	Song et al. (2005)	4B	46	Multiple loci		
Xgwm538	Röder et al. (1998)	4B	49	Not amplified		
Xbarc114	Song et al. (2005)	4B	59	Polymorphic	x	x
Xwmc125	Gupta et al. (2002)	4B	59	Not amplified		
Xwmc285	Gupta et al. (2002)	4D	10	Polymorphic	x	x
Xbarc1118	Song et al. (2005)	4D	10	Polymorphic		
Xbarc217	Song et al. (2005)	4D	27	Polymorphic	x	x
Xwmc720	Gupta et al. (2002)	4D	27	Not amplified		
Xgwm213	Röder et al. (1998)	4D	30	Multiple loci		
Xbarc91	Song et al. (2005)	4D	32	Polymorphic	x	x
Xwmc331	Gupta et al. (2002)	4D	43	Polymorphic	x	x
Xwmc399	Gupta et al. (2002)	4D	54	Polymorphic	x	x
Xcfd84	Sourdille et al. (2001)	4D	67	Polymorphic	x	x
Xbarc1183	Song et al. (2005)	4D	73	Polymorphic		
Xgwm194	Röder et al. (1998)	4D	82	Polymorphic	x	x
Xgwm624	Röder et al. (1998)	4D	89	Polymorphic	x	x
Xgwm609	Röder et al. (1998)	4D	91	Polymorphic	x	x
Xgwm443	Röder et al. (1998)	5A	24	Multiple loci		
Xwmc713	Gupta et al. (2002)	5A	28	Polymorphic	x	x
Xgwm205	Röder et al. (1998)	5A	33	Multiple loci		
Xgdm109	Pestova et al. (2000)	5A	34	Without exotic fragment		
Xgwm154	Röder et al. (1998)	5A	34	Polymorphic	x	x
Xgwm293	Röder et al. (1998)	5A	52	Artificial fragments		
Xgwm415	Röder et al. (1998)	5A	55	Polymorphic	x	x
Xgwm304	Röder et al. (1998)	5A	64	Polymorphic	x	x
Xgwm186	Röder et al. (1998)	5A	64	Polymorphic	x	x
Xbarc165	Song et al. (2005)	5A	65	Artificial fragments		
Xbarc1	Song et al. (2005)	5A	70	Artificial fragments		
Xgwm156	Röder et al. (1998)	5A	72	Artificial fragments		
Xgwm639	Röder et al. (1998)	5A	74	Multiple loci		
Xbarc330	Song et al. (2005)	5A	75	Polymorphic	x	x
Xgwm617	Röder et al. (1998)	5A	76	Multiple loci		

Marker	Reference	Chr.	Pos. (cM)	Specification	Genotyped	For analysis
Xgwm666	Röder et al. (1998)	5A	90	Multiple loci		
Xbarc230	Song et al. (2005)	5A	105	Polymorphic		
Xbarc319	Song et al. (2005)	5A	110	Polymorphic	x	x
Xbarc232	Song et al. (2005)	5A	111	Multiple loci		
Xwmc110	Gupta et al. (2002)	5A	127	Polymorphic		
Xgwm126	Röder et al. (1998)	5A	139	Artificial fragments		
Xgwm179	Röder et al. (1998)	5A	140	Artificial fragments	x	
Xwmc577	Gupta et al. (2002)	5A	142	Monomorphic		
Xgwm595	Röder et al. (1998)	5A	151	Not amplified		
Xwmc727	Gupta et al. (2002)	5A	155	Without exotic fragment		
Xgwm291	Röder et al. (1998)	5A	164	Artificial fragments	x	
Xcfd5	Sourdille et al. (2001)	5B	0	Artificial fragments		
Xwmc773	Gupta et al. (2002)	5B	8	Multiple loci	x	
Xbarc21	Song et al. (2005)	5B	13	Monomorphic		
Xcfd60	Sourdille et al. (2001)	5B	14	Polymorphic	x	x
Xgwm234	Röder et al. (1998)	5B	38	Polymorphic	x	x
Xgdm146	Pestova et al. (2000)	5B	54	Not amplified		
Xgwm159	Röder et al. (1998)	5B	57	Multiple loci		
Xgwm544	Röder et al. (1998)	5B	61	Polymorphic	x	x
Xgwm68	Röder et al. (1998)	5B	64	Multiple loci		
Xgwm67	Röder et al. (1998)	5B	65	Monomorphic		
Xbarc74	Song et al. (2005)	5B	67	Polymorphic		
Xgwm335	Röder et al. (1998)	5B	68	Monomorphic		
Xgwm371	Röder et al. (1998)	5B	73	Artificial fragments	x	
Xgwm499	Röder et al. (1998)	5B	75	Monomorphic		
Xgwm554	Röder et al. (1998)	5B	89	Multiple loci		
Xgwm408	Röder et al. (1998)	5B	117	Artificial fragments		
Xgwm604	Röder et al. (1998)	5B	124	Polymorphic	x	x
Xbarc140	Song et al. (2005)	5B	127	Polymorphic		
Xbarc142	Song et al. (2005)	5B	130	Monomorphic		
Xgdm116	Pestova et al. (2000)	5B	133	Not amplified		
Xwmc508	Gupta et al. (2002)	5B	141	Not amplified		
Xbarc130	Song et al. (2005)	5D	4	Polymorphic	x	x
Xgwm190	Röder et al. (1998)	5D	9	Monomorphic		
Xbarc205	Song et al. (2005)	5D	16	Polymorphic	x	x
Xbarc143	Song et al. (2005)	5D	23	Polymorphic	x	x
Xbarc44	Song et al. (2005)	5D	27	Not amplified		
Xwmc608	Gupta et al. (2002)	5D	28	Artificial fragments		
Xcfd266	Sourdille et al. (2001)	5D	34	Polymorphic	x	x
Xbarc49	Song et al. (2005)	5D	37	Multiple loci		
Xgwm583	Röder et al. (1998)	5D	44	Polymorphic	x	x
Xgwm182	Röder et al. (1998)	5D	50	Polymorphic	x	x
Xbarc347	Song et al. (2005)	5D	55	Polymorphic		
Xgwm174	Röder et al. (1998)	5D	58	Polymorphic	x	x
Xgwm121	Röder et al. (1998)	5D	61	Multiple loci		
Xgwm292	Röder et al. (1998)	5D	65	Monomorphic		
Xgwm212	Röder et al. (1998)	5D	67	Polymorphic	x	x
Xbarc322	Song et al. (2005)	5D	82	Polymorphic	x	x
Xgdm133	Pestova et al. (2000)	5D	84	Artificial fragments		
Xbarc110	Song et al. (2005)	5D	96	Artificial fragments		
Xcfd10	Sourdille et al. (2001)	5D	98	Monomorphic		
Xgwm469	Röder et al. (1998)	5D	110	Multiple loci	x	
Xgwm269	Röder et al. (1998)	5D	118	Artificial fragments		
Xgwm272	Röder et al. (1998)	5D	119	Polymorphic	x	x
Xgwm654	Röder et al. (1998)	5D	121	Artificial fragments		
Xgwm459	Röder et al. (1998)	6A	0	Artificial fragments	x	
Xgwm334	Röder et al. (1998)	6A	2	Artificial fragments		
Xbarc37	Song et al. (2005)	6A	35	Artificial fragments		
Xbarc113	Song et al. (2005)	6A	41	Artificial fragments		
Xbarc3	Song et al. (2005)	6A	44	Not amplified		
Xbarc171	Song et al. (2005)	6A	46	Artificial fragments		
Xgwm570	Röder et al. (1998)	6A	51	Not amplified		
Xwmc553	Gupta et al. (2002)	6A	52	Not amplified		
Xgwm169	Röder et al. (1998)	6A	83	Not amplified		
Xgwm427	Röder et al. (1998)	6A	93	Polymorphic	x	x

Marker	Reference	Chr.	Pos. (cM)	Specification	Genotyped	For analysis
Xwmc621	Gupta et al. (2002)	6A	115	Artificial fragments		
Xgwm613	Röder et al. (1998)	6B	0	Not amplified		
Xwmc486	Gupta et al. (2002)	6B	3	Without exotic fragment	x	
Xwmc487	Gupta et al. (2002)	6B	9	Without exotic fragment		
Xbarc1169	Song et al. (2005)	6B	14	Artificial fragments		
Xwmc104	Gupta et al. (2002)	6B	17	Artificial fragments		
Xgwm705	Röder et al. (1998)	6B	17	Not amplified		
Xgdm113	Pestova et al. (2000)	6B	27	Not amplified		
Xgwm518	Röder et al. (1998)	6B	27	Artificial fragments	x	
Xgwm508	Röder et al. (1998)	6B	32	Artificial fragments		
Xgwm193	Röder et al. (1998)	6B	36	Multiple loci	x	
Xgwm361	Röder et al. (1998)	6B	38	Artificial fragments		
Xgwm88	Röder et al. (1998)	6B	41	Artificial fragments		
Xgwm70	Röder et al. (1998)	6B	42	Monomorphic		
Xbarc198	Song et al. (2005)	6B	44	Polymorphic	x	x
Xbarc127	Song et al. (2005)	6B	47	Multiple loci	x	
Xgwm626	Röder et al. (1998)	6B	48	Polymorphic	x	x
Xbarc24	Song et al. (2005)	6B	55	Polymorphic		
Xgwm219	Röder et al. (1998)	6B	59	Polymorphic	x	x
Xbarc178	Song et al. (2005)	6B	60	Not amplified		
Xbarc134	Song et al. (2005)	6B	82	Monomorphic		
Xcfd49	Sourdille et al. (2001)	6D	0	Not amplified		
Xcfd135	Sourdille et al. (2001)	6D	5	Not amplified		
Xcfd75	Sourdille et al. (2001)	6D	19	Without exotic fragment		
Xcfd42	Sourdille et al. (2001)	6D	24	Polymorphic		
Xcfd132	Sourdille et al. (2001)	6D	35	Polymorphic	x	x
Xbarc54	Song et al. (2005)	6D	47	Not amplified		
Xbarc196	Song et al. (2005)	6D	51	Not amplified		
Xgwm325	Röder et al. (1998)	6D	53	Polymorphic	x	x
Xcfd76	Sourdille et al. (2001)	6D	61	Polymorphic		
Xbarc273	Song et al. (2005)	6D	70	Polymorphic	x	x
Xbarc1121	Song et al. (2005)	6D	80	Polymorphic		
Xbarc96	Song et al. (2005)	6D	92	Polymorphic	x	x
Xgwm233	Röder et al. (1998)	7A	5	Polymorphic	x	x
Xwmc158	Gupta et al. (2002)	7A	5	Not amplified		
Xgwm635	Röder et al. (1998)	7A	7	Multiple loci		
Xgwm350	Röder et al. (1998)	7A	11	Multiple loci		
Xgwm471	Röder et al. (1998)	7A	17	Artificial fragments		
Xwmc479	Gupta et al. (2002)	7A	22	Without exotic fragment	x	
Xgwm60	Röder et al. (1998)	7A	30	Polymorphic	x	x
Xbarc154	Song et al. (2005)	7A	41	Multiple loci		
Xcfa2028	Sourdille et al. (2001)	7A	42	Polymorphic		
Xbarc222	Song et al. (2005)	7A	53	Monomorphic		
Xwmc83	Gupta et al. (2002)	7A	54	Artificial fragments		
Xbarc174	Song et al. (2005)	7A	64	Not amplified		
Xgwm573	Röder et al. (1998)	7A	68	Multiple loci		
Xwmc17	Gupta et al. (2002)	7A	70	Without exotic fragment		
Xgwm260	Röder et al. (1998)	7A	70	Artificial fragments	x	
Xbarc108	Song et al. (2005)	7A	71	Not amplified		
Xwmc139	Gupta et al. (2002)	7A	78	Not amplified		
Xgwm276	Röder et al. (1998)	7A	84	Artificial fragments	x	
Xbarc192	Song et al. (2005)	7A	93	Artificial fragments	x	
Xgwm282	Röder et al. (1998)	7A	100	Monomorphic		
Xgwm332	Röder et al. (1998)	7A	100	Without exotic fragment		
Xgwm63	Röder et al. (1998)	7A	104	Artificial fragments		
Xcfa2019	Sourdille et al. (2001)	7A	107	Polymorphic	x	x
Xbarc275	Song et al. (2005)	7A	144	Polymorphic	x	x
Xwmc323	Gupta et al. (2002)	7B	1	Not amplified		
Xgwm569	Röder et al. (1998)	7B	8	Artificial fragments	x	
Xgwm537	Röder et al. (1998)	7B	35	Polymorphic	x	x
Xgwm400	Röder et al. (1998)	7B	40	Polymorphic	x	x
Xbarc65	Song et al. (2005)	7B	48	Polymorphic	x	x
Xbarc85	Song et al. (2005)	7B	49	Monomorphic		
Xgwm46	Röder et al. (1998)	7B	54	Polymorphic	x	x
Xgwm43	Röder et al. (1998)	7B	57	Monomorphic		

Marker	Reference	Chr.	Pos. (cM)	Specification	Genotyped	For analysis
Xgwm297	Röder et al. (1998)	7B	58	Polymorphic	x	x
Xbarc95	Song et al. (2005)	7B	62	Artificial fragments		
Xgwm333	Röder et al. (1998)	7B	63	Polymorphic	x	x
Xbarc176	Song et al. (2005)	7B	69	Not amplified		
Xbarc278	Song et al. (2005)	7B	77	Polymorphic	x	x
Xgwm302	Röder et al. (1998)	7B	86	Not amplified		
Xwmc723	Gupta et al. (2002)	7B	87	Monomorphic		
Xwmc311	Gupta et al. (2002)	7B	118	Polymorphic	x	x
Xgwm611	Röder et al. (1998)	7B	136	Artificial fragments		
Xgwm577	Röder et al. (1998)	7B	137	Polymorphic	x	x
Xwmc581	Gupta et al. (2002)	7B	138	Artificial fragments		
Xwmc276	Gupta et al. (2002)	7B	142	Polymorphic	x	x
Xbarc32	Song et al. (2005)	7B	142	Not amplified		
Xbarc182	Song et al. (2005)	7B	144	Not amplified		
Xbarc123	Song et al. (2005)	7B	149	Polymorphic	x	x
Xgwm146	Röder et al. (1998)	7B	150	Artificial fragments		
Xgwm344	Röder et al. (1998)	7B	151	Artificial fragments	x	
Xbarc184	Song et al. (2005)	7D	28	Polymorphic	x	x
Xcfd41	Sourdille et al. (2001)	7D	44	Not amplified		
Xgdm88	Pestova et al. (2000)	7D	51	Without exotic fragment		
Xcfd66	Sourdille et al. (2001)	7D	53	Polymorphic	x	x
Xgwm130	Röder et al. (1998)	7D	59	Artificial fragments		
Xbarc352	Song et al. (2005)	7D	66	Without exotic fragment		
Xwmc463	Gupta et al. (2002)	7D	72	Polymorphic		
Xgwm295	Röder et al. (1998)	7D	77	Monomorphic		
Xbarc214	Song et al. (2005)	7D	83	Artificial fragments		
Xgwm111	Röder et al. (1998)	7D	89	Monomorphic		
Xgwm437	Röder et al. (1998)	7D	92	Polymorphic	x	x
Xbarc172	Song et al. (2005)	7D	99	Not amplified		
Xcfd25	Sourdille et al. (2001)	7D	111	Artificial fragments		
Xbarc111	Song et al. (2005)	7D	115	Monomorphic		
Xbarc53	Song et al. (2005)	7D	130	Polymorphic		
Xgwm428	Röder et al. (1998)	7D	136	Polymorphic	x	x
Xgwm37	Röder et al. (1998)	7D	141	Artificial fragments		
Xwmc634	Gupta et al. (2002)	7D	143	Polymorphic	x	x
Xcfd175	Sourdille et al. (2001)	7D	154	Polymorphic	x	x
Total				451	159	117

Marker: Label of SSR marker. Reference: Study, where the marker was described at first. Chr.: Chromosomal location of the marker derived from Somers et al. (2004). Pos.: Position of the marker in cM on chromosome derived from Somers et al. (2004). Specification: Evaluation of the amplified fragments. Genotyped: Marker genotyped in the advanced backcross populations T84 and D84. For analysis: Marker used for calculation of the QTL.

Appendix 4: Genotype data of 94 markers detected in T84, including 223 BC_2F_4 lines and arranged according to chromosome position.

Marker	Reference	Chr.	Pos. (cM)	Bin	n [AA]	n [Aa]	n [aa]	[aa] (%)	Amb. genot. (%)	DS
Xgwm357	Röder et al. (1998)	1A	52	1AL1-0.17-0.61	198	12	10	7.3	1.3	n.s.
Xgwm99	Röder et al. (1998)	1A	126	1AL3-0.61-1.00	200	6	15	8.1	0.9	n.s.
Xbarc194[1]	Song et al. (2005)	1B	8	-	163	14	13	10.5	14.8	*
Xgwm413	Röder et al. (1998)	1B	26	C-1BS10-0.50	20	1	6	24.1	87.9	**
Xgwm498	Röder et al. (1998)	1B	31	C-1BL6-0.32	27	3	5	18.6	84.3	**
Xgwm18	Röder et al. (1998)	1B	34	C-1BS10-0.50	158	21	40	23.1	1.8	**
Xwmc44	Gupta et al. (2002)	1B	92	-	182	3	16	8.7	9.9	n.s.
Xwmc147	Gupta et al. (2002)	1D	16	-	145	11	14	11.5	23.8	n.s.
Xgwm337	Röder et al. (1998)	1D	48	C-1DS3-0.48	181	2	19	9.9	9.4	n.s.
Xgwm458	Röder et al. (1998)	1D	55	C-1DL4-0.18	195	1	22	10.3	2.2	n.s.
Xgwm642	Röder et al. (1998)	1D	75	1DL2-0.41-1.00	192	5	21	10.8	2.2	n.s.
Xgwm232	Röder et al. (1998)	1D	107	1DL2-0.41-1.00	203	6	12	6.8	0.9	n.s.
Xgdm111	Pestsova et al. (2000)	1D	116	-	175	10	18	11.3	9.0	n.s.
Xgwm95	Röder et al. (1998)	2A	53	C-2AS5-0.78	187	5	30	14.6	0.4	n.s.
Xgwm558	Röder et al. (1998)	2A	54	C-2AL1-0.85	166	15	24	15.4	8.1	n.s.
Xgwm294	Röder et al. (1998)	2A	76	C-2AL1-0.85	171	11	34	18.3	3.1	n.s.
Xgwm356	Röder et al. (1998)	2A	126	C-2AL1-0.85	186	5	20	10.7	5.4	n.s.

