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The Inheritance and Molecular Mapping of Genes for Post-anthesis Drought Tolerance (PADT) in Wheat

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ABBREVIATIONS

ABA	accumulation of abscisic acid
AFLPs	amplified fragment length polymorphisms
ALF	automated laser fluorescence express DNA sequencer
ANOVA	analysis of variance
APS	ammonium persulphate
ARC	agriculture research center
BC	back cross population
BP	base pairs
C	estimated centromere position
cM	centiMorgans
cm	centimeter
CTD	canopy temperature depression
DAF	DNA amplification fingerprinting
dATP	deoxyadenosinetriphosphate
dCTP	deoxycytosinetriphosphate
dGTP	deoxyguanosinetriphosphate
DH	doubled haploid
DNA	deoxyribonucleic acid
DIA	digital image analysis
dTTP	deoxythymidinetriphosphate
EDTA	ethylenediamine tetraacetic acid
EtBr	ethidium bromide
EtOH	ethanol
F_1	first filial generation, produced by crossing two parental lines
F_2	second filial generation, produced by selfing the F_1
F_3	third filial generation, produced by selfing the F_2
FAO	food and agriculture organization of the united nations
Flt	flowering time
G	gram
Gae	grain area
Gcc	grain circumference
Gdf	grain form density factor
GFS02	Gatersleben field season 2002
GFS03	Gatersleben field season 2003
Glt	grain length
Grs	grain roundness
Gwd	grain width
gwm	Gatersleben wheat microsatellite
H	hour(s)
HG	homoeologous group
Ht	Plant height
ITMI	international triticeae mapping initiative
IPK	Institut für Pflanzengenetik und Kulturpflanzenforschung
KI	potassium iodide
LOD	logarithm of odds
M	molar
MAS	marker-assisted selection
Min	minute(s)

MM	millimeters
µl	microliter
PADT	post-anthesis drought tolerance
PCR	polymerase chain reaction
PV	phenotypic variance
QTL	quantitative trait loci
RAPD	random amplified polymorphic DNA
RFLP	restriction fragment length polymorphism
RILs	recombinant inbred lines
RLWC	relative leaf water content
RNAse	ribonuclease
S	second(s)
SCARs	sequence characterized amplified regions
SDS	sodium dodecyl sulfate
SIM	simple interval mapping
SNPs	single nucleotide polymorphisms
Srm	stem reserve mobilization
SSD	single seed descent
SSRs	simple sequence repeats or microsatellite
STI	stress tolerance index
STMS	sequence-tagged microsatellite sites
STRs	short tandem repeats
STS	sequence tagged site
TBE	Tris-Borate-EDTA buffer
TE	Trise-EDTA (TE) buffer
TNS	total non-structural carbohydrate
Tris	2-amino-2-(hydroxymethyl)-propane-1,3-diol
WSC	water soluble carbohydrate
WUE	water use efficiency
W/V	weight/volume
V/V	volume/volume
U	unit
%	percent
*****	significant at 5% level of probability
******	significant at 1% level of probability

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1. INTRODUCTION

1.1. Wheat

1.1.1. Economic importance and taxonomy of the wheat

Wheat (*Triticum aestivum* L. em Thell.) is the first important and strategic cereal crop for the majority of world's populations. It is the most important staple food of about two billion people (36% of the world population). Worldwide, wheat provides nearly 55% of the carbohydrates and 20% of the food calories consumed globally (Breiman and Graur, 1995). It exceeds in acreage and production every other grain crop (including rice, maize, etc.) and is therefore, the most important cereal grain crop of the world, which is cultivated over a wide range of climatic conditions and the understanding of genetics and genome organization using molecular markers is of great value for genetic and plant breeding purposes.

The grass family *Poaceae* (*Gramineae*) includes major crop plants such as wheat (*Triticum aestivum* L.), barley (*Hordeum vulgare* L.), oat (*Avena sativa* L.), rye (*Secale cereale* L.), maize (*Zea mays* L.) and rice (*Oryza sativa* L.). *Triticeae* is one of the tribes containing more than 15 genera and 300 species including wheat and barley.

Wheat belongs to the tribe *Triticeae* (= *Hordeae*) in the grass family *Poaceae* (*Gramineae*) (Briggle and Reitz, 1963) in which the one to several flowered spikelets are sessile and alternate on opposite sides of the rachis forming a true spike. Wheats (*Triticum*) and ryes (*Secale*) together with *Aegilops, Agropyron, Eremopyron* and *Haynalidia* form the subtribe *Triticineae* (Simmonds, 1976).

Linnaeus in 1753 first classified wheat. In 1918, Sakamura reported the chromosome number sets (genomes) for each commonly recognized type. This was a turning point in *Triticum* classification. It separated wheat into three groups. Diploids had 14 (n=7), tetraploids had 28 (n=14) and the hexaploids had 42 (n=21) chromosomes. Bread wheat is *Triticum aestivum*. *T. durum* and *T. compactum* are the other major species. All three are products of natural hybridization among ancestrals no longer grown commercially (Briggle, 1967).

1.1.2. Cultivation and use of the wheat crop

Wheat is an edible grain, one of the oldest and most important of the cereal crops. Though grown under a wide range of climates and soils, wheat is best adapted to temperate regions with rainfall between 30 and 90 cm. Winter and spring wheats are the two major types of the crop, with the severity of the winter determining whether a winter or spring type is cultivated. Winter wheat is always sown in the fall; spring wheat is generally sown in the

spring but can be sown in the fall where winters are mild. Therefore, today wheat is grown all over the world, with different varieties sown according to the various climates. In 2002, the world's main wheat producing regions were China, India, United States, Russian Federation, France, Australia, Germany, Ukraine, Canada, Turkey, Pakistan, Argentina, Kazakhstan and United Kingdom (FAO, 2003). Most of the currently cultivated wheat varieties belong to hexaploid wheat (*Triticum aestivum* L.), which is known as common bread wheat and valued for bread making. The greatest portion of the wheat flour produced is used for bread making. Wheat grown in dry climates is generally hard type, having protein content of 11-15 percent and strong gluten (elastic protein). The sticky gluten of bread wheat entraps the carbon dioxide (CO2) formed during yeast fermentation and enables leavened dough to rise. The hard type of wheat produces flour best suited for bread making. The wheat of humid areas is softer, with protein content of about 8-10 percent and weak gluten. The softer type produces flour suitable for cakes, crackers, cookies, pastries and household flours. Durum wheat (*Triticum turgidum* L.), which is the main tetraploid type, is also important, although its large, very hard grains yield low gluten flour that is the main source of semolina suitable for pasta, couscous, burghul and other Mediterranean local end-products (Nachit, 1992). Apparently, no economically important diploid wheats are being cultivated as a crop anywhere in the world. Although most wheat is grown for human food and about 10 percent is retained for seed and industry (for production of starch, paste, malt, dextrose, gluten). Wheat grain contains all essential nutrients; kernel contains about 12 percent water, including carbohydrates (60-80% mainly as starch), proteins (8-15%) containing adequate amounts of all essential amino acids (except lysine, tryptophan and methionine), fats (1.5-2%), minerals (1.5-2%), vitamins (such as B complex, vitamin E) and 2.2% crude fibers.

1.1.3. The wheat genome

The haploid DNA content of hexaploid wheat (*Triticum aestivum* L. em Thell, 2n=42, AABBDD) is approximately 1.7 x 10^{10} bp, about 100 times larger than the *Arabidopsis* genome, 40 times that of rice and about 6 times that of maize (Bennett and Smith, 1976; Amuruganathan and Earle, 1991). The large genome of bread wheat has resulted from polyploidy and extensive duplications, such that over 80% of the genome consists of repetitive DNA sequences (Smith and Flavell, 1974). The average wheat chromosome is around 810 MB, 25 times that of the average rice chromosome (Table 1).

This huge size arises from the origins of the wheat genome (Talbert *et al.,* 1998), of its triple structure (ABD genomes) and the inclusion of extensive duplications such that more than 85% of the whole genome is composed of repetitive, highly methylated sequences (Moore *et al.,* 1993).

Current estimates of gene number in higher plants vary between 25,000 and 43,000 (Miklos and Rubin, 1996). According to current studies, effects of approximately 30,000 genes governed the wheat plant phenotype. A few hundred of these have been identified, mapped and their primary and pleiotropic effects are described.

Table (1): The genome characteristics of cereal crops compared with *Arabidopsis.*

Species	DNA/cell Picograms	Genome size (bp)	% Of repeated sequences	Genetic map size (cM)	Chromosome number
Arabidopsis thaliana	0.4	$0.07x10^9$	37	501	5
Oryza sativa	-	0.45×10^9	58-66	1,700	12
Hordeum vulgare	13.4	5×10^9	70-76	1,096	7
Zea mays	11	2.7×10^9	78	1,400-1,500	10
Triticum aestivum	36.2	17×10^9	83-85	3,500	7*3 (ABD)

1 picogram = 1 pg = 0.965×10^9 bp = 29 cM

1.2. Drought tolerance

1.2.1. Drought

World food production is limited primarily by environmental stresses. It is very difficult to find 'stress free' areas where crops may approach their potential yields. Abiotic environmental factors are considered to be the main source (71%) of yields reductions (Boyer, 1982). Drought is one of the most common environmental stresses that affects growth and development of plants through alterations in metabolism and gene expression (Leopold, 1990). It continues to be a challenge to agricultural scientists in general and to plant breeders in particular, despite many decades of research. It is a permanent constraint to agricultural production in many developing countries and an occasional cause of losses of agricultural production in developed ones (Ceccarelli and Grando, 1996).

Wheat production suffers from variability in yield from year to year and from location to location. One of the main environmental abiotic stress that is responsible for yield instability and limitations in wheat is drought stress, which may occur early in the season or terminally at grain filling and grain development. Improvement of productivity of wheat cultivars under drought conditions becomes one of the important breeding programs

objectives in wheat. Breeding for drought tolerant wheat cultivars is a major objective in arid and semi-arid regions of the world due to inadequate precipitation, shortage of irrigation water and high water demand for crop evapotranspiration in such climates.