Marker	Reference	Chr.	Pos. (cM)	Bin	n [AA]	n [Aa]	n [aa]	[aa] (%)	Amb. genot. (%)	DS
Xgwm148	Röder et al. (1998)	2B	47	2BS1-0.53-0.75	160	16	45	24.0	0.9	**
Xgwm120	Röder et al. (1998)	2B	79	2BL2-0.36-0.50	171	12	30	16.9	4.5	n.s.
Xwmc332	Gupta et al. (2002)	2B	93	-	167	5	35	18.1	7.2	n.s.
Xwmc503	Gupta et al. (2002)	2D	21	-	85	4	9	11.2	56.1	n.s.
Xgwm455	Röder et al. (1998)	2D	32	2DS5-0.47-1.00	182	13	23	13.5	2.2	n.s.
Xgwm102	Röder et al. (1998)	2D	48	2DS1-0.33-0.47	190	4	22	11.1	3.1	n.s.
Xwmc18	Gupta et al. (2002)	2D	64	-	194	0	17	8.1	5.4	n.s.
Xgwm157	Röder et al. (1998)	2D	73	2DL3-0.49-0.76	194	6	22	11.3	0.4	n.s.
Xgwm539	Röder et al. (1998)	2D	91	C-2DL3-0.49	174	15	24	14.8	4.5	n.s.
Xgwm349	Röder et al. (1998)	2D	93	C-2DL3-0.49	209	2	6	3.2	2.7	*
Xgwm320	Röder et al. (1998)	2D	101	C-2DL3-0.49	95	0	8	7.8	53.8	n.s.
Xgwm5	Röder et al. (1998)	3A	45	C-3AL3-0.42	195	7	13	7.7	3.6	n.s.
Xgwm480	Röder et al. (1998)	3A	116	C-3AL3-0.42	205	8	10	6.3	0.0	n.s.
Xbarc75	Song et al. (2005)	3B	0	3BS8-0.78-1.00	152	4	18	11.5	22.0	n.s.
Xgwm493	Röder et al. (1998)	3B	12	3BS8-0.78-1.00	202	6	10	6.0	2.2	n.s.
Xbarc73	Song et al. (2005)	3B	60	3BS1-0.33-0.57	206	3	7	3.9	2.7	*
Xbarc77	Song et al. (2005)	3B	111	C-3BL2-0.22	130	15	39	25.3	17.5	**
Xgwm340	Röder et al. (1998)	3B	148	-	196	14	6	6.0	3.1	**
Xgwm161	Röder et al. (1998)	3D	13	3DS6-0.55-1.00	196	5	16	8.5	2.7	n.s.
Xgwm383	Röder et al. (1998)	3D	20	3DL	194	5	16	8.6	3.6	n.s.
Xgwm52	Röder et al. (1998)	3D	30	-	189	6	25	12.7	1.3	n.s.
Xgwm3	Röder et al. (1998)	3D	43	3DL	182	5	33	16.1	1.3	n.s.
Xgwm610	Röder et al. (1998)	4A	12	C-4AS1-0.20	159	17	23	15.8	10.8	**
Xgwm397	Röder et al. (1998)	4A	18	4AL13-0.59-0.66	156	7	23	14.2	16.6	n.s.
Xwmc468	Gupta et al. (2002)	4A	38	-	64	2	19	23.5	61.9	**
Xgwm160	Röder et al. (1998)	4A	79	4AL4-0.80-1.00	191	11	21	11.9	0.0	n.s.
Xgwm113	Röder et al. (1998)	4B	25	C-4BS4-0.37	186	9	22	12.2	2.7	n.s.
Xgwm149	Röder et al. (1998)	4B	31	4BL1-0.86-1.00	201	5	14	7.5	1.3	n.s.
Xgwm251	Röder et al. (1998)	4B	36	4BL1-0.86-1.00	200	4	13	6.9	2.7	n.s.
Xbarc114[1]	Song et al. (2005)	4B	59	-	4	0	5	55.6	96.0	**
Xwmc285	Gupta et al. (2002)	4D	10	-	64	10	8	15.9	63.2	**
Xbarc91	Song et al. (2005)	4D	32	-	78	4	18	20.0	55.2	n.s.
Xwmc331	Gupta et al. (2002)	4D	43	-	196	6	8	5.2	5.8	n.s.
Xwmc399	Gupta et al. (2002)	4D	54	-	177	9	13	8.8	10.8	n.s.
Xcfd84	Sourdille et al. (2001)	4D	67	C-4DL9-0.31	163	15	11	9.8	15.2	**
Xgwm194	Röder et al. (1998)	4D	82	4DL	171	4	27	14.4	9.4	n.s.
Xgwm624	Röder et al. (1998)	4D	89	4DL	185	8	13	8.3	7.6	n.s.
Xgwm609	Röder et al. (1998)	4D	91	4DL	186	10	14	9.0	5.8	n.s.
Xgwm154	Röder et al. (1998)	5A	34	5AS3-0.75-0.98	188	7	13	7.9	6.7	n.s.
Xgwm415	Röder et al. (1998)	5A	55	C-5AS1-0.40	193	2	20	9.8	3.6	n.s.
Xgwm304	Röder et al. (1998)	5A	64	C-5AS1-0.40	196	4	19	9.6	1.8	n.s.
Xbarc319[1]	Song et al. (2005)	5A	110	-	147	12	20	14.5	19.7	n.s.
Xcfd60	Sourdille et al. (2001)	5B	14	-	31	0	5	13.9	83.9	n.s.
Xgwm234	Röder et al. (1998)	5B	38	5BS5-0.71-0.81	186	9	13	8.4	6.7	n.s.
Xgwm544	Röder et al. (1998)	5B	61	5BS8-0.56-0.71	199	5	8	5.0	4.9	n.s.
Xgwm604	Röder et al. (1998)	5B	124	5BL16-0.79-1.00	166	7	17	10.8	14.8	n.s.
Xbarc130	Song et al. (2005)	5D	4	5DS2-0.78-1.00	170	13	35	19.0	2.2	n.s.
Xbarc205[1]	Song et al. (2005)	5D	16	-	164	14	37	20.5	3.2	*
Xbarc143	Song et al. (2005)	5D	23	C-5DS1-0.63	132	12	30	20.7	22.0	**
Xcfd266	Sourdille et al. (2001)	5D	34	-	164	7	35	18.7	7.6	n.s.
Xgwm583	Röder et al. (1998)	5D	44	C-5DL1-0.60	172	12	29	16.4	4.5	n.s.
Xgwm182	Röder et al. (1998)	5D	50	5DL1-0.60-0.74	200	10	12	7.7	0.4	n.s.
Xgwm174	Röder et al. (1998)	5D	58	5DL1-0.60-0.74	163	4	17	10.3	17.5	n.s.
Xgwm212	Röder et al. (1998)	5D	67	5DL5-0.76-1.00	188	9	23	12.5	1.3	n.s.
Xbarc322[1]	Song et al. (2005)	5D	82	-	110	5	9	9.3	44.1	n.s.
Xgwm272	Röder et al. (1998)	5D	119	5DL5-0.76-1.00	199	12	9	6.8	0.9	*
Xgwm427	Röder et al. (1998)	6A	93	6AL8-0.90-1.00	179	10	27	14.8	3.1	n.s.
Xgwm626	Röder et al. (1998)	6B	48	C-6BS5-0.76	179	9	23	13.0	5.4	n.s.
Xgwm219	Röder et al. (1998)	6B	59	6BL5-0.40-1.00	192	10	19	10.9	0.9	n.s.
Xgwm325	Röder et al. (1998)	6D	53	-	188	12	20	11.8	1.3	n.s.
Xbarc273[1]	Song et al. (2005)	6D	70	-	3	0	6	66.7	96.0	**
Xbarc96	Song et al. (2005)	6D	92	-	167	20	30	18.4	2.7	**
Xgwm60	Röder et al. (1998)	7A	30	7AS8-0.45-0.59	176	6	28	14.8	5.8	n.s.

Marker	Reference	Chr.	Pos. (cM)	Bin	n [AA]	n [Aa]	n [aa]	[aa] (%)	Amb. genot. (%)	DS
Xcfa2019	Sourdille et al. (2001)	7A	107	7AL16-0.86-0.90	102	4	17	15.4	44.8	n.s.
Xgwm537	Röder et al. (1998)	7B	35	-	180	3	34	16.4	2.7	n.s.
Xgwm400	Röder et al. (1998)	7B	40	C-7BS1-0.27	175	11	35	18.3	0.9	n.s.
Xgwm46	Röder et al. (1998)	7B	54	7BS1-0.27-1.00	151	11	42	23.3	8.5	**
Xgwm297	Röder et al. (1998)	7B	58	C-7BS1-0.27	174	9	39	19.6	0.4	n.s.
Xwmc311	Gupta et al. (2002)	7B	118	-	184	11	19	11.4	4.0	n.s.
Xgwm577	Röder et al. (1998)	7B	137	7BL10-0.78-1.00	181	14	18	11.7	4.5	n.s.
Xwmc276	Gupta et al. (2002)	7B	142	-	147	1	14	9.0	27.4	n.s.
Xbarc123	Song et al. (2005)	7B	149	-	171	13	22	13.8	7.6	n.s.
Xbarc184	Song et al. (2005)	7D	28	-	160	13	42	22.6	3.6	**
Xgwm437	Röder et al. (1998)	7D	92	C-7DL5-0.30	187	6	22	11.6	3.6	n.s.
Xgwm428	Röder et al. (1998)	7D	136	7DL5-0.30-0.61	182	9	26	14.1	2.7	n.s.
Xwmc634	Gupta et al. (2002)	7D	143	-	62	8	21	27.5	59.2	**
Xcfd175	Sourdille et al. (2001)	7D	154	-	95	10	12	14.5	47.5	**
Sum					15,201	741	1,872			23
Mean					161.7	7.9	19.9	14.0	15.0	

Marker: Label of SSR marker. (1) Marker was not described by Somers et al. (2004) and Sourdille et al. (2004), respectively, estimated position in cM on chromosome by linked SSR marker positions described by Somers et al. (2004) and Song et al. (2005).

Reference: Puplication, where the marker was described at first.

Chr.: Chromosomal location of the marker derived from Somers et al. (2004).

Pos.: Position of the marker in cM on chromosome derived from Somers et al. (2004).

Bin: Marker was assigned to deletion bins described by Sourdille et al. (2004). (-) Marker was not described in bins.

n [AA]: Number of markers showing the cultivar genotype (Triso).

n [Aa]: Number of markers showing the heterozygous genotype.

n [aa]: Number of markers showing the exotic genotype (Syn-84).

[aa] (%): Proportion of exotic genotype in every BC2F4 line.

Amb. geno. (%): Ambiguous genotype.

DS: Distorted segregation specified the deviation from the expected genotype distribution of cultivar (86%) to heterozygous (3%) to exotic (11%) genotypes were computed with Chi-square test (** P = 0.01, *P = 0.05, n.s. P > 0.01).

Appendix 5: Genotype data of 106 markers detected in D84, including 176 BC_2F_4 lines and arranged according to chromosome position.

Marker	Reference	Chr.	Pos. (cM)	Bin	n [AA]	n [Aa]	n [aa]	[aa] (%)	Amb. geno. (%)	DS
Xgwm357	Röder et al. (1998)	1A	52	1AL1-0.17-0.61	145	11	18	13.5	1.1	n.s.
Xgwm164	Röder et al. (1998)	1A	56	C-1AL1-0.17	140	8	18	13.3	5.7	n.s.
Xgwm99	Röder et al. (1998)	1A	126	1AL3-0.61-1.00	146	6	20	13.4	2.3	n.s.
Xbarc194[1]	Song et al. (2005)	1B	8	-	134	15	23	17.7	2.3	**
Xgwm498	Röder et al. (1998)	1B	31	C-1BL6-0.32	42	3	21	34.1	62.5	**
Xgwm18	Röder et al. (1998)	1B	34	C-1BS10-0.50	126	6	33	21.8	6.3	*
Xwmc44	Gupta et al. (2002)	1B	92	-	66	0	14	17.5	54.5	*
Xwmc147	Gupta et al. (2002)	1D	16	-	59	2	14	20.0	57.4	*
Xgwm337	Röder et al. (1998)	1D	48	C-1DS3-0.48	143	2	21	13.3	5.7	n.s.
Xgwm458	Röder et al. (1998)	1D	55	C-1DL4-0.18	123	11	36	24.4	3.4	**
Xgwm642	Röder et al. (1998)	1D	75	1DL2-0.41-1.00	140	6	27	17.3	1.7	n.s.
Xgwm232	Röder et al. (1998)	1D	107	1DL2-0.41-1.00	154	3	18	11.1	0.6	n.s.
Xgdm111	Pestsova et al. (2000)	1D	116	-	131	8	15	12.3	12.5	n.s.
Xbarc212	Song et al. (2005)	2A	0	2AS5-0.78-1.00	143	10	21	14.9	1.1	n.s.
Xgwm95	Röder et al. (1998)	2A	53	C-2AS5-0.78	149	8	14	10.5	2.8	n.s.
Xgwm558	Röder et al. (1998)	2A	54	C-2AL1-0.85	147	6	17	11.8	3.4	n.s.
Xgwm445	Röder et al. (1998)	2A	68	C-2AL1-0.85	157	5	7	5.6	4.0	n.s.
Xgwm294	Röder et al. (1998)	2A	76	C-2AL1-0.85	141	8	23	15.7	2.3	n.s.
Xgwm356	Röder et al. (1998)	2A	126	C-2AL1-0.85	121	18	26	21.2	6.3	**
Xbarc279[1]	Song et al. (2005)	2A	138	-	148	1	17	10.5	5.7	n.s.
Xgwm148	Röder et al. (1998)	2B	47	2BS1-0.53-0.75	154	5	13	9.0	2.3	n.s.
Xgwm120	Röder et al. (1998)	2B	79	2BL2-0.36-0.50	150	1	17	10.4	4.5	n.s.
Xwmc332	Gupta et al. (2002)	2B	93	-	134	1	18	12.1	13.1	n.s.
Xwmc503	Gupta et al. (2002)	2D	21	-	138	7	17	12.7	8.0	n.s.
Xgwm455	Röder et al. (1998)	2D	32	2DS5-0.47-1.00	141	13	16	13.2	3.4	*
Xgwm102	Röder et al. (1998)	2D	48	2DS1-0.33-0.47	134	8	31	20.2	1.7	*

Marker	Reference	Chr.	Pos. (cM)	Bin	n [AA]	n [Aa]	n [aa]	[aa] (%)	Amb. geno. (%)	DS
Xwmc18	Gupta et al. (2002)	2D	64	-	117	5	32	22.4	12.5	**
Xgwm157	Röder et al. (1998)	2D	73	2DL3-0.49-0.76	134	10	26	18.2	3.4	n.s.
Xgwm539	Röder et al. (1998)	2D	91	C-2DL3-0.49	143	6	22	14.6	2.8	n.s.
Xgwm349	Röder et al. (1998)	2D	93	C-2DL3-0.49	145	8	17	12.4	3.4	n.s.
Xgwm320	Röder et al. (1998)	2D	101	C-2DL3-0.49	126	6	14	11.6	17.0	n.s.
Xbarc57[1]	Song et al. (2005)	3A	0	-	138	6	21	14.5	6.3	n.s.
Xgwm5	Röder et al. (1998)	3A	45	C-3AL3-0.42	145	7	13	10.0	6.3	n.s.
Xwmc559	Gupta et al. (2002)	3A	83	-	131	7	25	17.5	7.4	n.s.
Xgwm480	Röder et al. (1998)	3A	116	C-3AL3-0.42	142	6	27	17.1	0.6	n.s.
Xbarc133[1]	Song et al. (2005)	3B	7	-	133	10	11	10.4	12.5	n.s.
Xgwm493	Röder et al. (1998)	3B	12	3BS8-0.78-1.00	161	6	8	6.3	0.6	n.s.
Xbarc73	Song et al. (2005)	3B	60	3BS1-0.33-0.57	151	7	10	8.0	4.6	n.s.
Xbarc139[1]	Song et al. (2005)	3B	66	-	145	10	8	8.0	7.4	*
Xbarc77	Song et al. (2005)	3B	111	C-3BL2-0.22	152	4	16	10.5	2.3	n.s.
Xgwm340	Röder et al. (1998)	3B	148	-	159	3	7	5.0	4.0	n.s.
Xgwm161	Röder et al. (1998)	3D	13	3DS6-0.55-1.00	149	8	19	13.1	0.0	n.s.
Xgwm383	Röder et al. (1998)	3D	20	3DL	145	7	16	11.6	4.6	n.s.
Xgwm52	Röder et al. (1998)	3D	30	-	150	6	9	7.3	6.3	n.s.
Xgwm3	Röder et al. (1998)	3D	43	3DL	148	8	20	13.6	0.0	n.s.
Xbarc323[1]	Song et al. (2005)	3D	80	-	79	8	6	10.8	47.2	**
Xgwm610	Röder et al. (1998)	4A	12	C-4AS1-0.20	143	6	20	13.6	4.0	n.s.
Xgwm397	Röder et al. (1998)	4A	18	4AL13-0.59-0.66	136	2	18	12.2	11.4	n.s.
Xgwm160	Röder et al. (1998)	4A	79	4AL4-0.80-1.00	155	3	17	10.6	0.6	n.s.
Xgwm113	Röder et al. (1998)	4B	25	C-4BS4-0.37	151	7	15	10.7	1.7	n.s.
Xgwm149	Röder et al. (1998)	4B	31	4BL1-0.86-1.00	139	12	16	13.2	5.1	n.s.
Xgwm251	Röder et al. (1998)	4B	36	4BL1-0.86-1.00	145	10	16	12.3	2.8	n.s.
Xbarc114[1]	Song et al. (2005)	4B	59	-	151	6	14	9.9	2.8	n.s.
Xwmc285	Gupta et al. (2002)	4D	10	-	87	1	5	5.9	47.2	n.s.
Xbarc217[1]	Song et al. (2005)	4D	27	-	136	7	28	18.4	2.8	n.s.
Xbarc91	Song et al. (2005)	4D	32	-	76	2	10	12.5	50.0	n.s.
Xwmc331	Gupta et al. (2002)	4D	43	-	57	3	10	16.4	60.2	n.s.
Xwmc399	Gupta et al. (2002)	4D	54	-	112	3	23	17.8	21.6	n.s.
Xcfd84	Sourdille et al. (2001)	4D	67	C-4DL9-0.31	69	2	13	16.7	52.3	n.s.
Xgwm624	Röder et al. (1998)	4D	89	4DL	158	1	5	3.4	6.8	*
Xgwm609	Röder et al. (1998)	4D	91	4DL	162	2	9	5.8	1.7	n.s.
Xwmc713	Gupta et al. (2002)	5A	28	-	75	2	14	16.5	48.3	n.s.
Xgwm154	Röder et al. (1998)	5A	34	5AS3-0.75-0.98	138	12	19	14.8	4.0	n.s.
Xgwm415	Röder et al. (1998)	5A	55	C-5AS1-0.40	141	5	24	15.6	3.4	n.s.
Xgwm304	Röder et al. (1998)	5A	64	C-5AS1-0.40	142	7	22	14.9	2.8	n.s.
Xgwm186	Röder et al. (1998)	5A	64	C-5AL12-0.35	129	5	25	17.3	9.7	n.s.
Xbarc330[1]	Song et al. (2005)	5A	75	-	71	2	19	21.7	48.0	**
Xbarc319[1]	Song et al. (2005)	5A	110	-	67	1	5	7.5	58.5	n.s.
Xcfd60	Sourdille et al. (2001)	5B	14	-	141	4	19	12.8	6.8	n.s.
Xgwm544	Röder et al. (1998)	5B	61	5BS8-0.56-0.71	138	6	10	8.4	12.5	n.s.
Xgwm604	Röder et al. (1998)	5B	124	5BL16-0.79-1.00	112	15	25	21.4	13.6	**
Xbarc130	Song et al. (2005)	5D	4	5DS2-0.78-1.00	138	5	28	17.8	2.8	n.s.
Xbarc205[1]	Song et al. (2005)	5D	16	-	141	10	20	14.6	2.9	n.s.
Xbarc143	Song et al. (2005)	5D	23	C-5DS1-0.63	133	9	26	18.2	4.6	n.s.
Xcfd266	Sourdille et al. (2001)	5D	34	-	160	8	8	6.8	0.0	n.s.
Xgwm583	Röder et al. (1998)	5D	44	C-5DL1-0.60	142	4	22	14.3	4.5	n.s.
Xgwm182	Röder et al. (1998)	5D	50	5DL1-0.60-0.74	156	3	14	9.0	1.7	n.s.
Xgwm174	Röder et al. (1998)	5D	58	5DL1-0.60-0.74	74	6	9	13.5	49.4	n.s.
Xgwm212	Röder et al. (1998)	5D	67	5DL5-0.76-1.00	150	4	19	12.1	1.7	n.s.
Xbarc322[1]	Song et al. (2005)	5D	82	-	144	4	15	10.4	7.4	n.s.
Xgwm272	Röder et al. (1998)	5D	119	5DL5-0.76-1.00	155	6	15	10.2	0.0	n.s.
Xgwm427	Röder et al. (1998)	6A	93	6AL8-0.90-1.00	145	9	20	14.1	1.1	n.s.
Xbarc198	Song et al. (2005)	6B	44	C-6BS5-0.76	139	2	22	14.1	7.4	n.s.
Xgwm626	Röder et al. (1998)	6B	48	C-6BS5-0.76	153	3	15	9.6	2.9	n.s.
Xgwm219	Röder et al. (1998)	6B	59	6BL5-0.40-1.00	148	4	15	10.2	5.1	n.s.
Xcfd132	Sourdille et al. (2001)	6D	35	-	74	5	8	12.1	50.9	n.s.
Xgwm325	Röder et al. (1998)	6D	53	-	149	4	19	12.2	2.3	n.s.
Xbarc273[1]	Song et al. (2005)	6D	70	-	133	21	13	14.1	5.1	**
Xgwm233	Röder et al. (1998)	7A	5	7AS	108	6	18	15.9	25.0	n.s.