1.2.2. Mechanism of drought tolerance

Drought tolerance in wild plant species is often defined as survival, but in crop species it is defined in terms of productivity (Passioura, 1983). Rosielle and Hamblin (1981) defined drought tolerance as the difference in yield between stress and non-stress environments, while productivity is the average yield in stress and non-stress. A different definition regards drought tolerance as minimization of reduction in yield caused by stress compared to yield under non-stress environments (Fischer and Maurer, 1978; Langer *et al.,* 1979; Blum, 1983a; Blum, 1988). Also, it is defined as the relative yield of a genotype compared to other genotypes subjected to the same drought stress (Hall, 1993). Drought tolerance comprises drought escape, dehydration avoidance and dehydration tolerance mechanisms (Blum, 1988).

1.2.2.1. Drought escape

Drought escape through early flowering and/or short growth duration is advantageous in environments with terminal drought stress and where physical or chemical barriers inhibited root growth (Turner, 1986; Blum, 1988; Blum *et al.,* 1989). On other hand, later flowering can be beneficial in escaping early-season drought, if drought is followed by rains (Ludlow and Muchow, 1990). Under non-stress conditions, late-flowering varieties tend to yield higher than early-flowering ones (Turner, 1986; Lulow and Muchow, 1990). This is because the early-flowering varieties are likely to leave the yield potential unutilized (Muchow and Sinclair, 1986).

1.2.2.2. Dehydration avoidance

Dehydration avoidance can be defined as the plant's ability to retain a relatively higher level of 'hydration' under conditions of soil or atmospheric water stress (Blum, 1988). Levitt (1980) recognized two plant types with respect to dehydration avoidance: plant that avoid dehydration by reduced transpiration 'water savers' and plants that use means other than reduced transpiration 'water spenders'. Important features are root characteristics (increased water uptake), leaf and stomata characteristics (reduced water loss) and osmotic adjustment to lower the osmotic potential (Blum, 1988; Acevedo and Fereres, 1993).

1.2.2.3. Dehydration tolerance

Dehydration tolerance describes the ability of plants to continue metabolizing at low leaf water potential and to maintain growth despite dehydration of the tissue or to recover after release from stress conditions. According to Hsiao (1973) and Boyer (1976), translocation is one of the more dehydration tolerant processes in plants. It would proceed at levels of water deficit sufficient to inhibit photosynthesis. Ample information has been accumulated in the cereals to show that grain growth is partially supported by translocated plant reserves stored mainly in the stem during the pre-anthesis growth stages. When water stress occurs and the current photosynthetic source is inhibited, the role of stem reserves as a source for grain filling increases, both in relative and absolute terms. Stem reserves may therefore be considered as a powerful resource for grain filling in stress-affected plants during the grain filling stage.

1.2.3. A conceptual model for drought tolerance

The following model was described by Reynolds *et al*. **(**2000**).** Many anatomical, physiological and biochemical traits are mentioned in the literature as being drought adaptive (Blum, 1988; Loss and Siddique, 1994; Richards, 1996). This model will include those, which are currently considered of most potential value to the environment described, bearing in mind that not all traits are appropriate for all drought environments. The development of molecular probes for marker assisted screening of these traits would be an important objective, assuming their use is more efficient at identifying superior genotypes than conventional screening approaches.

- **Large seed size**

  Helps emergence, early ground cover and initial biomass.

- **Long coleoptiles**

  Helps for emergence from deep sowing (Radford, 1987). This is practiced to help seedlings reach the receding moisture profile and to avoid high soil surface temperatures which inhibit germination.

- **Early ground cover**

Thinner, wider leaves (i.e. with a relatively low specific leaf weight) and a more prostrate growth habit help to increase ground cover, thus conserving soil moisture and potentially

increasing radiation use efficiency (Richards, 1996). This trait would be more important in the Mediterranean type of drought environment where rain may occur during the early part of the cycle. It would be less useful in regions where the crop grows exclusively on stored soil moisture where dust mulching is practiced or where residue retention is practiced to avoid evaporation from the soil surface.

- **High pre-anthesis biomass**

Potential for vigorous growth prior to heading provides the opportunity to take advantage of relatively good growing temperatures and moisture availability earlier in the cycle. Up to 40% of available water may be lost by evaporation directly from the soil in Mediterranean types of environments (Loss and Siddique, 1994), so high early ground cover and biomass production may permit a more efficient use of soil water. Although most drought studies show that high water use efficiency (WUE) is not associated with better performance (Sayre *et al*., 1995), ideally early biomass should be achieved with maximal water use efficiency to improve water availability during grain filling.

- **Good capacity for stem reserves and remobilization**

Stored fructans can contribute substantially to grain filling especially when canopy photosynthesis is inhibited by drought (Rawson and Evans, 1971). Traits that may contribute include long and thick stem internodes, with extra storage tissue perhaps in the form of solid stems. In studies where crosses where made between lines contrasting in the solid stem trait, the solid-stem progeny contained more soluble carbohydrate per unit of stem length, though total stem carbohydrate was unaffected due to narrower and shorter stems (Ford *et al*., 1979).

- **High spike photosynthetic capacity**

Spikes have higher WUE than leaves and have been shown to contribute up to 40% of total carbon fixation under moisture stress (Evans *et al*., 1972). Awns contribute substantially to spike photosynthesis and longer awns are a possible selection criterion. While gas exchange measurement of spikes is time consuming and difficult to standardize, chlorophyll fluorescence should be considered as a more rapid means of screening for spike photosynthetic capacity under stress.

- **High RLWC/CTD during grain filling to indicate ability to extract water**

A root system that can extract whatever water is available in the soil profile is clearly drought adaptive (Hurd, 1968), but difficult to measure. Traits affected by the water relations

of the plant, such as relative leaf water content (RLWC) measured pre-dawn or canopy temperature depression (CTD) during the day and C_{13} discrimination or ash content of grain or other tissues, can give indications of water extraction patterns.

- **Osmotic adjustment**

Adjustment will help maintain leaf metabolism and root growth at relatively low leaf water potentials by maintaining turgor pressure in the cells (Morgan and Condon, 1986). Some research suggests that the trait can be assayed relatively easily by measuring coleoptile growth rate of seedlings in polyethylene glycol.

- **Accumulation of abscisic acid (ABA)**

The benefit of ABA accumulation under drought has been demonstrated (Innes *et al*., 1984). It appears to pre-adapt plants to stress by reducing stomatal conductance, rates of cell division, organ size and increasing development rate. However, high ABA can also result in sterility problems since high ABA levels may abort developing florets.

- **Leaf anatomy: waxiness, pubescence, rolling and thickness**

These traits decrease radiation load to the leaf surface (Richards, 1996). Benefits include a lower evapotranspiration rate and reduced risk of irreversible photo-inhibition. However, they may also be associated with reduce radiation use efficiency, which would reduce yield under more favorable conditions.

- **High tiller survival**

Comparison of old and new varieties have shown that under drought older varieties over-produce tillers many of which fail to set grain while modern drought tolerant lines produce fewer tillers most of which survive (Loss and Siddique, 1994).

- **Heat tolerance**

The contribution of heat tolerance to performance under moisture stress needs to be quantified, but it is relatively easy to screen for (Reynolds *et al*., 1998).

- **Stay green**

The trait may indicate the presence of drought avoidance mechanisms, but probably does not contribute to yield *per se* if there is no water left in the soil profile by the end of the cycle to support leaf gas exchange. It may be detrimental if it indicates lack of ability to

remobilize stem reserves (Blum, 1998). However, research in sorghum has indicated that stay-green is associated with higher leaf chlorophyll content at all stages of development and both were associated with improved yield and transpiration efficiency under drought (Borrell *et al*., 2000).

1.2.4. Stem reserve mobilization in wheat

1.2.4.1. Reserve accumulation

Reserve accumulation in the stem and the size of the storage strongly depend on the growing conditions before anthesis. Total stem nonstructural carbohydrate (TNS) at anthesis was shown to vary from 50 to 350 g kg^{-1} dry mass in different experiments (Kiniry, 1993). Under optimal growing conditions with regard to temperature, water regime (Davidson and Chevalier, 1992) and mineral nutrition (Papakosta and Gagianas, 1991), carbon assimilation rates are high and a proportion of the assimilation during stem elongation is reduced by stress, storage in stems is reduced. For example, remobilized water soluble carbohydrate (WSC) were 641 mg and 1047 mg in water stressed and irrigated wheat, respectively, because the former had less storage than the latter (Davidson and Chevalier, 1992). Under dry land field conditions only half amount of water-soluble carbohydrates was available for remobilization during grain filling, as compared with irrigated conditions. Stem length, as affected by height genes, is important in affecting stem reserve storage. The *Rht1* and *Rht2* dwarfing genes of wheat were found to reduce reserve storage by 35% and 39%, respectively as a consequence of a 21% reduction in stem length (Borrell *et al.*, 1993). However, under the favorable conditions the advantage of the tall (*rht*) genotype in reserve storage was not expressed in greater mobilization to ear. Under these favorable grain filling conditions only about 20% of grain yield was contributed by stem reserves in all genotypes. The contribution of stem reserves to grain yield was greater in a tall than a short barley cultivar, but absolute yield was the same in both, indicating that the taller cultivar was lacking in current assimilation compared with the shorter one (Daniels and Alcock, 1982).

1.2.4.2. Reserve utilization

Stem reserve mobilization is affected by sink size, by the environment and by cultivar. The demand by grain yield sink is a primary factor in determining stem reserve mobilization. Environmental conditions that decrease current assimilation during grain filling pose an increased demand for stem reserves for grain filling. When wheat plants were shaded during grain filling, up to 0.93g of grain was produced per gram of assimilates exported from the

stem (Kiniry, 1993). Stem reserve mobilization is affected by water deficit grain filling. Even the rate of development of water deficit may affect mobilization (Palta *et al.,* 1994). It is therefore to be expected that estimates of relative contributions of stem reserves to total grain mass per ear or to grain yield would vary among the different reports, according to the experimental conditions and cultivar used. These contributions were estimated to be anywhere between 6% and 100% (Austin *et al.,* 1980, Papakosta and Gagianas, 1991; Pheloung and Siddique, 1991; Davidson and Chevalier, 1992; Borrell *et al*., 1993; Blum *et al*., 1994; Gent, 1994; Palta *et al*., 1994; Khlestkina *et al*., 2001, Börner *et al*., 2002a, 2003, Salem and Börner 2003). It may be concluded that the reduction in current assimilation during grain filling, under different stresses, will induce an increase in stem reserve mobilization and utilization by grain. Drought conditions during grain filling often also involve heat stress, which reduces the duration of grain filling. There is normally an increase in the rate of grain dry matter accumulation under high temperatures, but it is not sufficient to compensate for the decrease in duration.