Marker	Reference	Chr.	Pos. (cM)	Bin	n [AA]	n [Aa]	n [aa]	[aa] (%)	Amb. geno. (%)	DS
Xgwm60	Röder et al. (1998)	7A	30	7AS8-0.45-0.59	134	18	20	16.9	2.3	**
Xcfa2019	Sourdille et al. (2001)	7A	107	7AL16-0.86-0.90	63	2	10	14.7	57.4	n.s.
Xbarc275[1]	Song et al. (2005)	7A	144	-	51	7	13	23.2	59.7	**
Xgwm537	Röder et al. (1998)	7B	35	-	148	0	20	11.9	4.5	n.s.
Xgwm400	Röder et al. (1998)	7B	40	C-7BS1-0.27	146	5	23	14.7	1.1	n.s.
Xbarc65[1]	Song et al. (2005)	7B	48	-	133	32	9	14.4	1.1	**
Xgwm46	Röder et al. (1998)	7B	54	7BS1-0.27-1.00	126	10	29	20.6	6.3	*
Xgwm297	Röder et al. (1998)	7B	58	C-7BS1-0.27	129	11	31	21.3	2.9	**
Xgwm333	Röder et al. (1998)	7B	63	7BL2-0.33-0.48	121	12	32	23.0	6.3	**
Xbarc278[1]	Song et al. (2005)	7B	77	-	63	1	9	13.0	58.5	n.s.
Xwmc311	Gupta et al. (2002)	7B	118	-	122	7	10	9.7	21.0	n.s.
Xgwm577	Röder et al. (1998)	7B	137	7BL10-0.78-1.00	152	7	12	9.1	2.9	n.s.
Xbarc123	Song et al. (2005)	7B	149	-	141	5	20	13.6	5.7	n.s.
Xbarc184	Song et al. (2005)	7D	28	-	152	4	10	7.2	5.7	n.s.
Xgwm437	Röder et al. (1998)	7D	92	C-7DL5-0.30	141	5	27	17.1	1.7	n.s.
Xgwm428	Röder et al. (1998)	7D	136	7DL5-0.30-0.61	137	6	25	16.7	4.5	n.s.
Xwmc634	Gupta et al. (2002)	7D	143	-	71	6	14	18.7	48.3	*
Sum					13,702	687	1,863			23
Mean					129.3	6.5	17.6	13.8	12.9	

Gloss based on Appendix 4.

Appendix 6: LS-means of 16 traits for T84, D84 and recurrent parents Triso and Devon, computed across environments.

Trait		T84		Triso		D84		Devon	
		N+	N-	N+	N-	N+	N-	N+	N-
BRT	n	442	442	17	17	351	351	20	20
	Min	1	1	1	1	1	1	1	1
	Max	2	2	1	1	2	2	1	2
	Mean	1.2	1.2	1.0	1.0	1.2	1.2	1.0	1.1
	SD	0.4	0.4	0.0	0.0	0.4	0.4	0.0	0.2
EAR	n	1,542	1,544	67	68	1,227	1,228	80	80
	Min	192.0	192.0	296.0	256.0	224.0	128.0	312.0	232.0
	Max	1,504.0	1,344.0	944.0	816.0	1,232.0	1,152.0	992.0	928.0
	Mean	611.0	533.4	590.6	518.9	571.7	520.7	587.4	537.5
	SD	191.3	158.1	164.4	141.3	156.1	147.2	146.4	161.1
GNE	n	438	434	16	17	351	349	20	20
	Min	4.2	4.4	26.4	27.3	7.2	5.3	26.9	26.7
	Max	60.6	82.7	35.0	36.8	57.7	50.2	35.4	34.2
	Mean	27.5	26.6	31.2	31.0	27.7	27.5	30.6	29.9
	SD	4.9	6.1	2.1	2.5	5.2	5.3	2.0	2.1
HEA	n	1,767	1,772	68	68	1,403	1,405	80	80
	Min	71.0	70.0	85.0	82.0	72.0	71.0	85.0	85.0
	Max	103.0	99.0	99.0	98.0	99.0	99.0	97.0	95.0
	Mean	86.0	85.5	92.1	91.2	86.2	85.7	91.8	90.9
	SD	5.7	6.0	3.8	4.2	6.0	6.0	3.0	3.5
HEI	n	1,767	1,772	68	68	1,403	1,405	80	80
	Min	65.0	60.0	80.0	85.0	70.0	70.0	75.0	70.0
	Max	136.0	128.0	117.0	109.0	143.0	142.0	112.0	107.0
	Mean	97.5	97.9	98.1	96.7	101.7	103.4	91.6	89.9
	SD	12.7	11.1	8.2	6.4	11.7	10.4	10.6	9.5
HI	n	441	435	17	17	350	342	20	19
	Min	0.1	0.1	0.4	0.4	0.2	0.1	0.4	0.4
	Max	0.7	0.5	0.5	0.5	0.6	0.6	0.5	0.6
	Mean	0.4	0.4	0.4	0.5	0.4	0.4	0.5	0.4
	SD	0.1	0.1	0.0	0.0	0.1	0.1	0.0	0.0
HLW	n	1,058	1,005	50	49	838	816	59	57
	Min	67.9	67.0	70.8	73.7	64.2	60.8	68.8	71.4
	Max	87.7	91.2	83.8	82.0	85.6	92.5	84.6	82.8
	Mean	78.4	78.0	77.9	77.6	77.2	77.7	78.3	78.1
	SD	3.4	3.1	3.7	2.9	4.1	3.4	4.6	3.4
LAH	n	1,326	1,326	34	34	1,050	1,052	40	40
	Min	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0

Trait		T84		Triso		D84		Devon	
		N+	N-	N+	N-	N+	N-	N+	N-
	Max	9.0	9.0	7.0	7.0	9.0	9.0	9.0	9.0
	Mean	3.3	2.1	1.7	1.9	4.0	2.6	2.6	1.8
	SD	2.5	1.5	1.2	1.4	2.7	1.7	2.6	2.1
TGW	n	1,317	1,319	51	50	1,043	1,038	59	59
	Min	29.7	30.7	36.6	39.0	30.9	31.9	35.6	33.1
	Max	55.8	54.8	48.3	50.5	61.0	76.7	52.7	49.5
	Mean	42.0	42.4	43.7	45.0	44.5	45.1	42.5	42.4
	SD	4.4	4.2	2.8	3.4	5.1	5.3	3.7	3.7
YLD	n	1,541	1,542	51	51	1,223	1,225	60	59
	Min	14.9	7.1	47.6	42.4	14.1	13.1	44.9	40.4
	Max	111.3	99.1	107.5	85.5	108.1	99.8	107.3	86.8
	Mean	65.4	58.2	81.6	69.5	62.1	57.3	76.2	67.7
	SD	17.3	15.5	15.1	12.1	17.7	15.5	19.9	13.7
GH	n	423	423	32	32	329	311	37	34
	Min	35.0	38.0	48.0	45.0	29.0	28.0	49.0	43.0
	Max	67.0	64.0	63.0	58.0	68.0	64.0	64.0	58.0
	Mean	55.1	52.7	56.3	53.1	55.8	53.3	56.6	52.5
	SD	6.4	5.6	4.7	3.6	6.7	5.6	4.9	3.9
GPC	n	645	646	32	32	505	487	37	35
	Min	10.0	7.7	10.5	10.0	9.7	8.3	11.2	9.6
	Max	17.8	17.2	15.1	11.3	17.2	16.0	14.9	12.8
	Mean	13.8	11.3	13.2	10.6	13.7	11.6	13.2	10.8
	SD	1.6	1.1	1.6	0.3	1.4	1.1	1.3	0.6
SED	n	331	222	27	17	279	176	35	20
	Min	22.0	19.0	31.0	27.0	28.0	23.0	32.0	28.0
	Max	72.0	46.0	57.0	31.0	72.0	48.0	62.0	32.0
	Mean	47.5	30.3	47.3	29.7	51.3	33.6	46.8	30.4
	SD	12.4	4.4	8.3	1.3	11.3	5.4	10.8	1.3
LR	n	723	-	63	-	540	-	36	-
	Min	1		1		1		1	
	Max	8		4		9		5	
	Mean	1.8		1.7		1.8		2.0	
	SD	1.2		0.9		1.5		1.3	
PM	n	1,771	-	160	-	1,405	-	96	-
	Min	1		1		1		1	
	Max	9		7		9		8	
	Mean	3.6		3.5		3.4		3.5	
	SD	2.0		1.6		2.0		1.7	
SEP	n	1,111	-	100	-	879	-	60	-
	Min	1		1		1		1	
	Max	9		8		9		7	
	Mean	4.3		4.0		3.7		3.7	
	SD	2.1		1.7		1.8		1.7	
[aa]	n	223	-		-	176	-		-
	Min	2.4				2.5			
	Max	30.5				29.3			
	Mean	12.6				13.6			
	SD	4.8				5.1			

Appendix 7: Localisation of 58 significant marker×trait associations in T84, specified as marker×environment interaction effects included 48 QTL, computed for high N-supply using the three-way ANOVA single-locus analysis (ANOVA I).

Trait	Marker	Chr.	Pos. (cM)	Sign.	F-val.	R^2 (%)	N+ [AA]	N+ [aa]	Diff. [aa]	RP [B04]	RP [B05]	RP [D04]	RP [D05]	RP [F04]	RP [F05]	RP [H04]	RP [H05]	QTL
BRT	Xgwm294	2A	76	**	21.3	2.0	1.2	1.2	0.0			12.3	-9.9					*QBRT.T84-2A*
BRT	Xbarc96	6D	92	*	7.2	0.8	1.2	1.1	-0.1			-11.4	2.7					*QBRT.T84-6D*
EAR	Xgwm356	2A	126	*	2.9	5.8	608.8	637.3	28.5	-1.1	-1.1	6.2	18.4	2.6	-2.8	5.7		*QEAR.T84-2A*
EAR	Xgwm544	5B	61	*	3.0	5.8	613.4	573.9	-39.5	-3.7	7.2	0.5	-27.3	-11.7	-4.4	1.0		*QEAR.T84-5B*
EAR	Xgwm577	7B	137	*	3.7	7.5	611.7	603.7	-8.0	-3.4	9.0	11.2	-16.1	-3.6	-2.0	-0.1		*QEAR.T84-7B*
GNE	Xgwm413×	1B	26	**	18.3	12.6	27.8	25.5	-2.3			-22.8	6.5					*QGNE.T84-1B*
GNE	Xgwm498	1B	31	*	9.1	5.5	28.2	27.2	-1.0			-14.2	7.1					"
HEA	Xgwm642	1D	75	*	2.7	0.9	85.9	86.5	0.6	2.0	0.0	0.7	1.6	0.3	0.9	-0.2	0.5	*QHEA.T84-1D*
HEA	Xgwm349	2D	93	*	2.8	0.9	85.9	87.3	1.4	1.8	-1.1	1.7	3.6	1.3	3.6	0.6	1.6	*QHEA.T84-2Dc*
HEA	Xgwm626	6B	48	*	3.0	1.1	86.1	85.2	-0.9	-1.3	-0.6	-1.2	-2.6	-0.6	-1.2	0.0	-0.6	*QHEA.T84-6B*
HEI	Xgwm604	5B	124	*	2.7	1.1	97.1	97.5	0.4	-2.5	5.6	-0.1	0.8	0.7	-1.6	0.2	0.5	*QHEI.T84-5B*
HEI	Xgwm325	6D	53	*	2.9	1.0	97.6	95.5	-2.1	0.5	1.5	-2.2	-2.7	-4.0	-2.0	-3.1	-4.7	*QHEI.T84-6D*
HEI	Xbarc123	7B	149	*	3.2	1.1	97.6	95.9	-1.7	-0.4	2.5	-3.3	-2.7	-3.7	-0.8	-1.9	-3.3	*QHEI.T84-7B*
HI	Xwmc44	1B	92	*	7.5	1.3	0.4	0.4	0.0			3.0	-7.1					*QHI.T84-1B*
HLW	Xgwm294	2A	76	**	6.3	5.1	78.3	78.4	0.1	0.0		-0.4	-0.3			0.1	1.8	*QHLW.T84-2A*
HLW	Xbarc319[1]	5A	110	**	7.2	7.2	78.3	78.6	0.3	-0.6		0.0	-0.9			1.9	1.5	*QHLW.T84-5Ab*
LAH	Xgwm415	5A	55	**	5.1	3.2	3.6	5.1	1.5	29.3	32.0	103.7	52.0		14.3			*QLAH.T84-5A*
LAH	Xgwm304×	5A	64	**	5.3	3.3	3.6	5.2	1.6	29.9	35.9	109.6	54.2		15.3			"
LAH	Xcfd60	5B	14	*	4.3	16.3	3.3	5.0	1.7	-2.5	44.4	140.4	111.2		12.2			*QLAH.T84-5B*
LAH	Xbarc205[1]×	5D	16	**	5.2	3.4	3.6	4.4	0.8	24.2	-9.4	58.4	37.6		13.5			*QLAH.T84-5Da*
LAH	Xbarc143	5D	23	*	4.1	3.3	3.6	4.5	0.9	27.6	-3.1	66.9	36.4		11.1			"
LAH	Xgwm182	5D	50	*	3.5	2.2	3.7	4.8	1.1	2.7	41.6	102.7	20.0		14.4			*QLAH.T84-5Db*
LAH	Xgwm212×	5D	67	*	4.3	2.8	3.7	4.6	0.9	27.4	-1.3	66.6	41.9		8.8			"
LAH	Xgwm60	7A	30	*	4.2	2.8	3.8	4.2	0.4	-13.8	0.9	28.6	31.6		-0.4			*QLAH.T84-7A*
LAH	Xgwm437	7D	92	*	3.5	2.3	3.8	4.0	0.2	21.2	-16.3	-14.8	30.1		1.5			*QLAH.T84-7D*
TGW	Xgwm455	2D	32	**	4.7	1.4	41.8	42.7	0.9	-1.7		3.0	0.4		5.9	4.3	2.2	*QTGW.T84-2Da*
TGW	Xwmc18	2D	64	**	5.9	1.7	41.8	42.8	1.0	-3.3		4.0	-0.5		5.2	4.8	4.1	*QTGW.T84-2Db*
TGW	Xgwm157×	2D	73	**	9.8	2.8	41.7	43.9	2.2	-1.1		7.0	2.7		5.7	8.2	9.9	"
TGW	Xgwm539	2D	91	**	9.2	2.8	41.7	43.6	1.9	-0.5		4.7	2.2		4.1	6.1	11.3	"
TGW	Xbarc77	3B	111	*	3.2	1.3	42.4	41.4	-1.0	0.6		-3.6	-2.7		-2.6	-2.3	-5.1	*QTGW.T84-3B*
TGW	Xbarc319[1]	5A	110	*	4.1	1.7	42.3	42.7	0.4	-3.0		0.6	-0.7		3.7	4.0	0.5	*QTGW.T84-5A*
YLD	Xgwm120	2B	79	*	2.8	1.9	66.0	63.2	-2.8	4.2	-6.2	-3.9	-3.4		-7.9	-9.8	-2.3	*QYLD.T84-2B*
YLD	Xgwm113	4B	25	*	3.5	2.0	66.0	61.9	-4.1	-0.2	-7.7	-10.4	-9.6		-6.0	-7.3	1.3	*QYLD.T84-4B*
YLD	Xgwm149	4B	31	*	3.5	1.9	65.6	62.5	-3.1	-4.7	-9.0	-11.2	-9.2		-3.2	-0.1	7.0	"
YLD	Xgwm251×	4B	36	**	3.8	2.1	65.8	64.0	-1.8	-2.8	-6.9	-10.4	-6.5		-4.3	5.0	9.1	"
YLD	Xgwm415×	5A	55	*	3.5	1.9	65.5	65.0	-0.5	-6.5	12.3	-0.6	-1.4		-9.7	4.2	0.6	*QYLD.T84-5A*
YLD	Xgwm304	5A	64	*	3.5	1.9	65.4	65.2	-0.2	-5.9	12.8	-0.5	-1.4		-10.2	4.5	2.2	"