1.2.4.3. Stem reserves mobilization under stress

In most wheat growing regions and especially in the Mediterranean grain filling is subjected to several physical and biotic stresses. Grain filling often occurs when temperatures are increasing and moisture supply is decreasing. Also foliar disease of wheat tends to spread and intensify towards and after flowering. Leaf rust, stripe rust and Septoria leaf blotch can result in total leaf destruction at grain filling. The common end result of all these stresses is the reduction in kernel weight, kernel shriveling, reduced test weight and loss in yield. The current source of carbon for grain filling is assimilation by light intercepting viable green surfaces. This source is normally diminishing due to natural senescence and the effect of various stresses, in addition to the demand posed by maintenance respiration of live plant biomass.

While root storage is important in some legumes and other species, there is no evidence that roots or leaves are as important as stems for reserve storage in the small grains. In most studies of stem reserves in the small grains, stems also include the leaf sheaths, which in themselves contain reserves. In small grains, stems store carbohydrates in the form of glucose, fructose, sucrose and starch, but the main reserve is fructan (Lopatecki *et al.,* 1962; Dubois *et al.,* 1990; Wardlaw and Willenbrink, 1994). Storage is commonly analyzed as total non-structural carbohydrates (TNS) or water soluble carbohydrates (WSC). Fructan accumulated in internodes while they were extending, although most of the fructan in an

internode accumulated after it was fully extended. When WSC was mobilized from the stem, the mass of fructose first increased then decreased, indicating that fructan was hydrolyzed at a faster rate than it is produced (Bonnett and Incoll, 1992).

1.2.4.4. Methodology and selection for stem reserve under post-anthesis drought stress

An important form of drought stress tolerance is the tolerance to post-anthesis stress. In wheat, as in other cereals, grain filling depends partly on actual photosynthesis during this period and partly on carbohydrates stored during pre-anthesis which are translocated from vegetative plant parts. Under conditions of terminal drought (and heat) stress, net photosynthesis decreases significantly in wheat (Acevedo, 1991) and the proportion of translocation of stored soluble carbohydrates as a source for grain filling becomes larger (Austin *et al*., 1977, 1980; Richards and Townley-Smith, 1987). Stem reserve mobilization is affected by water deficit grain filling. Genetic variation exists within cereal crop species in the ability to sustain kernel growth by remobilization of reserves (Austin *et al*., 1977; Acevedo and Ceccarelli, 1989).

Blum *et al.* (1983a, 1983b) developed a technique for revealing translocation-based grain filling in absence of photosynthesis under post-anthesis stress in wheat. With this method, small plots are sprayed to complete wetting by a solution of magnesium or sodium chlorate (4% active ingredient), at the initial part of the linear phase of kernel growth (approximately 14 days after anthesis), when final cell number of the kernel has been determined in each genotype. The chemical bleaches all plant surfaces upon contact without killing the plant. The desiccant kills all photosynthetic tissue including leaves, leaf sheaths, glumes and awns. The treatment does not simulate drought stress. However, it simulates the effect of stress by inhibiting current assimilation. When the plants are devoid of their chlorophyll, grain filling can proceed only with translocated plant reserves. At harvest, 1000 kernel weight was compared between treated and non-treated (control) plants, calculating the rate of reduction in kernel weight caused by treatment. The technique is being applied experimentally in Australia using potassium iodide as a desiccant (Turner and Nicholas, 1987; Nicholas and Turner, 1993).

The correlation across diverse genetic materials between the rate of reduction in kernel weight by chemical desiccation and the rate of reduction by drought stress was found to be significant. It was r = 0.81 *** and r = 0.79 ** over two years in Blum *et al*. (1983b) and r = 0.48 *** and r = 0.81** over two years in Nicholas and Turner (1993).

Chemical desiccation can be incorporated into breeding program in two ways. Firstly, it can be used to assess responses of individual advanced lines or families, always compared with non-treated controls under non-stress conditions. Secondly, it can be used in mass selection at the F_2-F_4 generation.

1.2.5. How to estimate drought tolerance?

Due to the complexity of drought tolerance in comparison to other traits, e.g., quality or disease traits, which are more clearly defined, efforts to increase drought tolerance could be achieved through selection for yield, which integrates all the unknown factors that will be important for improving drought tolerance. However, consideration should be given to whether the plants are grown in conditions which are representative of the target environments, genetic variation is maximum and the genotype x environment interactions are not too large.

Accordingly, many yield-based parameters were suggested to evaluate drought tolerance. Many of them were constructed in forms of indices, e.g., stress susceptibility index (SSI) suggested by Fischer and Maurer (1978). The stress susceptibility index is the ratio of relative reduction in yield of genotype due to drought compared to the mean relative reduction in yield of all tested genotypes. This SSI is found to be equivalent to the ratio of yield under stress (Yd) to yield under non-stress (Yw), (Yd/Yw) (Link *et al.,* 1999).

1.3. Molecular mapping in plants

Traditional methods of plant breeding have made a significant contribution to crop improvement, but they have been slow in targeting complex traits like grain yield, grain quality and abiotic stress such as drought. In traditional plant breeding, the plant breeder during selection of desirable plant from the segregation population faced the following problems: (i) a large segregating population needs to be screened for a desirable trait e.g., yield and its component, quality, drought tolerance, disease resistance, etc.; (ii) wait for advanced generations F_6 to start selection for quantitative traits, for which selection in early generation is not effective; (iii) it becomes very difficult to screen a segregating population for a desired trait when the trait is influenced by environment; (iv) contrasting forms are often not distinguishable at seedling stage, making it necessary to grow population up to the adult stage; (v) it is difficult to undertake pyramiding of resistance genes, since selection of additional genes in presence of an existing resistance gene would be difficult. To meet the great increase in food production necessitated by population growth and the higher standards of living expected by most of the developing countries, biotechnology brings new and powerful tools to plant breeders. One method receiving growing attention is the mapping of

chromosomal regions affecting qualitative or quantitative traits. Polygenic characters, which were very difficult to analyse using traditional plant breeding methods, can now be tagged using DNA molecular markers. Molecular markers allow geneticists and plant breeders to locate and follow the numerous interacting genes that determine a complex trait. Genetic linkage maps can provide a more direct method for selecting desirable genes *via* their linkage to easily detectable molecular markers (Tanksley *et al.,* 1989). Combining marker-assisted selection methods with conventional breeding schemes can increase the overall selection gain and, therefore, the efficiency of breeding program. With the use of molecular techniques it is possible to hasten the transfer of desirable genes between varieties and to introgress novel genes from wild species into crop plants. The plant breeder would like to exercise indirect marker aided selection (MAS) at the seedling stage in early generations, if possible. Availability of tightly linked molecular markers for a trait will facilitate such an indirect selection and help plant breeding by saving time and expense.

1.3.1. Molecular marker technologies for genetic mapping

The development of molecular marker technologies during the last ten years has revolutionized the genetic analysis of crop plants. A significant progress has been made towards the use of molecular approaches in plant breeding. From the time of Gregor Mendel until the mid-eighties, morphological characters had been the major types of markers readily available for genetic mapping. Molecular marker technology has changed dramatically during the past two decades. The first molecular markers were isozyme markers, which based on the different mobility of differently charged protein with the same enzymatic function on the gel. Enzyme markers have limited genome coverage and numbers. The term molecular marker is taken here to refer to markers identifying variation at the level of DNA, though biochemical markers such as isozymes have made a valuable contribution to the development of genetic maps in the late seventies and eighties for example, of tomato (Tanksley and Rick, 1980) and maize (Edwards *et al.,* 1987).

The molecular markers, so developed, may be used for improving the efficiency of traditional plant breeding by facilitating indirect selection through molecular markers linked to genes for the traits of interest, because, these markers are not influenced by the environment and can be scored at all stages of plant growth. This saves time, resources and energy that are needed not only for raising large segregating populations for several generations, but also for estimating the parameters used for selection. In addition to these applications, DNA markers can also be used for germplasm characterization, genetic

diagnostics, study of genetic diversity, study of genome organization, etc. (Rafalaski *et al.*, 1996). Molecular markers have already been used not only for the preparation of molecular maps but also for tagging genes, controlling traits of interest, for use in marker assisted selection (MAS). In plant, using markers, several genetic maps were initially prepared in tomato (Bernatzky and Tanksley, 1986). Subsequently, maps were constructed in different crops such as rice (McCouch *et al*., 1988, Kishimoto *et al*., 1989); maize (Burr *et al*., 1988; Beavis and Grant, 1991; Burr and Burr, 1991), barley (Heun *et al*., 1991; Graner *et al*., 1991; Hinze *et al*. 1991) or wheat (Chao *et al*., 1989; Liu and Tsunewaki, 1991; Liu *et al*., 1992; Devos *et al*., 1992; Devos and Gale, 1993; Röder *et al*., 1998).

There are two main types of molecular markers, isozyme markers and DNA markers. Markert and Moller (1959) were first to describe the differing forms of bands that they were able to visualize with specific enzyme stains and they were the first to introduce the term isozyme. Following this discovery further investigation showed that many of these enzymes were tissue specific and generally unaffected by environmental or other factors. Lately, it was found that this type of markers has many limitations and disadvantages (Tanksley, 1983). The other type is DNA based markers. Recombinant DNA technology has provided new more powerful tools for studying genetic variation with a greater resolution than all previous experimental methods, including protein electrophoresis. Recombinant DNA technology can be applied to a variety of *in vitro* techniques, which include DNA isolation and production of new combination of heritable material by the splicing of the nucleic acids *in vitro* (Old and Primrose, 1989). The main advantage of DNA based markers is that they give information of about any kind of sequence in the genome, not only of isozymes or highly expressed non-isozymatic proteins such as storage proteins but also unexpressed sequences.

On the basis of the principles and methods employed, molecular markers can be broadly classified in the following four groups according to Mohan *et al*., 1997; Gupta *et al*., 1999b; Gupta and Varshney, 2000, (i) hybridization based markers, (ii) PCR-based molecular markers and (iii) sequencing and DNA chip based markers.

1.3.1.1. Hybridization based markers

Now it is possible to gain information about the whole genome and any of its components, surpassing the limitations of protein electrophoresis, which only gives information on translated sequences. DNA based markers have overcome main limitations of protein electrophoresis since the detection of variation is not limited to coding regions and all categories of mutational events can, in principle, be detected.