Trait	Marker	Chr.	Pos. (cM)	Sign.	F-val.	R^2 (%)	N+ [AA]	N+ [aa]	Diff. [aa]	RP [B04]	RP [B05]	RP [D04]	RP [D05]	RP [F04]	RP [F05]	RP [H04]	RP [H05]	QTL
GH	Xgwm626	6B	48	**	11.9	0.8	54.8	54.8	0.0			-2.2				2.8		*QGH.T84-6B*
GPC	Xgwm480	3A	116	*	4.8	1.8	13.7	13.6	-0.1			0.1				4.5	-5.2	*QGPC.T84-3A*
GPC	Xgwm383	3D	20	*	5.3	2.1	13.7	13.6	-0.1			-2.9				3.8	-3.3	*QGPC.T84-3D*
GPC	Xgwm149	4B	31	**	8.0	3.2	13.7	14.3	0.6			5.6				10.5	-1.0	*QGPC.T84-4B*
GPC	Xgwm251[×]	4B	36	**	9.9	4.1	13.6	14.3	0.7			6.4				11.4	-1.7	*"*
GPC	Xbarc130	5D	4	**	7.3	3.0	13.7	13.6	-0.1			-3.5				-0.7	2.4	*QGPC.T84-5D*
SED	Xbarc194[1]	1B	8	*	10.5	1.3	44.6	47.2	2.6			-5.4				23.2		*QSED.T84-1B*
SED	Xgwm294	2A	76	*	7.7	0.7	45.2	41.3	-3.9			-1.7				-18.5		*QSED.T84-2A*
SED	Xbarc130	5D	4	*	8.1	0.8	45.8	37.0	-8.8			-20.7				-17.2		*QSED.T84-5D*
SED	Xgwm400	7B	40	*	7.1	0.7	45.0	43.0	-2.0			1.1				-12.7		*QSED.T84-7B*
LR	Xgwm157	2D	73	*	8.4	3.0	2.3	2.5	0.2			-22.3					65.7	*QLR.T84-2D*
LR	Xbarc73	3B	60	**	18.3	5.7	2.4	3.8	1.4			-33.0					216.0	*QLR.T84-3B*
PM	Xgwm356	2A	126	*	3.3	1.0	3.6	2.8	-0.8	-19.6	-13.5	-24.3	-38.5	-17.6	-23.2	-16.4	-19.8	*QPM.T84-2Ab*
PM	Xbarc73	3B	60	*	3.3	1.0	3.6	2.1	-1.5	-40.8	-8.7	-36.0	-61.9	-43.7	-37.6	-46.8	-34.8	*QPM.T84-3B*
PM	Xgwm3	3D	43	*	3.3	1.0	3.5	3.7	0.2	-13.1	-19.7	14.5	6.6	5.7	10.7	-6.5	9.1	*QPM.T84-3D*
PM	Xgwm544	5B	61	*	3.2	1.0	3.6	2.8	-0.8	19.6	1.2	-26.3	-37.7	-20.3	-38.4	-23.3	-22.1	*QPM.T84-5B*
SEP	Xgwm148	2B	47	*	4.0	4.7	4.8	4.8	0.0	2.1	-3.1	14.7				-9.9		*QSEP.T84-2Ba*
SEP	Xwmc332	2B	93	*	4.3	5.3	4.8	4.8	0.0	1.5	-1.8	16.1				-13.9		*QSEP.T84-2Bb*
SEP	Xbarc77	3B	111	*	5.1	7.0	4.8	5.0	0.2	15.1	-3.7	9.9				-3.2		*QSEP.T84-3B*
SEP	Xgwm604	5B	124	**	6.0	8.6	4.8	4.6	-0.2	-25.4	0.4	4.0				5.2		*QSEP.T84-5B*
SEP	Xgwm537	7B	35	*	4.2	4.9	4.8	4.9	0.1	-7.7	2.6	9.7				20.6		*QSEP.T84-7B*

Trait: BRT (Brittleness), EAR (Tillers per square meter), GNE (Grain number per ear), HEA (Days until heading), HEI (Plant height), HI (Harvest index), HLW (Grain test weight), LAH (Lodging at harvest), TGW (Thousand grain weight), YLD (Grain yield), GH (Grain hardness), GPC (Grain protein content), SED (Sedimentation value), LR (Leaf rust), PM (Powdery mildew), SEP (*Septoria* leaf blotch). Marker: Label of SSR marker. ([×]) Significant marker×trait association computed with the highest F-value in a linked QTL cluster with a ≤ 20 cM distance. (1) Marker was not described by Somers et al. (2004) and Sourdille et al. (2004), respectively, estimated position in cM on chromosome by linked marker positions described by Somers et al. (2004) and Song et al. (2005). Chr.: Chromosomal location of the marker derived from Somers et al. (2004). Pos.: Position of the marker in cM on chromosome derived from Somers et al. (2004). Sign.: Level of significance computed using the GLM procedure of the significant marker×trait associations for marker main effect (M) or marker×environment interaction effect (M×E), (**) P = 0.001, (*) P = 0.01. F-val.: F-value was computed using the GLM procedure. R^2 (%): Proportion of the genetic variance computed using the GLM procedure, which was explained the marker main effect (M) or the marker×environment interaction effect (M×E). N+ [AA]: LS-means of trait values for high N-supply (two or three mineral N-applications) across all tested environments for BC_2F_4 lines carrying the cultivar genotype (Triso) at the given marker locus. N+ [aa]: LS-means of trait values for high N-supply (two or three mineral N-applications) across all tested environments for BC_2F_4 lines carrying the exotic genotype (Syn-84) at the given marker locus. Diff. [aa]: Difference between LS-means of the exotic and the cultivar genotype, N+ [aa] - N+ [AA]. RP [B04] - [H05]: Relative performance of exotic genotype (Syn-84) at a given marker locus for each tested environment computed using the GLM procedure. Relative performance was computed as ([aa] - [AA])×100 / [AA], where [AA] or [aa] were LS-means of BC_2F_4 lines carrying the cultivar genotype (Triso) or the exotic genotype (Syn-84) at the given marker locus. [B04] - [H05] were combinations of the experimental location [Boldebuck (B), Dikopshof (D), Feldkirchen (F), Hovedissen (H)] and the experimental year [2004 (04), 2005 (05)]. QTL: A significant marker×trait association was specified as QTL, if marker main effect (M) or marker×environment interaction effect (M×E), was significant with P = 0.01 in the GLM procedure. Linked QTLs with a ≤ 20 cM distance were interpreted as one QTL. The QTL label is consisting of Q (for QTL), YLD (tested trait), T84 (tested population), 4Ab (chromosome, where the QTL was detected and b for the second YLD-QTL on the same chromosome).

Appendix 8: Localisation of 34 significant marker×trait associations in D84, specified as marker×environment interaction effects included 30 QTL, computed in high N-supply using the three-way ANOVA single-locus analysis (ANOVA I).

Trait	Marker	Chr.	Pos. (cM)	Sign.	F-val.	R^2 (%)	N+ [AA]	N+ [aa]	Diff. [aa]	RP [B04]	RP [B05]	RP [D04]	RP [D05]	RP [F04]	RP [F05]	RP [H04]	RP [H05]	QTL
BRT	Xbarc319[1]	3B	66	*	8.1	2.0	1.1	1.3	0.2			-7.6	24.2					*QBRT.D84-3Bb*
EAR	Xgwm610	4A	12	*	3.2	8.4	614.9	594.5	-20.4	-5.9	0.8	-5.1	0.0	1.4	-7.0	-5.9		*QEAR.D84-4A*
EAR	Xbarc130	5D	4	*	3.8	9.6	610.3	631.1	20.8	-3.1	-3.8	4.1	3.2	3.6	8.1	5.9		*QEAR.D84-5Da*
GNE	Xgwm5	3A	45	*	8.1	2.0	28.0	20.6	-7.4			-27.7	-25.4					*QGNE.D84-3A*
HEI	Xgwm102×	2D	48	*	3.5	1.7	97.7	95.1	-2.6	-3.1	-2.3	-2.2	-2.5	-2.6	-1.9	-3.0	-4.0	*QHEI.D84-2D*
HEI	Xwmc18	2D	64	*	3.2	1.5	97.7	95.3	-2.4	-1.3	-4.2	-3.3	-2.0	-1.3	-1.9	-1.3	-4.1	″
HEI	Xgwm480	3A	116	*	3.2	1.5	97.4	99.1	1.7	0.7	-0.5	2.5	1.5	3.0	1.8	2.6	2.0	*QHEI.D84-3A*
HEI	Xgwm577	7B	137	*	3.5	1.5	97.3	98.3	1.0	2.7	-1.8	-0.7	0.5	2.7	-0.3	4.5	1.6	*QHEI.D84-7B*
HI	Xgwm5	3A	45	**	30.3	7.0	0.4	0.3	-0.1			-20.3	-32.3					*QHI.D84-3A*
HLW	Xgwm415	5A	55	*	4.5	3.5	78.2	78.6	0.4	0.2		0.3	-0.4			1.6	1.0	*QHLW.D84-5A*
HLW	Xgwm304	5A	64	*	4.0	3.2	78.2	78.6	0.4	0.2		0.3	-0.5			1.6	1.1	″
HLW	Xgwm186×	5A	64	**	7.4	6.0	77.1	77.2	0.1	-2.4		0.7	0.5			0.4	0.9	″
HLW	Xgwm537×	7B	35	**	5.7	4.4	78.3	78.3	0.0	0.2		-0.1	-0.6			0.5	-0.1	*QHLW.D84-7Ba*
HLW	Xgwm400	7B	40	*	3.9	3.4	78.3	78.3	0.0	0.6		-0.1	-0.3			0.2	-0.1	″
TGW	Xgwm356	2A	126	*	3.8	1.8	42.0	41.9	-0.1	1.4		1.0	-4.5		1.8	-1.6	0.1	*QTGW.D84-2Ab*
TGW	Xbarc275[1]	7A	144	**	5.0	4.3	44.8	43.8	-1.0	-4.1		-5.2	-2.7		-2.1	-3.5	6.6	*QTGW.D84-7A*
YLD	Xgwm455	2D	32	**	4.1	4.4	65.8	64.4	-1.4	-4.7	-6.2	1.1	-1.8		-4.9	-1.5	1.4	*QYLD.D84-2D*
YLD	Xbarc217[1]	4D	27	**	4.3	4.1	61.9	64.1	2.2	4.2	7.6	4.7	8.3		4.9	-9.0	2.0	*QYLD.D84-4Da*
YLD	Xbarc322[1]	5D	82	**	5.1	5.4	64.8	66.8	2.0	-6.9	-2.2	-1.4	5.0		6.7	10.6	10.2	*QYLD.D84-5D*
YLD	Xbarc65[1]	7B	48	*	3.0	3.8	62.5	61.9	-0.6	2.8	0.8	-8.3	-2.8		-7.2	14.3	1.7	*QYLD.D84-7Ba*
YLD	Xgwm577	7B	137	**	4.1	4.1	65.2	64.2	-1.0	-0.5	-0.7	-0.8	-2.4		0.8	-9.4	3.5	*QYLD.D84-7Bb*
GPC	Xwmc332	2B	93	*	5.6	3.8	13.7	13.7	0.0			0.7				0.4	0.3	*QGPC.D84-2B*
GPC	Xgwm102	2D	48	**	7.3	4.0	13.7	13.7	0.0			0.2				2.0	-1.8	*QGPC.D84-2D*
GPC	Xgwm609	4D	91	**	8.3	4.9	13.7	13.8	0.1			1.8				-1.3	1.7	*QGPC.D84-4D*
SED	Xgwm99	1A	126	*	7.2	1.3	44.4	45.9	1.5			7.8				-3.0		*QSED.D84-1A*
SED	Xgwm356	2A	126	*	9.0	1.7	45.1	42.8	-2.3			-4.3				-6.2		*QSED.D84-2A*
PM	Xgwm539	2D	91	*	2.9	1.6	3.5	3.7	0.2	3.6	-8.4	10.7	10.2	9.5	1.7	-1.3	1.3	*QPM.D84-2D*
PM	Xbarc323[1]	3D	80	*	3.3	4.1	3.5	3.4	-0.1	17.0	-9.5	-13.5	-41.4	7.7	28.0	28.5	8.2	*QPM.D84-3Db*
PM	Xbarc322[1]	5D	82	*	3.4	2.0	3.4	4.3	0.9	4.1	59.0	23.4	17.6	19.0	12.3	56.9	27.0	*QPM.D84-5D*
PM	Xgwm427	6A	93	**	6.4	3.4	3.7	2.8	-0.9	1.4	-21.4	-25.8	-35.6	-23.4	-31.6	-11.6	-18.8	*QPM.D84-6A*
PM	Xbarc278[1]	7B	77	*	3.3	3.7	3.6	2.7	-0.9	15.8	-6.0	-50.2	-24.4	-27.1	-36.4	-15.5	-22.8	*QPM.D84-7Bb*
SEP	Xgwm113	4B	25	*	4.0	5.5	4.8	4.9	0.1	8.3	1.6	4.6				-4.6		*QSEP.D84-4B*
SEP	Xbarc330[1]	5A	75	*	4.2	10.4	4.2	4.5	0.3	21.9	-0.8	31.0				-6.6		*QSEP.D84-5Aa*
SEP	Xbarc319[1]	5A	110	**	6.5	20.0	4.8	5.0	0.2	-0.9	3.8	8.8				9.5		*QSEP.D84-5Ab*

Gloss based on Appendix 7.

Appendix 9: Relative performances of exotic genotype (Syn-84) of 128 significant marker×trait associations in T84, specified as marker main effect or marker×environment interaction effect in high N-supply, computed using the three-way ANOVA single-locus analysis (ANOVA I).

Chr.	Pos. (cM)	Marker	BRT	EAR	GNE	HEA	HEI	HI	HLW	LAH	TGW	YLD	GH	GPC	SED	LR	PM	SEP	QTLs	Fav. [aa]
1B	8	Xbarc194													5.8				3	1
	26	Xgwm413			-8.2															
	31	Xgwm498			-3.5															
	92	Xwmc44						-1.9												
1D	75	Xgwm642			6.2*	0.7													2	1
2A	53	Xgwm95									3.8*						25.1*		10	6
	54	Xgwm558					3.6*										26.0*			
	76	Xgwm294	1.3			-1.1*			0.2		6.2*				-8.5					
	126	Xgwm356		4.7													-22.9			
2B	47	Xgwm148															-20.3*	0.4	4	1
	79	Xgwm120										-4.2								
	93	Xwmc332																0.3		
2D	21	Xwmc503										-11.7*							7	4
	32	Xgwm455				-1.4*					2.2									
	64	Xwmc18				-1.5*					2.3									
	73	Xgwm157									5.3					9.2				
	91	Xgwm539									4.5									
	93	Xgwm349				1.6														
3A	45	Xgwm5	69.8*		-26.5*							-27.4*							5	0
	116	Xgwm480				1.9*								-0.4						
3B	12	Xgwm493			-11.5*														9	2
	60	Xbarc73	68.7*									-16.7*				58.7	-40.8			
	111	Xbarc77						-6.2*			-2.5		3.6*					3.7		
3D	20	Xgwm383												-1.1					4	0
	30	Xgwm52											-4.8*							
	43	Xgwm3													-8.3*		3.3			
4A	12	Xgwm610					4.4*				4.2*								5	3
	18	Xgwm397									4.2*									
	38	Xwmc468				-2.3*					6.3*									
	79	Xgwm160					-6.3*										25.2*			
4B	25	Xgwm113						-8.8*				-6.1							3	1
	31	Xgwm149										-4.8		4.8						
	36	Xgwm251						-9.0*				-2.8		5.1						
4D	10	Xwmc285					7.2*			32.7*									4	2
	43	Xwmc331									7.3*			5.8*						
	54	Xwmc399									5.5*									
5A	34	Xgwm154							0.9*										8	5

Chr.	Pos. (cM)	Marker	BRT	EAR	GNE	HEA	HEI	HI	HLW	LAH	TGW	YLD	GH	GPC	SED	LR	PM	SEP	QTLs	Fav. [aa]
	55	Xgwm415					4.5*			40.0		-0.6								
	64	Xgwm304					4.5*			42.3		-0.3								
	110	Xbarc319				-2.0*			0.4		0.8				14.0*					
5B	14	Xcfd60								48.5									8	2
	38	Xgwm234							-1.3*			-12.0*								
	61	Xgwm544		-6.4								-14.0*					-21.9			
	124	Xgwm604					0.4											-5.0		
5D	4	Xbarc130											-15.7*	-0.7	-19.3				9	1
	16	Xbarc205								23.4			-4.2*							
	23	Xbarc143			-4.8*					25.0										
	44	Xgwm583									3.6*									
	50	Xgwm182								29.7										
	67	Xgwm212					3.5*			25.9							28.3*			
6A	93	Xgwm427									-5.2*								1	0
6B	48	Xgwm626				-1.0					-6.0*		0.1	4.2*					5	4
	59	Xgwm219												3.8*	19.2*					
6D	53	Xgwm325					-2.1												2	2
	92	Xbarc96	-4.5																	
7A	30	Xgwm60		-8.1*						9.3	6.2*			2.8*					4	2
7B	35	Xgwm537																4.1	7	2
	40	Xgwm400				-1.0*									-4.5		22.6*			
	54	Xgwm46															25.0*			
	58	Xgwm297															27.7*			
	118	Xwmc311															34.0*			
	137	Xgwm577		-1.3													38.0*			
	142	Xwmc276															32.7*			
	149	Xbarc123					-1.8													
7D	28	Xbarc184						-4.5*											5	0
	92	Xgwm437					3.9*		-0.7*	6.2										
	136	Xgwm428															-35.4*			
	143	Xwmc634															-34.6*			
		QTLs	4	4	5	10	10	4	5	7	12	8	4	7	7	2	11	5	105	
		Fav. [aa]	1	1	1	7	3	0	3	0	9	0	2	4	3	0	4	1		39

Gray highlighted RP values were favourable QTL effects with a positive effect from the exotic genotype (Syn-84) compared with the cultivar genotype (Triso or Devon) at a given marker locus. (*) RP values from a significant marker×trait association (P = 0.01) specified as a marker main effect (M). Trait: BRT (Brittleness), EAR (Tillers per square meter), GNE (Grain number per ear), HEA (Days until heading), HEI (Plant height), HI (Harvest index), HLW (Grain test weight), LAH (Lodging at harvest), TGW (Thousand grain weight), YLD (Grain yield), GH (Grain hardness), GPC (Grain protein content), SED (Sedimentation value), LR (Leaf rust), PM (Powdery mildew), SEP (*Septoria* leaf blotch). Chr.: Chromosomal location of the marker derived from Somers et al. (2004). Pos.: Position of the marker in cM on chromosome derived from Somers et al. (2004). Marker: Label of SSR marker described by Somers et al. (2004) and Song et al. (2005). QTL: Number of QTL (P = 0.01) specified as a marker main effect (M) or a marker×environment interaction effect (M×E). Fav. [aa]: Relative performance of exotic genotype (Syn-84) at a given marker locus for N-supply N+ across all tested environments computed using the GLM procedure specified a favourable QTL effect (+) with a positive effect from the exotic genotype (Syn-84) compared with the cultivar genotype (Triso) at a given marker locus.