In 1980, it was suggested that large numbers of genetic markers might be found by studying differences in the DNA molecule itself, revealed as restriction fragment length polymorphisms (RFLP) (Botstein *et al.*, 1980). This technique involves restriction of genomic DNA followed by electrophoretic size separation of the fragments in a gel matrix. The fragments are then transferred to a membrane by Southern blotting and hybridized with a radioisotope labeled probe. Many sources of DNA can serve as probes, such as a small piece of genomic DNA, cDNA sequence or specific PCR products. Sometimes, probes can be adopted from other species as heterologous probes for comparative mapping, which allows comparison of genome organization and evolution between the related species (Tanksley *et al.,* 1988; Bonierbale *et al.,* 1988; Lagercrantz *et al.,* 1996; Lagercrantz, 1998). The polymorphisms detected by RFLP rely on the specific and characteristic nucleotide sequence, which is recognized and cut by restriction enzymes. Insertions or deletions between restriction sites or mutations occurring at restriction sites result in length polymorphisms of restriction fragments. The range of fragment length and number of fragments depends on different enzymes. RFLP markers are often co-dominant and, therefore, very informative. However, generating RFLP data is labor intensive and time consuming and requires a relatively large amount of DNA. RFLP maps have been developed for a number of species like maize (Helentjaris *et al.,* 1986, Helentjaris 1987), tomato (Bernatzky and Tanksley 1986, Helentjaris *et al.,* 1986, Zamir and Tanksley 1988), lettuce (Landry *et al.,* 1987), rice (McCouch *et al.,* 1988), pepper (Tanksley *et al.,* 1988), Arabidopsis (Chang *et al.,* 1988), rye (Börner and Korzun, 1998; Korzun *et al.,* 2001), barley (Graner *et al.,* 1991; Heun *et al.,* 1991) and peanut (Halward *et al.,* 1992). In wheat, due to low frequency of RFLP, this approach has been relatively less useful. This is sometimes attributed to polyploid nature, high proportion of repetitive DNA and large genome size. Despite these difficulties, sufficient applications of RFLP were practiced in wheat. These purposes included, genome mapping (Devos and Gale, 1993), variety identification (Gupta *et al.,* 1998) and marker aided selection (Gale *et al.,* 1995). In wheat, RFLP's have been used to map loci for seed storage protein (Dubcovsky *et al.,* 1997), flour colour (Parker *et al.,* 1998), vernalization and frost resistance (Galiba *et al.,* 1995), dwarfing and vernalization (Korzun *et al.,* 1997), resistance to pre-harvest sprouting (Anderson *et al.,* 1993), tissue culture response (Ben Amer *et al.,* 1997), resistance against cereal cyst nematode (Eastwood *et al.,* 1994; Williams *et al.,* 1996), milling yield (Parker *et al.,* 1999) and different important agronomic characters (Börner *et al.,* 2002b).

1.3.1.2. PCR-based molecular markers

The development of new methods to perform analysis with molecular markers has been the focus of many recent studies and most of these are based on PCR amplification of genomic DNA (Kochert, 1994). Polymerase chain reactions (PCR) have been considered to be the most revolutionary modern technique of molecular biology in 1980s. PCR is a powerful extremely sensitive technique with applications in many fields such as molecular biology diagnostics and population genetics. Recombinant DNA techniques have revolutionized genetics by permitting the isolation and characterization of genes, allowing the detailed study of their function and expression during development processes, or as a response to environmental factors. More of the cloning methods involved can be accelerated and sometimes even circumvented by using PCR, and novel applications of the technique now permit studies that were not possible before. The idea of PCR is a simple process in which a specific segment of DNA is synthesized repeatedly, resulting in the production of large amounts of a single DNA sequence starting from a minute quantity of template (Saiki *et al.,* 1985). The process depends on primer sequences of DNA, which match flanking sequences at both ends of targeted sequence. Through repeated denaturing, annealing and synthesized steps, the intervening sequence is synthesized in a 2^n amplification.

- **Random amplified polymorphic DNA (RAPD)**

Random Amplified Polymorphic DNA (RAPD) (William *et al.,* 1990; Welsh and McClelland, 1990) is a PCR-based technique for DNA fingerprinting. This assay, unlike the PCR, does not require knowledge of the target DNA sequence, and a single arbitrary primer will support DNA amplification from a genomic template if binding sites on opposite strands of the template exist within a distance that can be traversed by the thermo stable equation usually random oligonucleotides (or 10 bases) used as primer to amplify discrete fragments of genomic DNA. The primers are generally of random sequence and contain at least 50% G and C without internal inverted repeats. The products are easily separated by standard electrophoretic technique and visualized under ultraviolet (UV) illumination of ethidium bromide stained agarose gels. Polymorphism results from changes in either the sequence of the primer-binding site (point mutation), which prevents stable association with the primer or from changes, which alter the size or prevent amplification of target DNA (insertions, deletions or inversions). RAPDs can rapidly be used to construct linkage maps. These advantages have allowed mapping of a wide variety of plant genomes (Devos and Gale, 1992; Waugh and Powell 1992; Tingey and Del Tufo, 1993). RAPD markers were also instrumental

for map-based cloning of disease-resistance genes (Jones *et al.,* 1994; Mindrinos *et al.,* 1994; Whitham *et al.,* 1994; Martin *et al.,* 1991; Michelmore *et al.,* 1991). However RAPD markers, inherited usually in a dominant manner, are not transferable from one population to another and are poorly reproducible between different laboratories (Penner *et al.,* 1993; Jones, 1997). Consequently, RAPD is largely being replaced by a more robust DNA fingerprinting technique termed amplified fragment length polymorphism (AFLP).

- **DNA amplification fingerprinting (DAF)**

A modification of the RADP assay, named DNA amplification fingerprinting (DAF), has been described by Caetano-Anoles *et al.* (1991). The difference from the other procedures is that the PCR products are separated on polyacrylamide urea gels and visualized by silver stain. In the DAF procedure primers as short as five nucleotides, produce complex band patterns ideally suited for genome fingerprinting applications.

Denaturing polyacrylamide gradient gel-electrophoresis (DGGE) has been used to resolve DNA sequence differences among fragments of similar or identical size (Fischer and Lerman, 1983; Myers *et al.,* 1987). Using the DGGE procedure, single base differences result in altered migration of DNA fragments and thus produce polymorphic DNA fragments. Because of this the DGGE procedure is considered to be highly suitable for self-pollinating species.

- **Sequence-tagged site (STS)**

STS is a short, unique sequence that identified a specific locus and can be amplified by PCR. A pair of PCR primers, which are designed by sequencing an RFLP probe representing a mapped low-copy number sequence, characterizes each STS. Talbert *et al.* (1994) showed that PCR could be used to detect polymorphism in wheat with primer sequences derived from the α-amylase and γ-gladine genes. In another study in wheat, RFLP probe *Xbcd1231*, linked with *Pm4a* locus was converted into an STS marker (Liu *et al.,* 1998). Also, Roy *et al*. (1999) found an STS marker, which showed a strong association with pre-harvest sprouting tolerance in wheat. Conventionally, the term STS is used for the primers, which are designed on the basis of mapped low-copy RFLP loci.

- **Directed search (amplification of low copy DNA)**

In general, cereals have a high level of repetitive DNA sequences (about 70% of the DNA sequence in wheat are repetitive). Removal of repetitive DNA sequences before PCR

has been reported to produce polymorphic and reproducible DNA fragments (Eastwood *et al.,* 1994). Hydroxylapatite column chromatography is used to enrich low copy DNA sequences (Clarke *et al.,* 1992). Once the procedure is standardized, it could be useful to screen marker linked to disease resistance and other traits.

- **Sequence characterized amplified regions (SCARs)**

Paran and Michelmore (1993) developed a dependable PCR - based technique called sequence characterized amplified regions (SCARs). In this procedure, the polymorphic DNA fragment is cloned and sequenced.

- **Amplified fragment length polymorphisms (AFLPs)**

AFLP is a PCR based DNA fingerprint technique (Vos *et al.,* 1995; Zabeau and Vos, 1993). It involves restriction of genomic DNA followed by ligation of adaptors to restricted fragments and preselective and selective PCR amplification of a subset of these fragments. The amplified fragments are resolved on a sequencing gel and visualized either by autoradiography or fluorescent sequencing equipment (Meksem *et al.,* 1995; Zhang *et al.,* 1999; Schwarz *et al.,* 1999; Huang *et al.,* 2000b; Huang and Sun 1999; Hartl and Seefelder, 1998), depending on the method of labelling or silver staining (Cho *et al.,* 1996). In contrast to RAPD, AFLP is highly reproducible and also transferable between different populations (Jones *et al*., 1997; Yin *et al.,* 1999; Waugh *et al*., 1997; Li *et al.,* 1998; Rouppe van der Voort *et al.,* 1997). One major limitation of AFLPs is the dominant nature and the difficulty in identifying allelic variants at a specific locus although co-dominant AFLP markers have been found, however, in frequencies of 4-15 % among all polymorphic AFLP markers (Waugh *et al.*, 1997; Lu *et al.,* 1998; Boivin *et al.*, 1999). AFLP is now the first option to saturate a particular region of the genome when map-based cloning is applied to cloning target genes. Above all, one major application of AFLP is for molecular genetic mapping. It has been used to construct maps for barley (Becker *et al.*, 1995; Waugh *et al.,* 1997; Qi *et al.,* 1998), sugar beet (Schondelmaier *et al.,* 1996), soybean (Keim *et al.,* 1997), petunia (Gerats *et al.,* 1995), rice (Maheswaran *et al.,* 1997), wheat (Lotti *et al.,* 1998) and tomato (Haanstra *et al.,* 1999).

- **Simple sequence repeats (SSRs) or microsatellite**

DNA sequences with di-, tri-, tetra- or penta-nucleotide tandem repeats are described either as microsatellites (Litt and Luty, 1989), as simple sequence repeats (SSRs; Hearne *et*

al., 1992) or as short tandem repeats (STRs; Edwards *et al.,* 1991). The first report of microsatellites in plants was made by Condit and Hubbell (1991). These markers appear to be hypervariable, in addition to which their co-dominance and reproducibility make them ideal for genome mapping, as well as for population genetic studies (Dayanandan *et al.*, 1998). Inter-SSRs are a variant of the RAPD technique, although the higher annealing temperatures probably mean that they are more rigorous than RAPDs. They are present in the vast majority of eukaryotic genomes. The total number of different dinucleotide blocks has been estimated for several species (Ma *et al.,* 1996; Wu and Tanksley, 1993; Morgante and Olivieri, 1993). The number of sites ranged from 10^3 to 10^5 depending on the species and repeat motif. Polymorphism produced by a variable number of tandem repeats has been demonstrated in a large number of species. This feature has made microsatellites a very attractive molecular marker for species with a narrow genetic base such as wheat and barley. This methodology is based on the use of primers complementary to SSRs. Multilocus profiles have been generated using different kinds of oligonucleotide containing simple sequence repeats as single primer (Gupta *et al.,* 1994; Nagaoka and Ogihara, 1997) or in combination with arbitrary sequence oligonucleotides (Wu *et al.,* 1994). These studies have shown the reproducibility of the patterns generated the Mendelian inheritance of the polymorphic amplified bands and their usefulness in the investigation of the genetic relationships. Mapping of this kind of markers in barley (Becker and Heun, 1995) and rapeseed (Kresovich *et al.,* 1995; Szewe-MeFadden *et al.*, 1996; Uzunova and Ecke, 1999; Plieske and Struss, 2001) have been conducted. In wheat, Devos *et al.* (1995) searched sequence database and converted two microsatellite sequences into PCR based markers. Röder *et al.* (1995), Ma *et al.* (1996) and Plaschke *et al.* (1995) investigated the potential of microsatellite sequences as genetic markers in hexaploid wheat. These markers were genome specific and displayed high levels of variation. More recently, a detailed genetic map of 279 microsatellite loci (Röder *et al.,* 1998), another map of 50 loci (Stephenson *et al.,* 1998), 65 loci for the D genome (Pestsova *et al.,* 2000) and (Huang *et al.,* 2001) have been developed for bread wheat. The availability of extensive molecular maps of wheat microsatellites will help in tagging genes of economic importance for marker assisted selection. In wheat, microsatellite markers have been used to tag several genes or quantitative trait loci (QTLs) (see section 1.3.5.2.).

1.3.1.3. Sequencing and DNA chip based markers

Single nucleotide polymorphisms (SNPs) are single base pair positions in genomic DNA at which different sequence alternatives (alleles) exist in normal individuals in natural

populations (Brookes, 1999). Significant efforts towards large-scale characterization of SNPs were first initiated in human genome research. SNPs have since been shown to be the most common type of genetic variation in organisms. Of all the different types of sequence change including single nucleotide substitutions, insertions/deletions and copy number variation in nucleotide repeat motifs, SNP represents about 90 % of human DNA polymorphism (Collins *et al.,* 1998). SNPs have been found to occur with a frequency as high as 1 in every 202 bp in the mouse genome and 1 in 1000 bp in the human genome (Lindblad-Toh *et al.*, 2000; Wang *et al.,* 1998). There are various methods for SNP detection and scoring. More commonly used are gel-based sequencing and high-density variation-detection DNA chips (Wang *et al.,* 1998). SNP has many advantages and great potential for many applications. Since SNPs exist over the whole genome of organisms with a relatively high frequency, they could facilitate the development of highly dense genetic function maps that would be highly valuable for genome analysis. Moreover, as the sequence context of the SNPs is already known, it has the potential for automation and can facilitate the genetic study of associating sequence variations with heritable phenotypes on a large scale. Because of this, there has recently been considerable interest in SNP discovery and detection for genome analysis of plant (Cho *et al.,* 1999).

1.3.2. Comparison of different types of DNA markers

Several different types of DNA markers are currently available for genetic analysis and new marker types are being developed continuously. Markers differ from each other in many respects: the initial workload and costs for building up the marker system, running costs and ease of use, level of polymorphisms, inheritance, number of loci analyzed per assay, reproducibility and distribution on the chromosomes. Detection of polymorphism at the DNA level is usually based either on restriction patterns or differential amplification of DNA. In order to make a choice from a number of molecular markers that have now become available, it is necessary to make a comparison between different types of molecular markers (RFLPs, RAPDs, DAF, SSRs, AFLPs, etc.) described in this chapter. These markers have often been compared for convenience, reproducibility, speed of assay, cost effectiveness and feasibility of using automation and high throughput approaches (Table 2). The choice of the best marker system depends on whether it will be used in evolutionary or population studies, genetic mapping or fingerprinting. The ploidy level and reproductive system of the organism studied are also important. However, using suitably designed experiments in several crops including soybean, barley and wheat, these markers have also been compared for their relative effectiveness and efficiency in detecting DNA polymorphism for a variety of purpose.

Table (2): A comparison of general features of different types of molecular markers and their use. Modified from Rafalski and Tingey (1993), Kalendar *et al.* (1999) and Ridout and Donini (1999).

	RFLP	RAPD	DAF	SSRs	AFLP	SNPs
Principle	Endonuclease restriction, Southern blotting Hybridization	DNA amplification with random primers	DNA amplification with random primers	Amplification of simple sequence repeats using specific primers	Endonuclease restriction Ligation of Adapters & Selective primers	Sequence analysis
Types of polymorphism detected	Single base changes Insertions Deletions	Single base changes Insertions Deletions	Single base changes Insertions Deletions	Changes in number of repeats	Single base changes Insertions Deletions	Single base changes
Genomic abundance	High	Very high	Very high	Medium	Very high	Medium
Level of polymorphism	High	Medium	High	Very high	High	High
Inheritance	Co-dominant	Dominant	Dominant	Co-dominant	Dominant	Dominant
No. of loci detected	1-5	1-10	20-30 or more	1-3	100-150	1 biallelic
Quantity of DNA required	2-15 µg	10-50 ng	10-50 ng	50 ng	0.5-1.0 µg	
Need for sequence information	No	No	No	Yes	No	Yes
Cost	Medium	Low	Medium	High initially	High	High
Reproducibility	High	Low	Low	High	High	High
Technical difficulty	Medium	Low	Medium	Low	Medium/ Low	Medium/ high
Automation possible	-	-	-	+	+	+
Use: 1. Varietal fingerprinting and genetic diversity	+	++	++	+++	+++	++
2.Qualitative gene tagging	++	++	-	+	+++	+
3. QTL mapping	++	-/+	-	+	++	+
4. MAS	++	-	-	++	+++	++
5.Comparative mapping	++	+	-	++	++	++

The superiority of AFLP and SSR techniques was also demonstrated in several other earlier studies (Linn *et al.,* 1996; Janssen *et al.,* 1996; Schwengel *et al.,* 1994). As mentioned above, the SSR markers have high information content (estimated as either the polymorphic information content or as genetic diversity index or as expected heterozygosity) are locus

specific and co-dominant, thus making them the markers of choice for a variety of purposes including practical plant breeding. However, if SSR markers are developed for the first time, a very high cost of their development (due to cloning and sequencing) will restricted their use in many laboratories. But if SSR primers have already been developed in a crop, the use of SSR markers for this specific crop will be cost effective and can be used even in small laboratories (e.g., in wheat, ~1000 primer pairs are available through the efforts of wheat microsatellite and individual works). Polymorphic bands in RAPD and AFLP can also be converted into locus specific SCARs, which will then prove to be as effective as SSR markers.

1.3.3. Mapping populations

Mapping is putting markers (and genes or QTL) in order, indicating the relative distances among them and assigning them to their linkage groups on the basis of their recombination values from all pair wise combinations. Knowledge about the genetic concepts of segregation and recombination is essential to the understanding of mapping. The construction of a linkage map is a process that follows the segregation of molecular markers in a segregating population and put them in linear order based on pair wise recombination frequencies. Thus, a mapping population with high number of polymorphisms over the total genome is highly desirable. Towards this end, various ways have been used to create mapping populations, which are illustrated in Figure 1. Populations used for mapping are usually derived from F_1 hybrids between two lines (either homozygous or heterozygous), which show allelic differences for selected probes. Genetic maps of plants are constructed based on several different kinds of populations (Paterson, 2002), with each population structure having unique strengths and weaknesses. Four types of population are commonly used for map construction and mapping experiment, they are F_2 population, back cross population (BC), doubled haploid (DH) population, and recombinant inbred lines (RILs). Most genetic mapping populations in plants have been derived from crosses between largely homozygous parents.

1.3.3.1. F_2 population

Such populations can be quickly developed and harbor all possible combinations of parental alleles (Lander *et al.*, 1987). However, each F_2 individual has a different genotype and no replication or experimental design can be employed to effectively control environmental influence. To solve this problem, evaluation of F_3 progenies derived from

individual segregants by selfing can be used but gains in precision are partly sacrificed due to genetic heterogeneity (Paterson *et al.,* 1990; Paterson, 1997). A major disadvantage of F_2 population is that the data of marker genotypes cannot be repeatedly used.

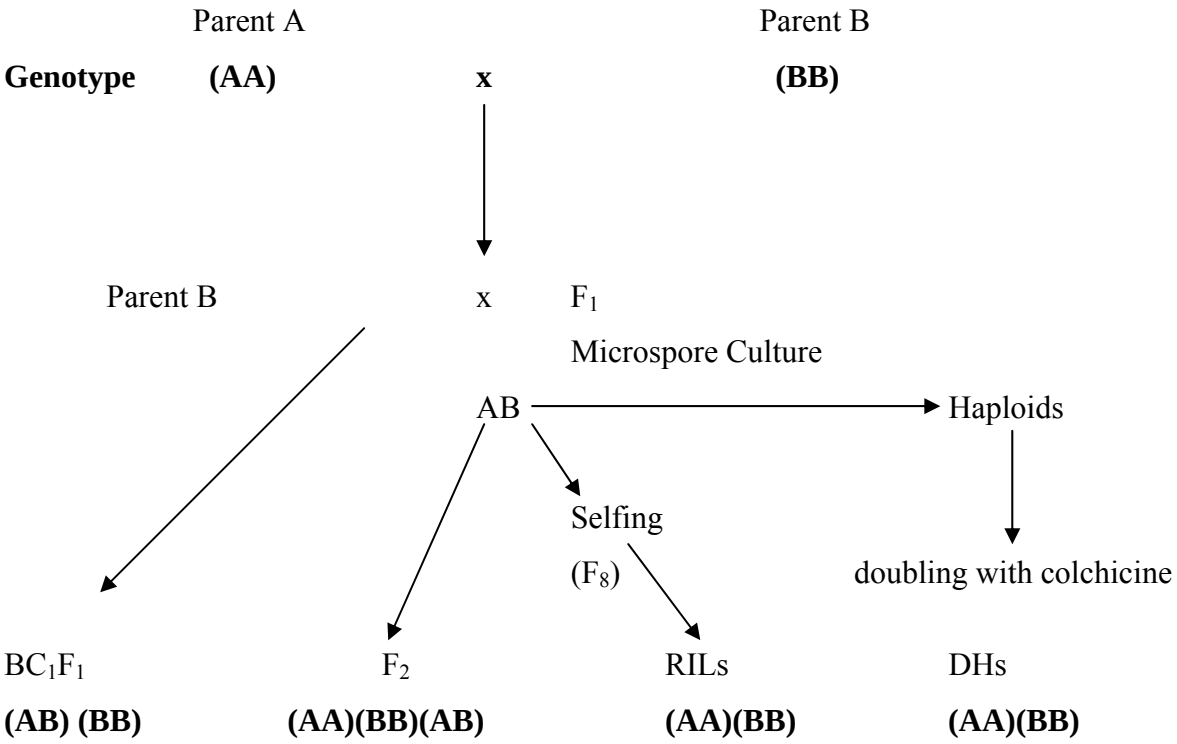


Figure (1): Common strategies for the construction of mapping populations with genotypes symbols (in bold).