Appendix 10: Relative performances of exotic genotype (Syn-84) at 92 significant marker×trait associations in D84, specified as marker main effect or marker×environment interaction effect for high N-supply, computed using the three-way ANOVA single-locus analysis (ANOVA I).

Chr.	Pos. (cM)	Marker	BRT	EAR	GNE	HEA	HEI	HI	HLW	LAH	TGW	YLD	GH	GPC	SED	LR	PM	SEP	QTLs	Fav. [aa]
1A	52	Xgwm357					4.1*												2	1
	126	Xgwm99													3.5					
1B	92	Xwmc44							1.5*										1	1
1D	75	Xgwm642													-9.5*				1	0
2A	53	Xgwm95					5.7*				5.7*								9	4
	54	Xgwm558					5.6*				5.2*									
	68	Xgwm445					5.3*													
	76	Xgwm294				-1.4*														
	126	Xgwm356				1.3*					-0.3				-5.0		-26.6*			
	138	Xbarc279				-2.0*												12.4*		
2B	47	Xgwm148										-9.7*							2	1
	93	Xwmc332												0.5						
2D	32	Xgwm455										-2							9	4
	48	Xgwm102					-2.7			21.5*				0.1						
	64	Xwmc18					-2.4													
	73	Xgwm157						-7.2*			6.6*		4.6*							
	91	Xgwm539			-10.6*						6.0*						4.7			
3A	45	Xgwm5			-26.5			-26.1				-13.4*							4	0
	116	Xgwm480					1.8													
3B	7	Xbarc133			-10.8*														6	0
	12	Xgwm493						-10.9*				-10.6*								
	60	Xbarc73						-8.5*				-7.8*								
	66	Xbarc319	9.1																	
3D	30	Xgwm52															34.3*		2	1
	80	Xbarc323															-1.4			
4A	12	Xgwm610		-3.3			4.1*							3.0*					3	1
	18	Xgwm397					4.3*													0
4B	25	Xgwm113																2.9	1	0
4D	10	Xwmc285													-16.1*				4	2
	27	Xbarc217										3.6								
	89	Xgwm624					7.4*													
	91	Xgwm609					5.0*							0.8						
5A	55	Xgwm415				-1.7*			0.6										6	2
	64	Xgwm304							0.5											
	64	Xgwm186							0.0	24*										
	75	Xbarc330					4.6*											9.1		
	110	Xbarc319																4.4		

Chr.	Pos. (cM)	Marker	BRT	EAR	GNE	HEA	HEI	HI	HLW	LAH	TGW	YLD	GH	GPC	SED	LR	PM	SEP	QTLs	Fav. [aa]
5D	4	Xbarc130		3.4									-14.6*						7	2
	16	Xbarc205			-12.1*															
	67	Xgwm212							-1.4*											
	82	Xbarc322										3.1	-8.2*				25.5			
6A	93	Xgwm427															-22.9		1	1
6B	44	Xbarc198			-9.9*				-1.1*	29.2*	-6.3*	-9.2*			10.5*				6	1
	48	Xgwm626			-11.5*						-6.2*	-6.6*			13.4*					
6D	35	Xcfd132										-10.1*							1	0
7A	144	Xbarc275									-2.1									0
7B	35	Xgwm537				-1.8*			0.0								26.2*		9	2
	40	Xgwm400							0.0							63.2*		9.5*		
	48	Xbarc65										-0.9								
	77	Xbarc278															-24.6			
	137	Xgwm577					1.1					-1.5								
7D	92	Xgwm437	12.9*					-5.5*									24.4*		3	0
		QTLs	2	2	5	5	8	5	5	3	5	11	3	4	5	1	9	5	78	
		Fav. [aa]	0	1	0	4	1	0	2	0	2	2	1	4	2	0	4	0		23

Gloss based on Appendix 9.

Appendix 11: Comparison of relative performances of exotic genotype (Syn-84) of 185 significant marker×trait associations in T84 and D84, specified as marker main effect or marker×environment interaction effect in high N-supply, computed using the three-way ANOVA single-locus analysis (ANOVA I).

Chr.	Pos. (cM)	Marker	Pop	BRT	EAR	GNE	HEA	HEI	HI	HLW	LAH	TGW	YLD	GH	GPC	SED	LR	PM	SEP	cQTL
1A	52	Xgwm357	D84					4.1*												0
	126	Xgwm99	D84													3.5				
1B	8	Xbarc194	T84													5.8				0
	26	Xgwm413	T84			-8.2														
	31	Xgwm498	T84			-3.5														
	92	Xwmc44	T84						-1.9											
	92	Xwmc44	D84							1.5*										
1D	75	Xgwm642	T84			6.2*	0.7													0
	75	Xgwm642	D84													-9.5*				
2A	53	Xgwm95	T84									3.8*						25.1*		4
	53	Xgwm95	D84					5.7*				5.7*								
	54	Xgwm558	T84					3.6*										26.0*		
	54	Xgwm558	D84					5.6*				5.2*								
	68	Xgwm445	D84					5.3*												
	76	Xgwm294	T84	1.3			-1.1*			0.2		6.2*				-8.5				

Chr.	Pos. (cM)	Marker	Pop	BRT	EAR	GNE	HEA	HEI	HI	HLW	LAH	TGW	YLD	GH	GPC	SED	LR	PM	SEP	cQTL
	76	Xgwm294	D84				-1.4*													
	126	Xgwm356	T84		4.7													-22.9		
	126	Xgwm356	D84				1.3*					-0.3				-5.0		-26.6*		
	138	Xbarc279	D84				-2.0*												12.4*	
2B	47	Xgwm148	T84															-20.3*	0.4	0
	47	Xgwm148	D84										-9.7*							
	79	Xgwm120	T84										-4.2							
	93	Xwmc332	T84																0.3	
	93	Xwmc332	D84												0.5					
2D	21	Xwmc503	T84										-11.7*							1
	32	Xgwm455	T84				-1.4*					2.2								
	32	Xgwm455	D84										-2.0							
	48	Xgwm102	D84					-2.7			21.5*				0.1					
	64	Xwmc18	T84				-1.5*					2.3								
	64	Xwmc18	D84					-2.4												
	73	Xgwm157	T84									5.3					9.2			
	73	Xgwm157	D84						-7.2*			6.6*		4.6*						
	91	Xgwm539	T84									4.5								
	91	Xgwm539	D84			-10.6*						6.0*						4.7		
	93	Xgwm349	T84				1.6													
3A	45	Xgwm5	T84	69.8*		-26.5*							-27.4*							2
	45	Xgwm5	D84			-26.5			-26.1				-13.4*							
	116	Xgwm480	T84				1.9*								-0.4					
	116	Xgwm480	D84					1.8												
3B	7	Xbarc133	D84			-10.8*														1
	12	Xgwm493	T84			-11.5*														
	12	Xgwm493	D84						-10.9*				-10.6*							
	60	Xbarc73	T84	68.7*									-16.7*				58.7	-40.8		
	60	Xbarc73	D84						-8.5*				-7.8*							
	66	Xbarc319	D84	9.1																
	111	Xbarc77	T84						-6.2*			-2.5		3.6*					3.7	
3D	20	Xgwm383	T84												-1.1					0
	30	Xgwm52	T84											-4.8*						
	30	Xgwm52	D84															34.3*		
	43	Xgwm3	T84													-8.3*		3.3		
	80	Xbarc323	D84															-1.4		
4A	12	Xgwm610	T84					4.4*				4.2*								1
	12	Xgwm610	D84		-3.3			4.1*							3.0*					
	18	Xgwm397	T84									4.2*								
	18	Xgwm397	D84					4.3*												
	38	Xwmc468	T84				-2.3*					6.3*								

Chr.	Pos. (cM)	Marker	Pop	BRT	EAR	GNE	HEA	HEI	HI	HLW	LAH	TGW	YLD	GH	GPC	SED	LR	PM	SEP	cQTL
	79	Xgwm160	T84					-6.3*										25.2*		
4B	25	Xgwm113	T84						-8.8*				-6.1							0
	25	Xgwm113	D84																2.9	
	31	Xgwm149	T84										-4.8		4.8					
	36	Xgwm251	T84						-9.0*				-2.8		5.1					
4D	10	Xwmc285	T84					7.2*			32.7*									0
	10	Xwmc285	D84													-16.1*				
	27	Xbarc217	D84										3.6							
	43	Xwmc331	T84									7.3*			5.8*					
	54	Xwmc399	T84									5.5*								
	89	Xgwm624	D84					7.4*												
	91	Xgwm609	D84					5.0*							0.8					
5A	34	Xgwm154	T84							0.9*										0
	55	Xgwm415	T84					4.5*			40.0		-0.6							
	55	Xgwm415	D84				-1.7*			0.6										
	64	Xgwm304	T84					4.5*			42.3		-0.3							
	64	Xgwm304	D84							0.5										
	64	Xgwm186	D84							0.0	24*									
	75	Xbarc330	D84					4.6*											9.1	
	110	Xbarc319	T84				-2.0*			0.4		0.8				14.0*				
	110	Xbarc319	D84																4.4	
5B	14	Xcfd60	T84								48.5									0
	38	Xgwm234	T84							-1.3*			-12.0*							
	61	Xgwm544	T84		-6.4								-14.0*					-21.9		
	124	Xgwm604	T84					0.4											-5.0	
5D	4	Xbarc130	T84											-15.7*	-0.7	-19.3				1
	4	Xbarc130	D84		3.4									-14.6*						
	16	Xbarc205	T84								23.4			-4.2*						
	16	Xbarc205	D84			-12.1*														
	23	Xbarc143	T84			-4.8*					25.0									
	44	Xgwm583	T84									3.6*								
	50	Xgwm182	T84								29.7									
	67	Xgwm212	T84					3.5*			25.9							28.3*		
	67	Xgwm212	D84							-1.4*										
	82	Xbarc322	D84										3.1	-8.2*				25.5		
6A	93	Xgwm427	T84									-5.2*								0
	93	Xgwm427	D84															-22.9		
6B	44	Xbarc198	D84			-9.9*				-1.1*	29.2*	-6.3*	-9.2*			10.5*				1
	48	Xgwm626	T84				-1.0					-6.0*		0.1	4.2*					
	48	Xgwm626	D84			-11.5*						-6.2*	-6.6*			13.4*				
	59	Xgwm219	T84												3.8*	19.2*				

Chr.	Pos. (cM)	Marker	Pop	BRT	EAR	GNE	HEA	HEI	HI	HLW	LAH	TGW	YLD	GH	GPC	SED	LR	PM	SEP	cQTL
6D	35	Xcfd132	D84										-10.1*							0
	53	Xgwm325	T84					-2.1												
	92	Xbarc96	T84	-4.5																
7A	30	Xgwm60	T84		-8.1*						9.3	6.2*			2.8*					0
	144	Xbarc275	D84									-2.1								
7B	35	Xgwm537	T84																4.1	0
	35	Xgwm537	D84				-1.8*			0.0								26.2*		
	40	Xgwm400	T84				-1.0*									-4.5		22.6*		
	40	Xgwm400	D84							0.0							63.2*		9.5*	
	48	Xbarc65	D84										-0.9							
	54	Xgwm46	T84															25.0*		
	58	Xgwm297	T84															27.7*		
	77	Xbarc278	D84															-24.6		
	118	Xwmc311	T84															34.0*		
	137	Xgwm577	T84		-1.3													38.0*		
	137	Xgwm577	D84					1.1					-1.5							
	142	Xwmc276	T84															32.7*		
	149	Xbarc123	T84					-1.8												
7D	28	Xbarc184	T84						-4.5*											0
	92	Xgwm437	T84					3.9*		-0.7*	6.2									
	92	Xgwm437	D84	12.9*					-5.5*									24.4*		
	136	Xgwm428	T84															-35.4*		
	143	Xwmc634	T84															-34.6*		
		QTLs	T84	2	1	4	7	7	3	3	1	8	5	3	3	3	0	7	0	11
		QTLs	D84	1	0	4	5	5	4	3	3	3	6	3	1	3	1	4	2	

Relative performance of exotic genotype (Syn-84) at a given marker locus for high N-supply across all tested environments computed using the GLM procedure specified a favourable QTL effect (+) with a positive effect from the exotic genotype (Syn-84) compared with the cultivar genotype (Triso or Devon) at a given marker locus. Gray highlighted RP values were favourable QTL effects with a positive effect from the exotic genotype (Syn-84) compared with the cultivar genotype (Triso or Devon) at a given marker locus. Framed RP values were common QTL for both advanced backcross populations T84 and D84. (*) RP values from a significant marker×trait association (P = 0.01) specified as a marker main effect (M). Chr.: Chromosomal location of the marker derived from Somers et al. (2004). Pos.: Position of the marker in cM on chromosome derived from Somers et al. (2004). Marker: Label of SSR marker described by Somers et al. (2004) and Song et al. (2005). Trait: BRT (Brittleness), EAR (Tillers per square meter), GNE (Grain number per ear), HEA (Days until heading), HEI (Plant height), HI (Harvest index), HLW (Grain test weight), LAH (Lodging at harvest), TGW (Thousand grain weight), YLD (Grain yield), GH (Grain hardness), GPC (Grain protein content), SED (Sedimentation value), LR (Leaf rust), PM (Powdery mildew), SEP (*Septoria* leaf blotch). QTLs: Number of QTLs (P = 0.01) specified as a marker main effect (M) or a marker×environment interaction effect (M×E). c QTLs: Number of common QTLs for both populations T84 and D84.

Appendix 12: Localisation of 58 significant marker×trait associations in T84, specified as marker main effects including 48 QTL, computed using a four-way ANOVA single-locus analysis (ANOVA II) for both N-levels.

Trait	Marker	Chr.	Pos. (cM)	n [aa]	Effect	Sign.	F-val.	R^2 (%)	N+ [AA]	N+ [aa]	$Diff._{N+}$ [aa]	N- [AA]	N- [aa]	$Diff._{N-}$ [aa]	$RP_{N+,N-}$ [aa]	QTL	QTL effect
BRT	Xgwm5	3A	45	13	M	**	93.9	37.3	1.1	1.9	0.8	1.1	1.8	0.7	70.4	*QBRT.T84-3A*	-

Trait	Marker	Chr.	Pos. (cM)	n [aa]	Effect	Sign.	F-val.	R^2 (%)	N+ [AA]	N+ [aa]	Diff.$_{N+}$ [aa]	N- [AA]	N- [aa]	Diff.$_{N-}$ [aa]	RP $_{N+,N-}$ [aa]	QTL	QTL effect
BRT	Xbarc73	3B	60	7	M	**	45.6	20.5	1.1	1.9	0.8	1.1	1.9	0.8	71.1	*QBRT.T84-3B*	-
EAR	Xgwm194	4D	82	27	M	*	8.3	3.7	617.7	596.9	-20.8	541.0	512.0	-29.0	-4.3	*QEAR.T84-4D*	-
EAR	Xgwm60	7A	30	28	M	*	13.5	8.6	619.2	569.2	-50.0	537.3	509.9	-27.4	-6.7	*QEAR.T84-7A*	-
GNE	Xgwm5	3A	45	13	M	**	88.9	21.2	28.0	20.6	-7.4	27.2	19.6	-7.6	-27.1	*QGNE.T84-3A*	-
HEA	Xgwm455	2D	32	23	M	*	7.9	4.0	86.2	85.0	-1.2	85.7	84.5	-1.2	-1.4	*QHEA.T84-2Da*	+
HEA	Xwmc18	2D	64	17	M	*	9.5	4.6	86.1	84.7	-1.4	85.6	84.0	-1.6	-1.7	*QHEA.T84-2Db*	+
HEA	Xwmc468	4A	38	19	M	**	18.1	20.0	86.3	84.4	-1.9	85.8	84.0	-1.8	-2.2	*QHEA.T84-4A*	+
HEA	Xbarc319[1]	5A	110	20	M	**	11.9	8.3	86.0	84.2	-1.8	85.4	83.9	-1.5	-1.9	*QHEA.T84-5A*	+
HEA	Xcfd266	5D	34	35	M	*	8.4	4.4	86.2	85.3	-0.9	85.7	84.6	-1.1	-1.2	*QHEA.T84-5D*	+
HEI	Xgwm558	2A	54	24	M	*	8.6	5.1	96.6	100.1	3.5	96.9	100.5	3.6	3.7	*QHEI.T84-2Aa*	-
HEI	Xgwm294	2A	76	34	M	*	7.4	3.5	97.1	99.9	2.8	97.4	100.2	2.8	2.9	*QHEI.T84-2Ab*	-
HEI	Xgwm610	4A	12	23	M	**	11.8	6.1	96.7	100.9	4.2	97.0	101.2	4.2	4.3	*QHEI.T84-4Aa*	-
HEI	Xgwm160	4A	79	21	M	**	24.2	11.3	98.3	92.1	-6.2	98.7	92.0	-6.7	-6.5	*QHEI.T84-4Ab*	+
HEI	Xwmc285	4D	10	8	M	*	7.5	9.5	96.8	103.8	7.0	97.8	102.3	4.5	5.9	*QHEI.T84-4D*	-
HEI	Xgwm415[×]	5A	55	20	M	**	11.4	5.4	97.0	101.4	4.4	97.4	101.7	4.3	4.5	*QHEI.T84-5A*	-
HEI	Xgwm304	5A	64	19	M	*	10.5	5.0	97.0	101.4	4.4	97.4	101.7	4.3	4.5	″	-
HEI	Xgwm212	5D	67	23	M	*	8.9	4.3	97.1	100.5	3.4	97.4	101.4	4.0	3.8	*QHEI.T84-5D*	-
HI	Xwmc503	2D	21	9	M	*	9.4	7.0	0.4	0.4	0.0	0.4	0.4	0.0	-9.2	*QHI.T84-2D*	-
HI	Xgwm113[×]	4B	25	22	M	*	12.2	4.8	0.4	0.4	0.0	0.4	0.4	0.0	-7.3	*QHI.T84-4B*	-
HI	Xgwm149	4B	31	14	M	*	7.1	2.8	0.4	0.4	0.0	0.4	0.4	0.0	-7.5	″	-
HI	Xbarc319[1]	5A	110	20	M	*	11.1	4.6	0.4	0.4	0.0	0.4	0.4	0.0	-6.5	*QHI.T84-5A*	-
HI	Xgwm234	5B	38	13	M	*	10.9	4.2	0.4	0.4	0.0	0.4	0.4	0.0	-8.5	*QHI.T84-5B*	-
HLW	Xgwm234	5B	38	13	M	**	12.7	4.7	78.4	77.4	-1.0	77.8	77.0	-0.8	-1.2	*QHLW.T84-5B*	-
LAH	Xgwm356	2A	126	20	M	*	7.1	3.3	3.7	4.5	0.8	2.2	2.8	0.6	23.7	*QLAH.T84-2A*	-
LAH	Xgwm3	3D	43	33	M	*	8.0	4.4	3.9	3.2	-0.7	2.4	1.7	-0.7	-21.0	*QLAH.T84-3D*	+
LAH	Xgwm160	4A	79	21	M	*	9.4	5.6	3.9	2.7	-1.2	2.3	1.7	-0.6	-29.5	*QLAH.T84-4A*	+
LAH	Xgwm154	5A	34	13	M	*	8.0	4.3	3.7	4.7	1.0	2.2	3.0	0.8	31.7	*QLAH.T84-5A*	-
LAH	Xgwm415	5A	55	20	M	*	13.4	14.3	3.6	5.1	1.5	2.1	3.6	1.5	50.4	″	-
LAH	Xgwm304[×]	5A	64	19	M	*	14.2	15.2	3.6	5.2	1.6	2.1	3.7	1.6	53.7	″	-
TGW	Xgwm294	2A	76	34	M	**	17.6	10.9	41.5	44.1	2.6	42.0	44.1	2.1	5.6	*QTGW.T84-2Ab*	+
TGW	Xgwm157	2D	73	22	M	*	10.7	6.9	41.7	43.9	2.2	42.1	44.4	2.3	5.4	*QTGW.T84-2Db*	+
TGW	Xgwm610	4A	12	23	M	*	7.2	3.9	41.8	43.6	1.8	42.2	43.7	1.5	3.8	*QTGW.T84-4A*	+
TGW	Xwmc468[×]	4A	38	19	M	**	15.6	17.9	42.0	44.6	2.6	42.4	44.6	2.2	5.7	″	+
TGW	Xwmc331[×]	4D	43	8	M	*	11.1	5.3	41.7	44.8	3.1	42.1	44.9	2.8	6.9	*QTGW.T84-4D*	+
TGW	Xwmc399	4D	54	13	M	*	9.3	4.7	41.7	44.0	2.3	42.0	44.1	2.1	5.2	″	+
TGW	Xgwm583	5D	44	29	M	*	10.5	5.0	41.7	43.2	1.5	42.0	43.8	1.8	3.9	*QTGW.T84-5D*	+
TGW	Xgwm427	6A	93	27	M	**	13.8	6.2	42.2	40.0	-2.2	42.5	40.9	-1.6	-4.6	*QTGW.T84-6A*	-
TGW	Xgwm626[×]	6B	48	23	M	**	22.1	11.1	42.2	39.7	-2.5	42.7	39.7	-3.0	-6.6	*QTGW.T84-6B*	-
TGW	Xgwm219	6B	59	19	M	*	11.0	4.9	42.1	40.4	-1.7	42.6	40.1	-2.5	-4.8	″	-
TGW	Xgwm60	7A	30	28	M	**	16.5	9.5	41.6	44.2	2.6	42.1	44.2	2.1	5.6	*QTGW.T84-7A*	+
YLD	Xwmc503	2D	21	9	M	*	7.4	7.0	66.3	58.9	-7.4	59.1	54.2	-4.9	-9.8	*QYLD.T84-2D*	-