1.3.3.2. Back cross (BC) population

This is widely used mapping population. It is derived by crossing F_1 individuals to one of the two parents and has similar advantages and drawbacks as F_2 populations. A major disadvantage of BC population is that the data of marker genotypes cannot be repeatedly used.

1.3.3.3. Doubled haploids (DH) population

A DH population can also be called a permanent population. Producing wheat haploids by crossing bread wheat with maize or pearl millet has become a significant procedure. Doubled haploids are commonly used in many plant species in recently, which are amenable to anther or microspore culture (from F_1 plants), followed by chromosome doubling. Because the plant has two identical homologues, the amount of recombinational information is exactly equivalent to a backcross. However, DH individuals are completely

homozygous and can be self-pollinated to produce large numbers of progeny, which are all genetically identical. This permits replicated testing of phenotypes and also facilitates distribution of identical DH populations to many different researchers. A major disadvantage of DH population is, it is not possible to estimate dominance effects and related types of epistasis and the rates of pollens or microspores successfully turned into DH plants may vary with genotypes, thus causing segregation distortion and false linkage between some marker loci.

1.3.3.4. Recombinant inbred lines (RILs) or single seed descent (SSD) population

Homozygous or 'permanent' populations can also be made by traditional means i.e., by selfing or sib-mating individuals for many generations starting from F_2 by the single seed descent (SSD) approach until almost all of the segregating loci become homozygous. Each of the loci having allelic difference in parents has two genotypes with equal frequencies. However genetic distances based on RILs population are enlarged compared to those obtained from F_2, BC or DHs populations, because many generations of selfing or sib mating will increase the chance of recombination. Also, the RILs populations have several advantages, including reproduction, which favors the genetic analysis of quantitative traits because experiments can be replicated over years and locations; and the use of dominant marker types with the same efficiency as the co-dominant ones (Saliba-Colombi *et al.* 2000). A major shortcoming of RILs populations is that development of RILs population takes long time and it is not possible for all individuals to be homozygous at all segregating loci through limited generations of selfing or sib mating, which decreases the efficiency for QTL mapping to some extent. Also, replicated testing is possible like with DHs.

1.3.4. Mapping quantitative trait loci (QTLs)

1.3.4.1. Quantitative traits

Characters exhibiting continuous variation are termed quantitative traits. Quantitative traits show continuous phenotypic variation in a population resulting from the combined allelic effects of many genes and environmental conditions (Falconer and Mackay 1996). In crop plants most traits of agricultural and economical significance exhibit quantitative inheritance, such as yield, plant maturity, disease resistance and stress tolerance. The genetic loci, which control quantitative traits, are referred to as QTL (quantitative trait loci). QTL analysis has been a major area of genetically study for many decades. The earliest documented experiments on linkage analysis between quantitative effects and marker

genotypes have been reported by Sax (1923) and Thoday (1961). However, for most of the period up to 1980, the study of quantitative traits has largely involved biometrical approaches based on means, variances, covariance of relatives and, consequently, very little was known about the biological nature of quantitative or natural variation in terms of number and location of the genes that underlie them (Fisher, 1918; Wright, 1934; Mather, 1949). It is only during the past decade with the appearence of efficient molecular marker technologies and specific statistical methods that it became possible to follow the segregation of quantitative traits via linked markers (Tanksley, 1993) and to detect effects, numbers and map positions of QTL.

1.3.4.2. Methods of QTL mapping

The identification of QTL for economically important traits has been achieved primarily by two approaches, either through linkage mapping to anonymous markers or through association studies involving candidate genes.

1.3.4.2.1 QTL analysis through a molecular marker approach

The principle of QTL mapping is to associate the phenotypically evaluated trait(s) with molecular markers using statistic tools. The map locations of QTL can then be estimated by the means of highly associated markers. Typically, the detection and location of the loci underlying quantitative trait variation involves three essential steps. First, a segregation population is created and characterized with molecular markers. This usually leads to the construction of a genome wide genetic map of the population. Second, the individuals of the same population are phenotypically evaluated for the traits under investigation. Finally, genotypic molecular markers are analyzed for association with the phenotypic trait data using appropriate statistical methods. This type of QTL analysis can lead to the elucidation of QTL parameters in terms of number, position, effects and interactions between them. Association of morphological markers with quantitative traits in plants was observed early on (Sax, 1923; Everson and Schaller, 1955) and the first steps towards mapping of QTLs or polygenes were taken based on the scarce markers available (Thoday, 1961). Currently, complete genetical maps exist for many crop species and algorithms have been developed for QTL mapping in a wide range of pedigrees (Paterson, 1995). The simplest methods were based on single marker analysis, where the differences between the phenotypic means of the marker classes are compared using F-statistics, linear regression or nonparametric tests (Sax, 1923, Edwards *et al.*, 1987; Soller *et al.,* 1976). The computer program Mapmaker (Lander *et al.*, 1987) has been used extensively for performing interval mapping in plant studies. Interval mapping,

now called simple interval mapping (SIM), searches for a single target QTL throughout a mapped genome.

1.3.4.2.2. QTL analysis through a candidate gene approach

The candidate-gene approach is a powerful and robust method. Compared to the genome wide mapping strategy, the chances of finding markers linked to putative QTL are maximized, since the selection of candidate gene markers is based on known relationships between biochemistry, physiology and the agronomic character under study. This approach has been applied successfully in various QTL analyses, such as mapping QTL for defense response to diseases in wheat (Faris *et al.,* 1999; Pflieger *et al.*, 1999), for resistance to corn earworm in maize (Byrne *et al*. 1996, 1998) and early growth traits in maize (Causse *et al.*, 1995).

1.3.4.3. Conclusions from QTL mapping experiments for abiotic stress

In the traditional models of quantitative genetics simplifying assumptions were made about equality and strict additivity of gene effects (Falconer and Mackay, 1996). From the results of the QTL mapping experiments it has become clear that such assumptions are incorrect. In many mapping experiments, a relatively small number of QTLs accounts for very large portions of phenotypic variance, with increasing numbers of genes accounting for progressively smaller portions of variance, until the significance threshold is reached (Paterson, 1995). The number of QTLs located for particular traits in individual studies varies from one to sixteen, usually being below five (Kearsey and Farquhar, 1998). The proportion of phenotypic variation explained by each QTL and all QTLs together depends on heritability of the trait as well as on the portion of revealed QTLs. QTLs are usually spread over all chromosomes, but clusters of QTLs in certain chromosomal regions have been observed as well. Differences occur in QTL incidence when quantitative traits are scored in many environments or during many years. However, comparative studies between related species have revealed conservation not only in marker order but also in locations of some QTLs (Lin *et al.,* 1995). Examples of QTL studies for different traits in various mapping crosses of different plants for stress tolerance are shown in Appendix Table 1.

1.3.5. Applications of molecular markers

The invention of molecular marker technology such as RFLP, RAPD, AFLP, and SSR as outlined in the previous sections has opened up a new era for genetic analysis of plant genomes. Genetic mapping using molecular marker technology is of great significance to plant breeding, plant genetics and evolutionary studies. The most common applications of genetic linkage maps are concentrated on the following areas. First, genetic linkage maps can be used for marker-assisted selection (MAS) in plant breeding. They could help to identify DNA markers linked to single genes of major agronomic importance and the tightly linked DNA markers can be used as diagnostic tools for MAS. This is particularly suitable and powerful for screening for monogenic disease resistance. One of the successful examples is MAS for soybean cyst nematode resistance (*SCN*) (Cregan *et al.,* 1999). The SSR marker *Satt309*, which is located 1-2 cM away from the gene *rhg1* for resistance to *SCN*, has been developed and used for tagging and tracking the gene through breeding programs, leading to the development of resistant lines. The use of SSR markers has largely decreased the time and effort involved as compared to phenotypic selection. Second, genetic linkage maps can be used for the genetic analysis of quantitative traits. With the construction of molecular linkage maps, characterization of quantitative traits has been greatly facilitated in identifying the genomic regions responsible for the traits and estimating the possible number of genetic factors controlling the traits of interest (Tanksley, 1993). Third, genetic linkage mapping can be used to correlate the phenotypic traits with the genes controlling the trait, which includes map-based cloning of a gene of known heritable phenotype and postulating candidate genes for a trait with known biochemical basis. Finally, genetic linkage maps provide insights into chromosomal organization and could be useful in map-based evolutionary studies by comparative mapping.