Trait	Marker	Chr.	Pos. (cM)	n [aa]	Effect	Sign.	F-val.	R^2 (%)	N+ [AA]	N+ [aa]	Diff.$_{N+}$ [aa]	N- [AA]	N- [aa]	Diff.$_{N-}$ [aa]	RP $_{N+,N-}$ [aa]	QTL	QTL effect
YLD	Xgwm5	3A	45	13	M	*	20.9	39.7	66.6	48.3	-18.3	59.4	39.6	-19.8	-30.2	*QYLD.T84-3A*	-
YLD	Xbarc73	3B	60	7	M	**	13.3	8.6	65.9	54.9	-11.0	58.6	46.5	-12.1	-18.6	*QYLD.T84-3B*	-
YLD	Xgwm234	5B	38	13	M	**	12.4	6.7	66.2	58.3	-7.9	58.8	52.8	-6.0	-11.1	*QYLD.T84-5Ba*	-
YLD	Xgwm544	5B	61	8	M	**	11.6	5.9	65.7	56.5	-9.2	58.3	48.8	-9.5	-15.0	*QYLD.T84-5Bb*	-
GH	Xgwm558	2A	54	24	M	*	7.3	3.2	54.5	56.8	2.3	52.1	54.3	2.2	4.2	*QGH.T84-2Aa*	+
GH	Xgwm294	2A	76	34	M	**	12.4	5.3	54.6	56.7	2.1	52.1	54.9	2.8	4.6	*QGH.T84-2Ab*	+
GH	Xgwm52	3D	30	25	M	**	12.0	5.0	55.4	52.7	-2.7	53.0	50.1	-2.9	-5.1	*QGH.T84-3D*	-
GH	Xgwm251	4B	36	13	M	*	7.2	2.8	54.7	57.5	2.8	52.3	55.3	3.0	5.5	*QGH.T84-4B*	+
GH	Xbarc130$^{\times}$	5D	4	35	M	**	215.8	63.1	56.5	47.7	-8.8	53.9	45.3	-8.6	-15.8	*QGH.T84-5D*	-
GH	Xbarc205[1]	5D	16	37	M	*	8.5	3.8	55.5	53.2	-2.3	52.9	51.1	-1.8	-3.8	″	-
GPC	Xgwm413	1B	26	6	M	*	10.8	22.6	13.3	14.1	0.8	10.9	11.5	0.6	5.5	*QGPC.T84-1B*	+
GPC	Xgwm455	2D	32	23	M	*	7.8	2.8	13.7	13.9	0.2	11.2	11.7	0.5	2.9	*QGPC.T84-2D*	+
GPC	Xwmc331$^{\times}$	4D	43	8	M	**	15.3	5.5	13.7	14.5	0.8	11.3	12.1	0.8	6.6	*QGPC.T84-4D*	+
GPC	Xwmc399	4D	54	13	M	*	11.5	5.3	13.6	14.1	0.5	11.2	12.0	0.8	5.0	″	
GPC	Xgwm626$^{\times}$	6B	48	23	M	**	24.4	7.8	13.6	14.2	0.6	11.2	11.8	0.6	4.9	*QGPC.T84-6B*	+
GPC	Xgwm219	6B	59	19	M	**	15.2	4.9	13.7	14.2	0.5	11.2	11.7	0.5	4.3	″	+

Trait: BRT (Brittleness), EAR (Tillers per square meter), GNE (Grain number per ear), HEA (Days until heading), HEI (Plant height), HI (Harvest index), HLW (Grain test weight), LAH (Lodging at harvest), TGW (Thousand grain weight), YLD (Grain yield), GH (Grain hardness), GPC (Grain protein content). Marker: Label of SSR marker. ($^{\times}$) Significant marker×trait association computed with the highest F-value in a linked QTL cluster with a ≤ 20 cM distance. (1) Marker was not described by Somers et al. (2004) and Sourdille et al. (2004), respectively, estimated position in cM on chromosome by linked marker positions described by Somers et al. (2004) and Song et al. (2005). Chr.: Chromosomal location of the marker derived from Somers et al. (2004). Pos.: Position of the marker in cM on chromosome derived from Somers et al. (2004). n [aa]: Number of markers showing the exotic genotype (Syn-84). Effect: A significant marker×trait association (P = 0.01) was specified with marker main effect (M). Sign.: Level of significance computed using the GLM procedure of the significant marker×trait associations for marker main effect (M), (**) P = 0.001, (*) P = 0.01. F-val.: F-value was computed using the GLM procedure. R^2 (%): Proportion of the genetic variance computed using the GLM procedure, which was explained the marker main effect (M). N+ or N- [AA]: LS-means of trait values for high N-supply or low N-supply across all tested environments for BC_2F_4 lines carrying the cultivar genotype (Triso) at the given marker locus. N+ or N- [aa]: LS-means of trait values for high N-supply or low N-supply across all tested environments for BC_2F_4 lines carrying the exotic genotype (Syn-84) at the given marker locus. Diff.$_{N+}$ or $_{N-}$ [aa]: Difference between LS-means of the exotic and the cultivar genotype, N+ [aa] - N+ [AA] or N- [aa] – N- [AA]. RP$_{N+,N-}$ [aa]: Mean of relative performances (RP$_{N+}$, RP$_{N-}$) of exotic genotype (Syn-84) at a given marker locus across all tested environments computed using the GLM procedure. Relative performance was computed as ([aa] - [AA])×100 / [AA], where [AA] or [aa] were LS-means of BC_2F_4 lines carrying the cultivar genotype (Triso) or the exotic genotype (Syn-84) at the given marker locus. QTL: A significant marker×trait association was specified as QTL, if marker main effect (M), was significant with P = 0.01 in the GLM procedure. Linked QTL with a ≤ 20 cM distance were interpreted as one QTL. The QTL label is consisting of Q (for QTL), YLD (tested trait), T84 (tested population), 4Ab (chromosome, where the QTL was detected and b for the second YLD-QTL on the same chromosome). QTL effect: Relative performance of exotic genotype (Syn-84) at a given marker locus for HIGH N-supply or LOW N-supply computed using the GLM procedure specified a favourable QTL effect (+) with a positive effect from the exotic genotype (Syn-84) compared with the cultivar genotype (Triso), a not favourable QTL effect (-) with a negative effect from the exotic genotype (Syn-84) compared with the cultivar genotype (Triso) at a given marker locus.

Appendix 13: Localisation of 62 significant marker×trait associations in D84, specified as marker main effects including 48 QTL, computed using a four-way ANOVA single-locus analysis (ANOVA II) for both N-levels.

Trait	Marker	Chr.	Pos. (cM)	n [aa]	Effect	Sign.	F-val.	R^2 (%)	N+ [AA]	N+ [aa]	Diff.$_{N+}$ [aa]	N- [AA]	N- [aa]	Diff.$_{N-}$ [aa]	RP $_{N+,N-}$ [aa]	QTL	QTL effect
BRT	Xgwm5	3A	45	13	M/M×N	**	110.2	40.3	1.1	1.7	0.6	1.2	2.0	0.8	61.5	*QBRT.D84-3A*	-
BRT	Xbarc73	3B	60	10	M	**	26.4	11.7	1.1	1.5	0.4	1.2	1.7	0.5	37.6	*QBRT.D84-3Ba*	-

Trait	Marker	Chr.	Pos. (cM)	n [aa]	Effect	Sign.	F-val.	R^2 (%)	N+ [AA]	N+ [aa]	Diff.$_{N+}$ [aa]	N- [AA]	N- [aa]	Diff.$_{N-}$ [aa]	RP $_{N+,N-}$ [aa]	QTL	QTL effect
EAR	Xgwm544	5B	61	10	M	*	7.9	3.8	577.0	544.0	-33.0	525.5	491.1	-34.4	-6.1	*QEAR.D84-5B*	-
EAR	Xbarc205[1]	5D	16	20	M	*	8.6	4.5	568.5	597.0	28.5	517.1	545.6	28.5	5.3	*QEAR.D84-5Db*	+
EAR	Xgwm46[×]	7B	54	29	M	*	10.5	6.7	575.0	547.1	-27.9	526.7	499.7	-27.0	-5.0	*QEAR.D84-7B*	-
EAR	Xgwm297	7B	58	31	M	*	10.4	6.8	576.4	545.4	-31.0	526.6	500.0	-26.6	-5.2	″	-
GNE	Xgwm102	2D	48	31	M	*	7.2	3.2	28.1	26.7	-1.4	28.0	25.9	-2.1	-6.3	*QGNE.D84-2Da*	-
GNE	Xgwm157	2D	73	26	M	**	16.6	8.1	28.3	25.1	-3.2	27.9	25.2	-2.7	-10.7	*QGNE.D84-2Db*	-
GNE	Xgwm493	3B	12	8	M	**	13.2	5.6	28.0	23.7	-4.3	27.8	23.5	-4.3	-15.6	*QGNE.D84-3Bb*	-
GNE	Xbarc205[1]	5D	16	20	M	**	13.6	7.0	28.2	24.8	-3.4	27.9	24.9	-3.0	-11.5	*QGNE.D84-5D*	-
GNE	Xgwm626	6B	48	15	M	*	7.8	3.4	28.0	24.8	-3.2	27.6	25.7	-1.9	-9.2	*QGNE.D84-6B*	-
HEA	Xgwm294	2A	76	23	M	*	7.1	4.3	86.3	85.1	-1.2	85.8	84.8	-1.0	-1.3	*QHEA.D84-2Aa*	+
HEA	Xgwm356	2A	126	26	M	*	8.3	5.7	86.1	87.3	1.2	85.7	86.8	1.1	1.3	*QHEA.D84-2Ab*	-
HEA	Xgwm415[×]	5A	55	24	M	*	9.9	6.6	86.4	84.9	-1.5	85.9	84.7	-1.2	-1.6	*QHEA.D84-5A*	+
HEA	Xgwm304	5A	64	22	M	*	7.2	4.6	86.3	85.1	-1.2	85.9	84.8	-1.1	-1.4	″	+
HEA	Xgwm537[×]	7B	35	20	M	*	11.0	6.6	86.3	84.8	-1.5	85.9	84.5	-1.4	-1.7	*QHEA.D84-7B*	+
HEA	Xgwm400	7B	40	23	M	*	7.9	4.6	86.3	85.2	-1.1	85.9	84.7	-1.2	-1.3	″	+
HEI	Xgwm357	1A	52	18	M	*	8.7	5.6	101.2	105.4	4.2	103.0	106.8	3.8	3.9	*QHEI.D84-1A*	-
HEI	Xgwm95	2A	53	14	M	**	12.9	10.0	101.1	106.9	5.8	102.9	109.0	6.1	5.9	*QHEI.D84-2A*	-
HEI	Xgwm558[×]	2A	54	17	M	**	16.8	11.5	101.1	106.7	5.6	102.8	109.0	6.2	5.8	″	-
HEI	Xgwm445	2A	68	7	M	*	9.6	6.5	101.3	106.7	5.4	102.9	110.3	7.4	6.3	″	-
HEI	Xgwm610	4A	12	20	M	*	9.8	5.8	101.2	105.4	4.2	103.0	106.7	3.7	3.8	*QHEI.D84-4A*	-
HEI	Xgwm397[×]	4A	18	18	M	*	11.0	6.9	101.1	105.4	4.3	102.8	107.1	4.3	4.3	″	-
HEI	Xgwm624[×]	4D	89	5	M	*	9.8	5.7	101.5	109.0	7.5	103.2	110.3	7.1	7.1	*QHEI.D84-4D*	-
HEI	Xgwm609	4D	91	9	M	*	7.9	4.4	101.4	106.4	5.0	103.1	107.9	4.8	4.8	″	-
HEI	Xgwm304	5A	64	22	M	*	7.8	4.6	101.3	104.5	3.2	103.0	106.5	3.5	3.3	*QHEI.D84-5A*	-
HEI	Xgwm186	5A	64	25	M	*	7.1	4.6	101.1	103.9	2.8	102.8	106.0	3.2	2.9	″	-
HEI	Xbarc330[1×]	5A	75	19	M	**	15.7	14.7	101.0	105.7	4.7	102.7	107.0	4.3	4.4	″	-
HI	Xgwm157	2D	73	26	M	**	11.8	5.0	0.4	0.4	0.0	0.4	0.4	0.0	-5.8	*QHI.D84-2D*	-
HI	Xgwm493	3B	12	8	M	**	13.1	5.5	0.4	0.4	0.0	0.4	0.4	0.0	-10.8	*QHI.D84-3Ba*	-
HLW	Xwmc44	1B	92	14	M	*	8.4	8.7	76.9	78.0	1.1	77.4	78.3	0.9	1.4	*QHLW.D84-1B*	+
HLW	Xgwm337	1D	48	21	M	*	8.0	4.5	77.0	77.7	0.7	77.3	78.2	0.9	1.0	*QHLW.D84-1D*	+
HLW	Xgwm212	5D	67	19	M	*	8.2	4.3	77.3	76.2	-1.1	77.6	77.0	-0.6	-1.0	*QHLW.D84-5D*	-
HLW	Xbarc198	6B	44	22	M	*	8.9	3.9	77.2	76.4	-0.8	77.6	76.9	-0.7	-1.0	*QHLW.D84-6B*	-
HLW	Xgwm626[×]	6B	48	15	M	*	9.8	4.3	77.2	76.4	-0.8	77.6	76.5	-1.1	-1.3	″	-
HLW	Xcfd132	6D	35	8	M	*	8.6	8.5	77.2	76.2	-1.0	77.7	76.1	-1.6	-1.7	*QHLW.D84-6D*	-
HLW	Xgwm46	7B	54	29	M	*	8.1	4.5	77.2	76.7	-0.5	77.6	76.7	-0.9	-0.9	*QHLW.D84-7Bb*	-
LAH	Xgwm356	2A	126	26	M	*	7.3	4.7	4.4	5.1	0.7	2.6	3.2	0.6	18.4	*QLAH.D84-2A*	-
LAH	Xgwm102	2D	48	31	M/M×N	*	8.5	5.2	4.4	5.3	0.9	2.7	3.1	0.4	19.0	*QLAH.D84-2D*	-
LAH	Xgwm610	4A	12	20	M	*	8.7	5.7	4.5	5.5	1.0	2.7	3.4	0.7	23.1	*QLAH.D84-4A*	-
LAH	Xbarc217[1]	4D	27	28	M	*	9.9	5.6	4.7	3.9	-0.8	2.8	2.2	-0.6	-18.9	*QLAH.D84-4D*	+
LAH	Xgwm186	5A	64	25	M	*	10.9	7.0	4.4	5.5	1.1	2.7	3.3	0.6	23.4	*QLAH.D84-5A*	-
LAH	Xbarc198	6B	44	22	M/M×N	*	12.4	8.4	4.4	5.7	1.3	2.7	3.3	0.6	27.5	*QLAH.D84-6B*	-

Trait	Marker	Chr.	Pos. (cM)	n [aa]	Effect	Sign.	F-val.	R^2 (%)	N+ [AA]	N+ [aa]	Diff.$_{N+}$ [aa]	N- [AA]	N- [aa]	Diff.$_{N-}$ [aa]	RP $_{N+,N-}$ [aa]	QTL	QTL effect
TGW	Xgwm95	2A	53	14	M	*	8.1	5.4	44.3	46.8	2.5	44.8	47.5	2.7	5.8	*QTGW.D84-2Aa*	+
TGW	Xgwm157[×]	2D	73	26	M	**	20.7	12.0	44.1	47.0	2.9	44.7	47.2	2.5	6.1	*QTGW.D84-2D*	+
TGW	Xgwm539	2D	91	22	M	**	14.4	8.3	44.1	46.7	2.6	44.6	46.9	2.3	5.6	″	+
TGW	Xbarc198[×]	6B	44	22	M	**	12.8	9.5	45.0	42.1	-2.9	45.5	42.7	-2.8	-6.2	*QTGW.D84-6B*	-
TGW	Xgwm626	6B	48	15	M	*	11.0	7.6	44.8	42.0	-2.8	45.3	42.2	-3.1	-6.5	″	-
YLD	Xgwm148	2B	47	13	M	**	12.7	6.8	62.6	56.6	-6.0	57.6	53.2	-4.4	-8.7	*QYLD.D84-2B*	-
YLD	Xgwm5	3A	45	13	M	*	13.6	16.4	62.6	54.2	-8.4	57.7	49.8	-7.9	-13.5	*QYLD.D84-3A*	-
YLD	Xgwm493	3B	12	8	M	**	16.0	9.4	62.3	55.7	-6.6	57.6	48.4	-9.2	-13.2	*QYLD.D84-3Ba*	-
YLD	Xbarc73	3B	60	10	M	*	10.3	6.5	62.2	57.4	-4.8	57.6	51.1	-6.5	-9.5	*QYLD.D84-3Bb*	-
YLD	Xgwm624[×]	4D	89	5	M	*	7.9	6.0	62.2	55.0	-7.2	57.5	48.9	-8.6	-13.2	*QYLD.D84-4Db*	-
YLD	Xgwm609	4D	91	9	M	*	7.9	4.7	62.4	57.9	-4.5	57.6	51.8	-5.8	-8.6	″	-
YLD	Xbarc330[1]	5A	75	19	M	*	7.7	8.6	62.6	58.8	-3.8	58.1	53.7	-4.4	-6.8	*QYLD.D84-5A*	-
YLD	Xbarc198[×]	6B	44	22	M	**	17.5	10.0	63.0	57.3	-5.7	57.9	53.8	-4.1	-8.1	*QYLD.D84-6B*	-
YLD	Xgwm626	6B	48	15	M	*	8.2	5.1	62.4	58.3	-4.1	57.7	53.1	-4.6	-7.3	″	-
YLD	Xcfd132	6D	35	8	M	*	8.9	10.8	62.5	56.2	-6.3	58.0	51.2	-6.8	-10.9	*QYLD.D84-6D*	-
GH	Xbarc130	5D	4	28	M	**	177.3	44.7	56.9	48.6	-8.3	54.2	46.4	-7.8	-14.6	*QGH.D84-5Da*	-
GH	Xbarc322[1]	5D	82	15	M	**	16.3	8.1	56.2	51.5	-4.7	53.5	49.8	-3.7	-7.7	*QGH.D84-5Db*	-
GPC	Xbarc319[1]	5A	110	5	M	*	11.7	12.4	13.6	14.4	0.8	11.4	12.1	0.7	6.2	*QGPC.D84-5A*	+
GPC	Xgwm583	5D	44	22	M	*	7.9	3.4	13.6	13.8	0.2	11.4	11.8	0.4	2.6	*QGPC.D84-5D*	+

Gloss based on Appendix 12.

Appendix 14: Listing of all detected 130 QTLs in T84, computed using the three-way ANOVA I single-locus analysis, four-way ANOVA II single-locus analysis, three-way REML I single-locus analysis and REML II forward selection method, four-way REML III single-locus analysis and REML IV forward selection method.

Trait	Chr.	QTL	three-way methods			four-way methods			cQTL
			ANOVA I	REML I	REML II	ANOVA II	REML III	REML IV	
BRT	2A	*QBrt.T84-2A*	M×E						2
	3A	*QBrt.T84-3A*	M			M			
	3B	*QBrt.T84-3B*	M			M			
	6D	*QBrt.T84-6D*	M×E						
EAR	2A	*QEar.T84-2A*	M×E						1
	7A	*QEar.T84-7A*	M	M	M	M			
	5B	*QEar.T84-5B*	M×E						
	7B	*QEar.T84-7B*	M×E						
	4D	*QEar.T84-4D*				M			
GNE	3A	*QGne.T84-3A*	M			M			1
	1B	*QGne.T84-1B*	M×E						
	3B	*QGne.T84-3B*	M						
	1D	*QGne.T84-1D*	M						
	5D	*QGne.T84-5D*	M						
HEA	2A	*QHea.T84-2A*	M						4
	3A	*QHea.T84-3A*	M						
	4A	*QHea.T84-4A*	M	M	M	M	M	M	
	5A	*QHea.T84-5A*	M/M×E	M		M			
	1D	*QHea.T84-1D*	M×E						
	2D	*QHea.T84-2Da*	M			M			
	2D	*QHea.T84-2Db*	M			M			
	2D	*QHea.T84-2Dc*	M×E						
	5D	*QHea.T84-5D*				M			
	6B	*QHea.T84-6B*	M×E						
	7B	*QHea.T84-7B*	M						
HEI	2A	*QHei.T84-2Aa*	M			M			7
	2A	*QHei.T84-2Ab*				M			
	4A	*QHei.T84-4Aa*	M			M			
	4A	*QHei.T84-4Ab*	M	M	M	M	M	M	
	5A	*QHei.T84-5A*	M/M×E			M			
	5B	*QHei.T84-5B*	M×E						
	7B	*QHei.T84-7B QHei-N.T84-7B*	M×E			M×N			
	4D	*QHei.T84-4D*	M			M			
	5D	*QHei.T84-5D*	M			M			
	6D	*QHei.T84-6D*	M×E						
	7D	*QHei.T84-7D*	M						
HI	5A	*QHi.T84-5A*				M			1
	1B	*QHi.T84-1B*	M×E						
	3B	*QHi.T84-3B*	M						
	4B	*QHi.T84-4B*	M			M			
	5B	*QHi.T84-5B*				M			
	6B	*QHi-N.T84-6B*				M×N			
	2D	*QHi.T84-2D*				M			
	7D	*QHi.T84-7D*	M						
HLW	2A	*QHlw.T84-2A*	M×E						1
	5A	*QHlw.T84-5Aa*	M						
	5A	*QHlw.T84-5Ab*	M×E						
	4B	*QHlw-N.T84-4B*				M×N			
	5B	*QHlw.T84-5B*	M			M			
	4D	*QHlw-N.T84-4D*				M×N			
	5D	*QHlw-N.T84-5D*				M×N			
	7D	*QHlw.T84-7D*	M						
LAH	2A	*QLah.T84-2A*				M			3
	4A	*QLah.T84-4A*				M			
	5A	*QLah.T84-5A*	M×E			M			
	7A	*QLah.T84-7A QLah-N.T84-7A*	M×E			M×N			

APPENDIX

Trait	Chr.	QTL	three-way methods			four-way methods			cQTL
			ANOVA I	REML I	REML II	ANOVA II	REML III	REML IV	
	5B	*QLah.T84-5B*	M×E						
	3D	*QLah.T84-3D*				M			
	4D	*QLah.T84-4D QLah-N.T84-4D*	M			M×N			
	5D	*QLah.T84-5Da*	M×E						
	5D	*QLah.T84-5Db*	M×E						
	7D	*QLah.T84-7D*	M×E						
TGW	2A	*QTgw.T84-2Aa*	M						8
	2A	*QTgw.T84-2Ab*	M/M×E	M	M	M			
	4A	*QTgw.T84-4A*	M			M			
	5A	*QTgw.T84-5A*	M×E						
	6A	*QTgw.T84-6A*	M			M			
	7A	*QTgw.T84-7A*	M/M×E	M		M			
	3B	*QTgw.T84-3B*	M×E						
	5B	*QTgw-N.T84-5B*				M×N			
	6B	*QTgw.T84-6B*	M			M	M	M	
	2D	*QTgw.T84-2Da*	M×E						
	2D	*QTgw.T84-2Db*	M×E			M			
	4D	*QTgw.T84-4D*	M			M			
	5D	*QTgw.T84-5D*	M			M			
YLD	3A	*QYld.T84-3A*	M/M×E	M	M	M	M	M	6
	5A	*QYld.T84-5A QYld-N.T84-5A*	M×E			M×N			
	2B	*QYld.T84-2B*	M×E						
	3B	*QYld.T84-3B*	M/M×E			M	M		
	4B	*QYld.T84-4B*	M×E						
	5B	*QYld.T84-5Ba*	M	M	M	M			
	5B	*QYld.T84-5Bb*	M			M			
	7B	*QYld-N.T84-7B*				M×N			
	2D	*QYld.T84-2D*	M			M			
	2D	*QYld-N.T84-2D*				M×N			
GH	2A	*QGh.T84-2Aa*				M			2
	2A	*QGh.T84-2Ab*				M			
	3B	*QGh.T84-3B*	M						
	4B	*QGh.T84-4B*				M			
	6B	*QGh.T84-6B*	M×E						
	3D	*QGh.T84-3D*	M			M			
	5D	*QGh.T84-5D*	M			M			
GPC	3A	*QGpc.T84-3A*	M×E						2
	7A	*QGpc.T84-7A*	M						
	1B	*QGpc.T84-1B*				M			
	4B	*QGpc.T84-4B*	M×E						
	6B	*QGpc.T84-6B*	M			M			
	2D	*QGpc.T84-2D*				M			
	3D	*QGpc.T84-3D*	M×E						
	4D	*QGpc.T84-4D*	M			M			
	5D	*QGpc.T84-5D*	M×E						
SED	2A	*QSed.T84-2A*	M×E						0
	5A	*QSed.T84-5A*	M						
	1B	*QSed.T84-1B*	M×E						
	6B	*QSed.T84-6B*	M						
	7B	*QSed.T84-7B*	M×E						
	3D	*QSed.T84-3D*	M						
	5D	*QSed.T84-5D*	M×E						
LR	3B	*QLr.T84-3B*	M×E						0
	2D	*QLr.T84-2D*	M×E						
PM	2A	*QPm.T84-2Aa*	M						2
	2A	*QPm.T84-2Ab*	M×E						
	4A	*QPm.T84-4A*	M						
	2B	*QPm.T84-2B*	M/M×E						
	3B	*QPm.T84-3B*	M×E						
	5B	*QPm.T84-5B*	M×E						
	7B	*QPm.T84-7Ba*	M/M×E						
	7B	*QPm.T84-7Bb*	M	M					
	3D	*QPm.T84-3D*	M×E						

Trait	Chr.	QTL	three-way methods			four-way methods			cQTL
			ANOVA I	REML I	REML II	ANOVA II	REML III	REML IV	
	5D	*QPm.T84-5D*	M/M×E						
	7D	*QPm.T84-7D*	M/M×E	M	M				
SEP	2B	*QSep.T84-2Ba*	M×E						0
	2B	*QSep.T84-2Bb*	M×E						
	3B	*QSep.T84-3B*	M×E						
	5B	*QSep.T84-5B*	M×E						
	7B	*QSep.T84-7B*	M×E						
Total		130	105	10	7	59	5	4	40

Gray highlighted QTLs were stable across QTL mapping methods. Trait: BRT (Brittleness), EAR (Tillers per square meter), GNE (Grain number per ear), HEA (Days until heading), HEI (Plant height), HI (Harvest index), HLW (Grain test weight), LAH (Lodging at harvest), TGW (Thousand grain weight), YLD (Grain yield), GH (Grain hardness), GPC (Grain protein content), SED (Sedimentation value), LR (Leaf rust), PM (Powdery mildew), SEP (*Septoria* leaf blotch). QTL: A significant marker×trait association was specified as QTL, if marker main effect (M) or marker×environment interaction effect (M×E) or marker×nitrogen interaction effect (M×N) was significant with P = 0.01 in the ANOVA or REML analysis. Linked QTL with a ≤ 20 cM distance were interpreted as one QTL. The QTL label is consisting of Q (for QTL), YLD (tested trait), N (computed for two N supplies), T84 (tested population), 4Ab (chromosome, where the QTL was detected and b for the second YLD-QTL on the same chromosome). ANOVA I and II: A significant marker×trait association was specified with a marker main effect (M), marker×environment interaction effect (M×E) or marker×nitrogen interaction effect (M×N) at P = 0.01. These results were computed using a three-way ANOVA single-locus analysis (I) and four-way ANOVA single-locus analysis (II). REML I to IV: A significant marker×trait association was specified with marker main effect (M) at P = 0.01. These results were computed with a three-way REML I single-locus analysis and REML II forward selection, a four-way REML III single-locus analysis and REML IV forward selection. cQTL: Number of common QTLs detected in not less than two different calculations.

Appendix 15: Listing of all detected 109 QTLs in D84, computed using the three-way ANOVA I single-locus analysis, four-way ANOVA II single-locus analysis, three-way REML I single-locus analysis and REML II forward selection method, four-way REML III single-locus analysis and REML IV forward selection method.

Trait	Chr.	QTL	three-way methods			four-way methods			cQTL
			ANOVA I	REML I	REML II	ANOVA II	REML III	REML IV	
BRT	2A	*QBrt-N.D84-2A*				M×N			0
	3A	*QBrt.D84-3A*				M/M×N			
	3B	*QBrt.D84-3Ba*				M			
	3B	*QBrt.D84-3Bb*	M×E						
	7B	*QBrt.D84-7D*	M						
EAR	3A	*QEar-N.D84-3A*				M×N			0
	4A	*QEar.D84-4A*	M×E						
	5B	*QEar.D84-5B*				M			
	7B	*QEar.D84-7B*				M			
	5D	*QEar.D84-5Da*	M×E						
	5D	*QEar.D84-5Db*				M			
GNE	3A	*QGne.D84-3A*	M×E						2
	3B	*QGne.D84-3Ba*	M						
	3B	*QGne.D84-3Bb*				M			
	6B	*QGne.D84-6B*	M			M			
	2D	*QGne.D84-2Da*				M			
	2D	*QGne.D84-2Db*				M			
	2D	*QGne.D84-2Dc*	M						
	5D	*QGne.D84-5D*	M			M			
HEA	2A	*QHea.D84-2Aa*	M			M			4
	2A	*QHea.D84-2Ab*	M			M			
	2A	*QHea.D84-2Ac*	M/M×E						
	5A	*QHea.D84-5A*	M/M×E			M			
	7B	*QHea.D84-7B*	M			M			
HEI	1A	*QHei.D84-1A*	M			M			5
	2A	*QHei.D84-2A*	M/M×E	M	M	M	M	M	
	3A	*QHei.D84-3A*	M×E						
	4A	*QHei.D84-4A*	M			M			
	5A	*QHei.D84-5A*	M	M		M	M		
	7B	*QHei.D84-7B*	M×E						
	2D	*QHei.D84-2D*	M×E						
	4D	*QHei.D84-4D*	M			M			

Trait	Chr.	QTL	three-way methods			four-way methods			cQTL
			ANOVA I	REML I	REML II	ANOVA II	REML III	REML IV	
	5D	*QHei-N.D84-5D*				M×N			
HI	3A	*QHi.D84-3A*	M×E						2
	3B	*QHi.D84-3Ba*	M			M			
	3B	*QHi.D84-3Bb*	M						
	2D	*QHi.D84-2D*	M			M			
	7D	*QHi.D84-7D*	M						
HLW	1B	*QHlw.D84-1B*	M			M			4
	5A	*QHlw-N.D84-5Aa*				M×N			
	5A	*QHlw.D84-5A*							
		QHlw-N.D84-5Ab	M×E			M×N			
	6B	*QHlw.D84-6B*	M			M			
	7B	*QHlw.D84-7Ba*	M×E						
	7B	*QHlw.D84-7Bb*				M			
	7B	*QHlw-N.D84-7Ba*				M×N			
	7B	*QHlw-N.D84-7Bb*				M×N			
	1D	*QHlw.D84-1D*				M			
	3D	*QHlw-N.D84-3D*				M×N			
	5D	*QHlw.D84-5D*	M			M			
	6D	*QHlw.D84-6D*				M			
LAH	2A	*QLah.D84-2A*				M			3
	4A	*QLah.D84-4A*				M			
	5A	*QLah.D84-5A*	M			M			
	6B	*QLah.D84-6B*	M			M/M×N			
	2D	*QLah.D84-2D*	M			M/M×N			
	4D	*QLah.D84-4D*				M			
TGW	2A	*QTgw.D84-2Aa*	M			M			3
	2A	*QTgw.D84-2Ab*	M×E						
	7A	*QTgw.D84-7A*	M×E						
	6B	*QTgw.D84-6B*	M			M			
	2D	*QTgw.D84-2D*	M	M	M	M	M	M	
YLD	3A	*QYld.D84-3A*	M/M×E			M			6
	5A	*QYld.D84-5A*				M			
	2B	*QYld.D84-2B*	M			M			
	3B	*QYld.D84-3Ba*	M			M	M	M	
	3B	*QYld.D84-3Bb*	M			M			
	6B	*QYld.D84-6B*	M	M		M			
	7B	*QYld-N.D84-7B*				M×N			
	7B	*QYld.D84-7Ba*	M×E						
	7B	*QYld.D84-7Bb*	M×E						
	2D	*QYld.D84-2D*	M×E						
	2D	*QYld-N.D84-2Da*				M×N			
	2D	*QYld-N.D84-2Db*				M×N			
	4D	*QYld.D84-4Da*	M×E						
	4D	*QYld.D84-4Db*				M			
	5D	*QYld.D84-5D*	M×E						
	6D	*QYld.D84-6D*	M			M			
GH	2D	*QGh.D84-2D*	M						2
	5D	*QGh.D84-5Da*	M			M			
	5D	*QGh.D84-5Db*	M			M			
	5D	*QGh-N.D84-5D*				M×N			
GPC	4A	*QGpc.D84-4A*	M						0
	5A	*QGpc.D84-5A*				M			
	2B	*QGpc.D84-2B*	M×E						
	1D	*QGpc-N.D84-1D*				M×N			
	2D	*QGpc.D84-2D*	M×E						
	4D	*QGpc.D84-4D*	M×E						
	5D	*QGpc.D84-5D*				M			
SED	1A	*QSed.D84-1A*	M×E						0
	2A	*QSed.D84-2A*	M×E						
	6B	*QSed.D84-6B*	M						
	1D	*QSed.D84-1D*	M						
	4D	*QSed.D84-4D*	M						
LR	7B	*QLr.D84-7B*	M						0
PM	2A	*QPm.D84-2A*	M						0
	6A	*QPm.D84-6A*	M×E						

Trait	Chr.	QTL	three-way methods			four-way methods			cQTL
			ANOVA I	REML I	REML II	ANOVA II	REML III	REML IV	
	7B	*QPm.D84-7Ba*	M						
	7B	*QPm.D84-7Bb*	M×E						
	2D	*QPm.D84-2D*	M×E						
	3D	*QPm.D84-3Da*	M						
	3D	*QPm.D84-3Db*	M×E						
	5D	*QPm.D84-5D*	M×E						
	7D	*QPm.D84-7D*	M/M×E						
SEP	2A	*QSep.D84-2A*	M						0
	5A	*QSep.D84-5Aa*	M×E						
	5A	*QSep.D84-5Ab*	M×E						
	4B	*QSep.D84-4B*	M×E						
	7B	*QSep.D84-7B*	M						
Total		109	78	4	2	61	4	3	31

Gloss based on Appendix 14.