1.3.5.1. Linkage maps

Construction of a genetic linkage map is based on observed recombination between marker loci in the experimental cross. Segregating families, e.g. F_2 population or BC progenies, DHs population or RILs lines are commonly used. In barley the use of doubled haploid progenies produced from the F_1 generation simplifies genetic analysis. Doubled haploid lines have undergone only one meiotic cycle and carry a completely homozygous chromosome set. This means that the genetic information per plant is constant irrespective of the marker system used (Graner *et al.,* 1996). Genetic map distances are based on recombination fractions between loci. The Haldane (1919) or Kosambi (1944) mapping functions are

commonly used for converting the recombination fractions to map units or centiMorgans (cM). The Haldane mapping function takes into account the occurrence of multiple crossovers but the Kosambi mapping function accounts also for interference, which is the phenomenon of one crossing-over inhibiting the formation of another in its neighborhood (Ott, 1985). Computer programs performing full multipoint linkage analysis include Mapmaker (Lander *et al.,* 1987) and JoinMap (Stam, 1993). Linkage map of human genome based on segregation analysis of 814 (CA)n microsatellite loci was initially constructed (Weissenbach *et al.,* 1992). However in plants, mapping with STMS markers did not reach this level of resolution so far (Weising *et al.,* 1998), although the very first attempt to map sequence-tagged microsatellite sites (STMS) loci in any species, was made as early as 1992, in rice using $(GGC)_n$ microsatellites (Zhao and Kochert, 1992; 1993). Several barley maps based on SSRs (Liu *et al*., 1996) and randomly amplified SSRs (Dávila *et al.*, 1999) have been developed. Mapping of the whole genome using microsatellite loci are also currently in progress in many crops i.e. Brassica (Moule *et al.,* 2000), soybean (Csanádi *et al*., 2001) and maize (Sharopova *et al.,* 2000). Microsatellite loci, other than STMS markers, have also been used for mapping in different plant species. In bread wheat, two microsatellite maps, one with 279 loci (Röder *et al.,* 1998) and another with 50 loci (Stephenson *et al.,* 1998) have been prepared. Also in tetraploid wheat, 14 microsatellite loci were mapped on chromosomes 5A and 5B, which carry genes for protein content, vernalization response and resistance to Hessian fly. Utilizing International Triticeae Mapping Initiative (ITMI) population, an integrated map of wheat genome (with 1200 RFLP earlier mapped; Leroy, 1997a, b) became available, to which 279 *gwm* microsatellite loci were added (Röder *et al.,* 1998). Later, Gene and Genome Mapping Group, Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK), Gatersleben, Germany has successfully assigned a set of another 70 microsatellite loci to specific chromosomes using nulli-tetrasomic lines (Röder *et al.,* 1999). Additional microsatellite loci have been mapped by Leroy (2000). Comparative mapping within the *Poaceae* family has also revealed high levels of conservation of gene order (Devos and Gale, 1997).

1.3.5.2. Mapping qualitative traits for marker assisted selection (MAS)

Qualitative genes are inherited in a Mendelian fashion and their allelic forms give qualitatively distinct phenotypes. The phenotypes in a segregating progeny can be scored in a similar fashion as molecular markers. A normal segregation analysis will reveal linkages to any of the markers. Mapping a gene to a certain location on the chromosomes demands a linkage map of the whole genome, but genes can also be tagged with molecular markers

without any previous information of the map location of markers used. Two approaches have been proposed for this purpose, i.e., use of near-isogenic lines, NILs (Martin *et al.,* 1991; Muehlbauer *et al.,* 1988) and pooled DNA samples (Michelmore *et al.*, 1991). NILs differ only by the presence or absence of the target gene and a small region of flanking DNA. Hundreds of arbitrarily primed PCR-based markers can easily be screened to identify differences between isogenic lines and these differences are likely to be linked to the target gene. The NILs have been used in barley to tag a powdery mildew resistance gene (Hinze *et al.,* 1991) and a spot blotch resistance gene (Hakim, 1996). In bulked segregant analysis (BSA), DNA pools of individuals of a crossing progeny are made based on their phenotype and screened for differences in the molecular markers (Michelmore *et al.*, 1991). BSA has successfully been used in barley for tagging several disease resistance genes with RAPD markers locating 1.6-12 cM from the target locus (Weyen *et al.,* 1996; Borovkova *et al.,* 1997; Poulsen *et al.,* 1995; Barua *et al.,* 1993). Also, BSA has been proposed for tagging quantitative loci with a major effect: theoretically QTL alleles with phenotypic effects of 0.75-1.0 standard deviations should be detectable in DH populations of 100-200 lines (Wang and Paterson, 1994).

The first example of a gene linked to a microsatellite (AT) was a soybean mosaic virus resistance gene (*Rsv*) (Yu *et al.,* 1994; 1996). Several other resistance genes including those for resistance to peanut mottle virus (*Rpv*), Phytophthora (*Rps3*) and Javanese root knot nematode, were found to be clustered in the same region of soybean genome where this (AT)n microsatellite was found to be associated with *Rsv*. Microsatellite markers, associated with soybean cyst nematode (*SCN*) resistance locus, sclerotinia stem rot resistance and brown stem rot resistance, were also reported by (Mudge *et al.,* 1997; Moreiral *et al.,* 1999). In wheat, microsatellite markers have been applied widely for tagging genes or QTLs determining dwarfing (Korzun *et al.,* 1997, Korzun *et al.,* 1998, Worland *et al.,* 1998b), vernalization response (Korzun *et al.,* 1997; Tóth *et al.,* 2003), disease resistance (Fahima *et al.,* 1997; 1998; Peng *et al*., 1999; Börner *et al.,* 2000b; Huang *et al.,* 2000a; del Blanco *et al.,* 2003; Shen *et al.,* 2003; Schnurbusch *et al.,* 2003; 2004 ; Huang *et al.,* 2003b), flour colour and milling yield (Garry *et al.,* 1997), grain protein content (Prasad *et al.,* 1999; 2003), pre-harvest sprouting tolerance (Roy *et al.,* 1999), grain yield and its components (Varshney *et al.,* 2000; Huang *et al.,* 2003a) and frost (Tóth *et al.,* 2003). In durum wheat, some microsatellites have been mapped in two regions of chromosome 5A each carrying a QTL, for high grain protein content and for heading (Korzun *et al*., 1999).

1.3.5.3. Fingerprinting and variety identification

The ability to discriminate between and identify varieties of agricultural crops is central to the operation of seed trade. Plant breeder's rights offer protection for varieties, but in turn require that new varieties are Distinct from others, Uniform and Stable in their characteristics (the so called D, U and S criteria) (Cooke, 1995). Varietal identification and purity are also important for consumers, and especially for industry, which uses the harvested yield for large-scale processing. DNA markers have been introduced as a promising method of fingerprinting different crop varieties. For example, DNA fingerprints of 65 registered six-rowed barley varieties in Canada have been generated using RAPD markers. All varieties could be identified from each other based on 18 polymorphic bands (Baum *et al.* 1998). AFLP and RAPD markers have also been successfully used for barley malt fingerprinting (Faccioli *et al*. 1999). Using a number of SSRs, oligonuclotide fingerprinting has been successfully utilized in a variety of crops (Weising *et al.,* 1995). In a study involving 105 hexaploid wheat varieties from Argentina, closely related wheat varieties having high similarity co-efficients, could be discriminated using selected microsatellites, located on different chromosomes (Manifesto *et al.,* 1999).

1.3.5.4. Genetic diversity studies

DNA polymorphisms can also be used to explore issues of genetic diversity. Knowledge of genetic diversity and the genetic relationship between genotypes is an important consideration for efficient rationalization and utilization of germplasm resources. Information on genetic diversity is also needed for the optimal design of plant breeding programmes, influencing the choice of genotypes to cross for the development of new populations. Molecular approaches have been used to group barley cultivars into morphologically distinct groups and further into subgroups that have a similar genetic background. RFLPs (Melchinger *et al*. 1994, Graner *et al*., 1994, Casas *et al.,* 1998), RAPDs (Dweikat *et al*., 1993; Tinker *et al.,* 1993), AFLPs (Schut *et al.,* 1997; Ellis *et al.,* 1997) and SSRs (Dávila *et al.,* 1999; Russell *et al.,* 1997) have been used for assessing variation in local and global collections of barley germplasm. Microsatellites have been considered to be the markers of choice for assessment of genetic diversity among cultivars and their wild relatives (Karp *et al.,* 1998; Doldi *et al*., 1997). Using set of 12 microsatellite markers, Prasad *et al.* (2000) studied the genetic diversity of 55 elite genotypes. In bread wheat, 42 microsatellite markers clearly distinguished varieties in three different agro-ecological areas namely Hungary, Austria and Germany (Lelley and Stachel, 1998). The usefulness of these markers

for estimation of genetic relatedness has been demonstrated in many crops including maize (Taramino and Tingey, 1996), barley (Russell *et al.,* 1997), wheat (Plaschke *et al*., 1995; Donini *et al*., 1998; Lelley *et al*., 2000; Stachel *et al*., 2000; Pestsova *et al*., 2000; Hammer *et al*., 2000; Prasad *et al.,* 2000; Stachel *et al.,* 2000; Ben Amer *et al.,* 2001; Fahima *et al.*; 2002; Huang *et al.,* 2002), rice (Wu and Tanksley, 1993; Ahn *et al.,* 2000), sorghum (Brown *et al.,* 1996), sunflower (Paniego *et al.,* 1999), *Aegilops tauschii* (Lelley *et al*., 2000) and potato (Provan *et al.,* 1996).

1.3.5.5. Genetic fidelity and germplasm characterization

Microsatellite markers have been utilized to find out wether or not the germplasm accessions maintain their genetic fidelity during storage and conservation (i.e. detect duplications, seed mixtures and inadvertent out crossing). One should realize that the failure to detect polymorphism might not indicate genetic fidelity, although reproducibility of polymorphism between the two taxa after storage may suggest some degree of genetic fidelity (Gupta and Varshney, 1999; Börner *et al.,* 2000a; Chebotar *et al*., 2003). The microsatellite have been used to characterize and conserve the germplasm in many plant species i.e. soybean (Rongwen *et al.,* 1995), rapeseed (Poulsen *et al.,* 1993) and *Phaseolus* (Hamann *et al.,* 1995).

1.4. Outline of the thesis

Molecular markers are powerful tools that have been used for marker-assisted selection and as landmarks for map-based cloning of genes. Molecular markers associated with QTLs have been reported for many important traits. After a linkage between a QTL and molecular marker has been determined, the QTL can be transferred into any genetic background by marker-assisted selection. Therefore, the objectives of the present study are:

1. To define genotypes with high stem reserve mobilization ability.
2. To characterize the expression and inheritance of traits associated with post-anthesis drought tolerance and grain development.
3. To determine of the number, chromosome position and effects of the QTLs conditioning drought tolerance.
4. To identify SSR and RFLP markers associated with the QTLs for drought tolerance.
5. To explore the potential of marker-assisted selection in improving wheat drought tolerance.