Appendix 16: Listing of 17 QTLs detected using three-way and/or four-way REML mapping methods validated by other AB-QTL, QTL and candidate gene studies in wheat.

Trait	QTL	Marker	REML mapping methods	F-val.	R^2 (%)	QTL or candidate gene	R^2	Distance to QTL (cM)	Reference
EAR	*QEar.T84-7A*	Xgwm60	I, II	16.1	24.2	*Qyld.csdh. 7AS1*	-	0	Quarrie et al. (2006)
						QTn.ipk-7A	10.8	4	Huang et al. (2003b)
						QTn.ipk-7A	13.6	> 20	Huang et al. (2004)
						QTp.ccsu-7A.3	3.7	> 20	Kumar et al. (2007)
						Qyld.csdh.7AL	-	> 20	Quarrie et al. (2006)
						tiller number-7A	-	u.p.	Snape et al. (2007)
HEA	*QHea.T84-4A*	Xwmc468	I, II	20.4	22.2	*QFlt.nau-4A.1*	10.6	0	Lin et al. (2008)
			III, IV	15.7	20.5	*QFlt.nau-4A.2*, *Ppd*	19.1	8	Lin et al. (2008)
						MQTL7-HD	8.1	19	Hanocq et al. (2007)
						QEet.ipk-4A	-	> 20	Börner et al. (2002)
						QDh.ccsu-4A.1	7.7	> 20	Kulwal et al. (2003)
						QEet.ipk-4A	22.7	4AL	Huang et al. (2004)
						QEet.ocs-4A.1, *Wx-B1*	46.0	4AL	Araki et al. (1999)
						Eps	-	u.p.	Hoogendoorn (1985)
HEA	*QHea.T84-5A*	Xbarc319[1]	I, II	13.9	9.4	*QHea.T84-5A.a*	7.9	0	Mohamed (2007)
						DSF6-DSF7-HD	-	0	Peng et al. (2003)
						VRQTL_5A, Vrn-A1, Fr-A1	5.9	5	Hanocq et al. (2004)
						Vrn-A1	-	7	Chao et al. (2007)
						QEet.fcu-5A, Vrn-A1	41.0	7	Chu et al. (2008)
						Xgwm271-Hea, Vrn-A1	41.0	20	Kuchel et al. (2006)
						MQTL10-HD, Vrn-A1	10.3	> 20	Hanocq et al. (2007)
						QEet.whs-5A, Vrn-A1	22.6	> 20	Klahr et al. (2007)
						QHdg.crc-5A, *B1*	14.6	> 20	Cuthbert et al. (2008)
						QHea.Z86-5A.a	9.6	> 20	Kunert (2007a)
						QEet.ipk-5A	9.0	> 20	Huang et al. (2003b)
						Xcdo412-Xpsr574-Head, Eps	12.5	> 20	Ahmed et al. (2000)
						QEet.ocs-5A.2, Eps	-	5AS	Kato et al. (1999b)
						Xcdo504–Xpsr426-HD, Vrn-A^{m}1, Nse-5A^m	10.0	5AL	Shindo et al. (2002)

Trait	QTL	Marker	REML mapping methods	F-val.	R^2 (%)	QTL or candidate gene	R^2	Distance to QTL (cM)	Reference
						QEet.ocs-5A.1, Vrn-A1, Q	51.0	5AL	Kato et al. (1999a, 2003)
						QEet.fcu-5AL, Q	38.0	5AL	Liu et al. (2005)
						Xpsr574a-VS, Ppd	19.1	5AL	Shindo et al. (2003)
						Xtam75-HT, *Xglk407-LD*, *Ppd*	8.2	5AL	Sourdille et al. (2003)
						Xtam75-HT	8.7	5AL	Sourdille et al. (2000b)
						Eps-5A	-	u.p.	Snape et al. (2001)
HEI	*QHei.D84-2A*	Xgwm558	I, II	15.4	10.3	*QPh.ccsu-2A.1*	8.9	1	Kulwal et al. (2003)
			III, IV	13.2	7.3	*QPht.nfcri-2A*	23.5	2	Hai et al. (2008)
						QHei.B22-2A.a	14.9	> 20	Kunert (2007a)
						QHei.Z86-2A.a	1.1	> 20	Kunert (2007a)
						plant height-2A	29.3	2AS	Keller et al. (1999a)
						Eps-2AS	-	2AS	Snape et al. (2001)
						Ppd-A1	-	2AL	Mohler et al. (2004)
						crop height-2A	-	u.p.	Snape et al. (2007)
						Rht7	-	u.p.	Worland et al. (1980)
HEI	*QHei.T84-4Ab*	Xgwm160	I, II	21.8	11.1	*QHt.inra-4A*	15.0	2	Gervais et al. (2003)
			III, IV			*QHt.ipk-4A*	-	4	Börner et al. (2002)
						QPht.nfcri-4A	20.6	11	Hai et al. (2008)
						QHei.B22-4A.a	6.4	> 20	Kunert (2007a)
						QHei.Z86-4A.a	5.2	> 20	Kunert (2007a)
						plant height-4A	22.0	> 20	Keller et al. (1999a)
						QHt.ocs-4A.2, *Wx-B1*	26.0	4AS	Araki et al. (1999)
						QHt.ipk-4A	11.8	4AS	Huang et al. (2004)
						QHt.ocs-4A.1	29.0	4AL	Araki et al. (1999)
						Eps	-	u.p.	Hoogendoorn (1985)
HEI	*QHei.D84-5A*	Xbarc330[1]	I, II	15.3	16.0	*QHei.B22-5A.a*	11.7	0	Kunert (2007a)
			III	13.0	11.4	*Qt.ocs-5A.1, Vrn-A1, B1, Q*	10.7	1	Cadalen et al. (1998)
						Qph5A-2	-	1	Zhang et al. (2008a)
						plant height-5A, Q, Vrn-A1	11.0	1	Kato et al. (1999a)
						culm length-5A, Q, Vrn-A1	-	9	Kato et al. (2003)

Trait	QTL	Marker	REML mapping methods	F-val.	R^2 (%)	QTL or candidate gene	R^2	Distance to QTL (cM)	Reference
						DSF6-HT	-	11	Peng et al. (2003)
						Qph5A-1	-	11	Zhang et al. (2008a)
						QHt.ipk-5A.1	29.7	11	Huang et al. (2004)
						QHt.inra-5A	10.8	11	Gervais et al. (2003)
						Rht9	23.0	19	Ellis et al. (2005)
						QHt.fcu-5A, Vrn-A1	8.0	> 20	Chu et al. (2008)
						QHt.ipk-5A.2	37.3	> 20	Huang et al. (2004)
						DSF7-HT	-	> 20	Peng et al. (2003)
						plant height-5A.2	23.1	> 20	Keller et al. (1999a)
						Rht12	76.0	> 20	Ellis et al. (2005)
						plant height-5A.1	31.4	5AL	Keller et al. (1999a)
						Eps-5A	-	u.p.	Snape et al. (2001)
TGW	*QTgw.T84-2Ab*	Xgwm294	I, II	17.4	12.4	*QTgw.T84-2A.a*	2.4	0	Mohamed (2007)
						QGwt.crc-2A	3.0	0	McCartney et al. (2005)
						DSF4-GWH	-	0	Peng et al. 2003)
						QTgw-N.Z86-2A.a	0.7	8	Kunert (2007a)
						QTgw.ipk-2A	10.3	16	Huang et al. (2004)
						Xgwm312-Xgwm448-SW	17.6	20	Verma et al. (2005)
						QTgw.Z86-2A.a	6.4	> 20	Kunert (2007a)
						QTgw.ipk-2A	17.2	> 20	Huang et al. (2003b)
						Eps-2AS	-	2AS	Snape et al. (2001)
						1000-grain weight-2A	-	u.p.	Snape et al. (2007)
						Ppd-A1	-	u.p.	Snape et al. (2001)
TGW	*QTgw.D84-2D*	Xgwm157	I, II	20.0	14.2	*QTgw.B22-2D.a*	3.2	0	Kunert (2007a)
			III, IV	16.5	12.3	*Xwmc18-20 kernels weight*	-	9	Breseghello and Sorrells (2007)
						QTgw.crc-2D.1	4.7	9	Cuthbert et al. (2008)
						QTgw.Z86-2D.b	9.4	18	Kunert (2007a)
						QTgw.ipk-2D, Ppd	15.8	18	Huang et al. (2004)
						QTgw.ipk-2D, Ppd	15.4	18	Huang et al. (2003b)

Trait	QTL	Marker	REML mapping methods	F-val.	R^2 (%)	QTL or candidate gene	R^2	Distance to QTL (cM)	Reference
						QTgw.crc-2D.2	5.5	> 20	Cuthbert et al. (2008)
						QTgw.Z86-2D.a, Ppd-D1	7.3	> 20	Kunert (2007a)
						QTgw.crc-2D	9.2	> 20	Huang et al. (2006)
						QTgw.ipk-2D	-	> 20	Pshenichnikova et al. (2008)
						QTgw.ipk-2D	-	> 20	Börner et al. (2002)
						Xgwm484-Xgwm102-SW, Ppd	14.9	> 20	Verma et al. (2005)
						Xgwm261-TKW	6.8	> 20	Groos et al. (2003)
						Ppd-D1, Rht8	-	> 20	Chao et al. (2007)
						Tg1	-	> 20	Nalam et al. (2007)
						Eps-2DL	-	2DL	Snape et al. (2001)
						1000-grain weight-2D	-	u.p.	Snape et al. (2007)
TGW	*QTgw.T84-6B*	Xgwm626	III, IV	24.6	11.5	*Xm87p78.5a-TGW*	20.0	0	Quarrie et al. (2005)
						QTgw.B22-6B.a	4.5	1	Kunert (2007a)
						Xgwm582a-TKW	5.4	4	Elouafi and Nachit (2004)
						QTgw.D84-6B.a	3.0	4	Mohamed (2007)
						QTgw.ipk-6B	-	5	Börner et al. (2002)
						QTgw.Z86-6B.a	4.8	7	Kunert (2007a)
						Xgwm518-TKW	12.8	9	Elouafi and Nachit (2004)
						QTgw.T84-6B.b	12.0	11	Mohamed (2007)
						QTgw.T84-6B.a	14.0	12	Mohamed (2007)
						QTgw.ipk-6B	-	> 20	Börner et al. (2002)
						Eps-6BL.1, Eps-6BL.2	-	6BL	Snape et al. (2001)
						Vrn, Ppd	-	u.p.	Snape et al. (2001)
TGW	*QTgw.T84-7A*	Xgwm60	I, II	17.2	10.8	*Qyld.csdh. 7AS1*	-	0	Quarrie et al. (2006)
						QGw1.inra-7A, Vrn	10.3	2	Groos et al. (2003)
						Wx	-	2	Chao et al. (2007)
						QTgw.ipk-7A.1	3.3	20	Huang et al. (2004)

Trait	QTL	Marker	REML mapping methods	F-val.	R^2 (%)	QTL or candidate gene	R²	Distance to QTL (cM)	Reference
						Qyld.csdh. 7AC	-	> 20	Quarrie et al. (2006)
						QTgw.ipk-7A.2	4.2	> 20	Huang et al. (2004)
						QTgw.ipk-7A	14.5	> 20	Huang et al. (2003b)
						GWH-7A	-	u.p.	Peng et al. (2003)
						GW50-7A	-	u.p.	Hyne et al. (1994)
						QPpd.agt-7A	-	u.p.	Kuchel et al. (2007)
						Eps-7AS, Eps-7AL	-	u.p.	Snape et al. (2001)
						Vrn	-	u.p.	Law and Worland (1997)
YLD	*QYld.T84-3A*	Xgwm5	I, II	16.3	38.7	*LDb1.GY-3A*	-	0	Crossa et al. (2007)
			III, IV	23.7	40.0	*QYld.Z86-3A.a*	2.8	0	Kunert (2007a)
						Br-A1	-	0	Nalam et al. (2006)
						QGyld.unl-3A.2	28.1	2	Campbell et al. (2003)
						DSF5-YLD	-	2	Peng et al. (2003)
						S-A1	-	8	Salina et al. (2000)
						QGyld.unl-3A.2	21.0	18	Dilbirligi et al. (2006)
						QGyld.unl-3A.5	17.0	> 20	Dilbirligi et al. (2006)
						QYld.B22-3A.a	9.9	> 20	Kunert (2007a)
						QGyld.unl-3A.1	19.0	> 20	Dilbirligi et al. (2006)
						QGyld.unl-3A.1	28.1	> 20	Campbell et al. (2003)
						R-A1	-	> 20	Nalam et al. (2006)
						Eps-3S	-	3AS	Shah et al. (1999)
						Eps-3AL	-	3AL	Snape et al. (2001)
						yield-3A	-	u.p.	Snape et al. (2007)
						Vrn, Ppd	-	u.p.	Miura and Worland (1994)
YLD	*QYld.D84-3Ba*	Xgwm493	III, IV	18.5	7.6	*QYld.B22-3B.a*	1.2	0	Kunert (2007a)
						QYld.idw-3B	18.1	0	Maccaferri et al. (2008)
						Xgwm389-Xcfd79-Y	6.5	0	Groos et al. (2003)
						QYld.ipk-3B.1	9.6	0	Huang et al. (2003b)
YLD	*QYld.T84-3B*	Xbarc73	III	14.1	5.1	*QYld.crc.3B*	4.1	0	Cuthbert et al. (2008)
						QYld.T84-3B.a	2.1	0	Mohamed (2007)

Trait	QTL	Marker	REML mapping methods	F-val.	R^2 (%)	QTL or candidate gene	R²	Distance to QTL (cM)	Reference
						QGy.sdau-3B.e3	10.4	1	Li et al. (2007a)
						QYld.B22-3B.b	1.8	1	Kunert (2007a)
						QYld-N.B22-3B.a	0.3	1	Kunert (2007a)
						QYld.ipk-3B.2	21.6	2	Huang et al. (2003b)
						Br-B1	-	2	Nalam et al. (2006)
						LDb3.GY-3B	-	6	Crossa et al. (2007)
						QGy.sdau-3B.e2	12.4	6	Li et al. (2007a)
						S-B1	-	6	Salina et al. (2000)
						QGy.ccsu-3B.3	18.7	> 20	Kumar et al. (2007)
						Rht5	48.0	> 20	Ellis et al. (2005)
						R-B1	-	> 20	Nalam et al. (2006)
						Eps-3BL	-	3BL	Snape et al. (2001)
						yield-3B	-	u.p.	Snape et al. (2007)
						Vrn, Ppd	-	u.p.	Miura and Worland (1994)
YLD	*QYld.T84-5Ba*	Xgwm234	I, II	15.6	9.6	*QYld.T84-5B.a*	3.9	0	Mohamed (2007)
						QYld.ipk-5B	15.0	0	Huang et al. (2003b)
						LDb1.GY-5B	-	2	Crossa et al. (2007)
						ACC.AGC7/AAG.CTA1-GY	11.2	11	Marza et al. (2006)
						LDb2.GY-5B, Vrn	-	> 20	Crossa et al. (2007)
						QYld.B22-5B.a	1.3	> 20	Kunert (2007a)
						QYld.Z86-5B.a	2.6	> 20	Kunert (2007a)
						Xwg232.2-Xbarc074-YLD	21.6	> 20	Quarrie et al. (2005)
						QGy.ndsu-5B	11.0	> 20	Gonzalez-Hernandez et al. (2004)
						QYld.ipk-5B	10.0	> 20	Huang et al. (2004)
						Xgwm371-Xgwm604-Y	6.8	> 20	Groos et al. (2003)
						Vrn-B1	-	> 20	Chao et al. (2007)
						Eps-5B	-	u.p.	Snape et al. (2001)
YLD	*QYld.D84-6B*	Xbarc198	I, II	22.4	16.6	*QYld.ipk-6B*	11.8	3	Huang et al. (2004)
						yield-6BC	-	4	Ayala et al. (2002)
						GCTG.CTT1/GTG.GAC9-GY	7.3	5	Marza et al. (2006)
						QYld.D84-6B.a	3.8	8	Mohamed (2007)

Trait	QTL	Marker	REML mapping methods	F-val.	R^2 (%)	QTL or candidate gene	R^2	Distance to QTL (cM)	Reference
						LDb5.GY-6B	-	> 20	Crossa et al. (2007)
						LDb6.GY-6B	-	> 20	Crossa et al. (2007)
						Eps-6BL.1, Eps-6BL.2	-	6BL	Snape et al. (2001)
						Vrn, Ppd	-	u.p.	Snape et al. (2001)
PM	*QPm.T84-7Bb*	Xgwm577	I, II	13.5	7.2	*LDb6.PM-7B*	-	0	Crossa et al. (2007)
						Xgwm577-XpdaC01-PM	1.7	0	Chantret et al. (2001)
						Pm5d	-	0	Nematollahi et al. (2008)
						XpdaC01-XgbxP035b-PM	22.8	13	Minegot et al. (2002)
						Xglk750-Xmwg710a-PM	31.8	> 20	Keller et al. (1999b)
						Xpsr593c-Xpsr129c-PM, Pm5	11.3	> 20	Keller et al. (1999b)
						Pm5e	-	> 20	Huang et al. (2003a)
						Pm5a, Pm5b, Pm5c	-	u.p.	Hsam et al. (2001)
PM	*QPm.T84-7D*	Xwmc634	I, II	14.3	21.9	*Xgwm1220-Xswm10-PM*	-	> 20	Lillemo et al. (2008)
						Pm38, Lr34/Yr18		> 20	Lillemo et al. (2008)
						LDb7.PM-7D	-	> 20	Crossa et al. (2007)
						Ltn-Xgwm295.1-PM	12.0	> 20	Liang et al. (2006)
						QPm.ipk-7D	-	> 20	Börner et al. (2002)
						Pm15	-	7DS	Tosa and Sakai (1990)
						Pm29	-	7DL	Zeller et al. (2002)
						PM-7D	-	u.p.	Peusha et al. (2008)
						Pm19	-	u.p.	Lutz et al. (1995)

Trait: EAR (Tillers per square meter), HEA (Days until heading), HEI (Plant height), TGW (Thousand grain weight), YLD (Grain yield), PM (Powdery mildew). QTL: A significant marker×trait association was specified as QTL, if marker main effect was significant with P = 0.01 in the MIXED procedure. The QTL label is consisting of Q (for QTL), YLD (tested trait), T84 (tested population), 4Ab (chromosome, where the QTL was detected and b for the second YLD-QTL on the same chromosome). Marker: Label of SSR markers described by Somers et al. (2004), Sourdille et al. (2004) and Song et al. (2005), respectively. REML mapping methods: A significant marker×trait association was specified with marker main effect (M) at P = 0.01. These results were computed with a three-way REML I single-locus analysis and REML II forward selection, a four-way REML III single-locus analysis and REML IV forward selection. F-val.: F-value was computed using the MIXED procedure. R^2 (%): Proportion of the genetic variance computed using the MIXED procedure, which was explained the marker main effect (M). u.p.: QTL with an unknown position on a chromosome.

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