2. MATERIALS AND METHODS

2.1. Genetic materials

2.1.1. Screening plant materials

77 wheat genotypes from Genebank department, Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK), Gatersleben, Germany and Agriculture Research Center (ARC), Giza, Egypt were used to establish the experimental materials for this investigation (Appendix Table 3). The genotypes used in the study differ from each other in morphological as well as phenological characters. They had been originated in different regions.

2.1.2. Developing of $F_{2:3}$ mapping population

The post-anthesis drought tolerance (PADT) mapping population consisting of 81 F_3 families was developed from an interspecific cross between the spring wheat accession 'ATRI 5283' as a male parent (*Triticum durum* L.) and 'ATRI 15010' as a female parent (*Triticum aestivum* L.). These two genotypes were chosen according to their behavior to the post-anthesis drought stress. The percentage and degrees of tolerance of these genotypes are listed in Appendix Table 3. 'ATRI 5283' is a post-anthesis drought tolerant parent. On the other hand, the 'ATRI 15010' was post-anthesis drought sensitive.

2.1.3. Recombinant inbred lines (RILs)

A set of 114 recombinant inbred lines (RILs) from the International Triticeae Mapping Initiative (ITMI) population was also used for mapping of genes/QTLs for post-anthesis drought tolerance. This population was derived by single seed descent F_8 from the cross of 'W 7984' x 'Opata 85'. The parent 'W 7984' was an amphihexaploid wheat synthesized from *Triticum tauschii* (DD) and *Triticum durum* (AABB) variety 'Alter 84', while 'Opata 85' was a Mexican wheat variety developed at CIMMYT (Centro Internacional de Mejoramiento de Maizy Trigo). The development of these RILs was described by Börner *et al.* (2002b).

2.2. Drought experiments

2.2.1. Field experiments

2.2.1.1. Screening plant materials

This investigation was carried out at Gatersleben, during the wheat growing season 2001/2002. The experiments were arranged in a randomized complete block design with two replicates. Each replicate consisted of one plot per genotype with four rows, 1 m long, with 20

cm between rows. The soil type at the experimental site was silty loam. All plants in each plot were harvested in bulk when the plants reached maturity.

2.2.1.2. $F_{2:3}$ mapping population

The cross was initiated for F_1 and F_2. In 2002 season, 81 F_3 families and the two parents were planted on the experimental field of the Genbank, Gatersleben, in 4 rows 100 cm long with 20 cm between rows. In 2003 season, the same experiment was repeated. All plants in each plot were harvested in bulk when the plants reached maturity. Each plot was threshed separately after they all were dried**.**

2.2.1.3. Recombinant inbred lines (RILs)

This investigation was carried out at the experimental fields of the Genebank, IPK, Gatersleben, during the wheat growing seasons 2001 and 2003. The experiment was arranged in one replicate. The replicate consisted of one plot per genotype with four rows, 1 m long, with 20 cm between rows. The soil type at the experimental site was silty loam. All plants in each plot were harvested in bulk when the plants reached maturity.

2.2.2. Drought test

Anthesis was recorded when about 50% of the plant showed spikes with exerted anthers in the central third of the spikes as shown in Fig. 2. Fourteen days after anthesis, chemical desiccation was applied to two rows of the plot of each genotype, while the other two rows were kept untreated (without desiccation). The desiccation treatment was applied by spraying the whole plant canopy to full wetting with an aqueous solution of potassium iodide (KI, 0.5 % *w/v*). The desiccant was applied using a hand-held boom sprayer allowing spray penetration to the whole plant canopy Fig. 3.

Figure (2): Wheat spike with exerted anthers

Figure (3): Spray treatment with KI in field

2.2.3. Drought scoring

At maturity, the spikes were collected and threshed on a plot basis. After harvest, 1000-grain weight was estimated for treated and non-treated rows. In the final testing, the post-anthesis drought tolerance index of a pre-specified seed bulk was estimated from the performance of the stressed rows (S) relative to its respective non-stressed control rows (C) within the same replicate and calculated as percent according to Blum *et al*. (1983a, b): Calculation of stress tolerance index (STI) % = [(S/ C) x 100], where C = 1000-grain weight under control and S = 1000-grain weight under potassium iodide (KI) treatment.

2.2.4. Evaluation of phenotypic traits

Plants were selected at random for subsequent measurements as follows

2.2.4.1. Vegetative traits

2.2.4.1.1. Flowering time (days)

It was determined as the number of days from date of sowing to the date of the first anthers exertion of 50% of the ears of each genotype.

2.2.4.1.2. Plant height (cm)

Length of the main culm (in centimeters) was measured from the soil surface to the tip of the main ear at maturity, excluding awns.

2.2.4.2. 1000-grain weight (g)

It was recorded as the weight of 1000 random wheat grain.

2.2.4.3. Grain characters

A separate preliminary experiment was conducted to determine the grain sample size. Five Digital Image Analysis (DIA) parameters were measured and compared among samples of kernels of genotypes grown under treated and non-treated rows. A method similar to that described by Symons and Fulcher (1988) was used for DIA. The captured image was displayed as a digitized grey level image on a computer monitor. Calibration was in mm. The initial image was subjected to normalization. The discriminated grains were automatically identified and measured for: Grain area (mm^2), Grain width (mm), Grain length (mm), Grain circumference (mm) and Grain Roundness. Also, Grain form density factor was estimated. Grain form density factor, defined as grain weight/grain area (g/mm^2), could be considered as a grain quality character. Based on the measurements of grains originated from the treated and non-treated samples, STI was calculated (see section 2.2.3.).

2.2.5. Gene symbols

In total 9 characters were scored in the different experiments and divided into vegetative traits, grain yield and grain characters traits. The symbolisation of the QTLs follows the rules of McIntosh *et al*. (2003) (Table 3).

Table (3): Gene symbol for studied traits

Trait	Gene Symbol	Scale
Flowering time	*Flt*	days
Plant height	*Ht*	cm
Stem reserve mobilization	*Srm*	%
Grain area STI	*Gae*	%
Grain width STI	*Gwd*	%
Grain length STI	*Glt*	%
Grain circumference STI	*Gcc*	%
Grain Roundness STI	*Grs*	%
Grain form density factor STI	*Gdf*	%

2.3. Molecular mapping

2.3.1. Enzymes, buffers and solutions

2.3.1.1. Enzymes

- RNAse A (10 mg/ml)

100 mg of RNAse was dissolved in a sterile solution of 10 mM Tris-HCL (pH 7.5) and 15 mM NaCl and boiled for 15 min in a water bath. After cooling RNAse was tested and stored at -20 °C.

- *Taq*-DNA Polymerase

2.3.1.2. Basic buffers and solutions

- **0.5 M Ethylene diamine tetra acetate (EDTA, $Na_2EDTA.\ 2H_2O$) pH 8**

186.12 g $Na_2EDTA.\ 2H_2O$ (MW = 372.2) was dissolved in 800 ml distilled water by stirring vigorously and pH was adjusted to 8.0 with NaOH (~20 g of NaOH pellets). Solution was sterilized by autoclaving.

- **(24:1, *v/v*) Chloroform: Iso-amyl alcohol ($CHCl_3$: IAA)**

40 ml *iso*-amyl alcohol was added to 960 ml chloroform. Store the mixture at 4°C in dark glass bottles.

- **Ethidium bromide (Et Br, 10 mg/ml) Stock**

1g ethidium bromide was added to 100 ml of H_2O and stirred vigorously on a magnetic stirrer for several hours to ensure that the dye has dissolved. The container was wrapped in aluminium foil and stored at 4°C.

- **3 M Sodium acetate (NaOAc) pH 5.2**

408.1 g of sodium acetate was dissolved in 800 ml of distilled water; pH was adjusted to 5.2 with glacial acetic acid and sterilized by autoclaving.

- **5 M Sodium chloride (NaCl)**

292.2 g of NaCl (MW = 58.44) was dissolved in 800 ml of distilled water (dH_2O) and volume adjusted to 1000 ml and solution was sterilized by autoclaving.

- **(20 %, *w/v*) Sodium dodecyl sulphate (SDS)**

20 g of lauryl dodecyl sulphate sodium salt (SDS) was dissolved in 100 ml of distilled water by heating at 70 °C and pH was adjusted to 7.2 by adding a few drops of concentrated HCl.

- **1 M Tris-HCl pH 8**

121.1 g of Tris base was dissolved in 800 ml of distilled water and the pH to desired value (pH 8) was adjusted by adding concentrated HCl. The volume was made up to 1L and sterilized by autoclaving.

- **Tris-EDTA (TE) buffer**

(1,2114 g) of 1M Tris-HCl pH 8.0 and (0,37224 g) of 0.5M Na_2 EDTA pH 8.0 was added to 900 ml of distilled water (dH_2O). The volume was made up to 1L and sterilized by autoclaving.

- **(50 X) Tris-acetate-EDTA (TAE)**

242 g Tris, 57.1 ml glacial acetic acid and 37.2 g Na_2EDTA. 2H2O was added to 900 ml of distilled water (dH_2O), pH was adjusted to 8. The volume was made up to 1L.

- **(10 X) Tris-Borate-EDTA (TBE) buffer**

(108.0 g) of 0.89M Tris, (55.0 g) of 0.89M boric acid and (8.3 g) of 20mM EDTA was added to 900 ml of distilled water (dH_2O). The volume was made up to 1L.

- **10 mM dNTPs**

Equal amounts of 10mM dATP, 10mM dCTP, 10mM dGTP and 10 mMdTTP was mixed. Store in 10 µl aliquots at -20 °C.

- **(10 X) PCR buffer**

1 ml of 1M Tris-HCl pH 8.0, 5 ml of 1M KCl, 150 µl of 1M $MgCl_2$ and 10 mg of gelatin (Sigma G-2500) was added to 3.85 ml of distilled water (dH_2O). The volume was made up to 10 ml and sterilized by autoclaving.

2.3.2. Solution for DNA isolation

Mix from 100 ml of 5M NaCl, 100 ml of 1M Tris-HCl pH 8.0, 100 ml of 0.5M EDTA pH 8.0 and 62.5 ml of 20% SDS was added to 500 ml of distilled water (dH_2O). The volume was made up to 1L and sterilized by autoclaving.

- 75% EtOH

Absolute EtOH was diluted to 75% with distilled water (dH_2O).

2.3.3. Genomic DNA isolation

2.3.3.1. Plant growing and leave material preparation

Young leaves from eight-weeks-old F_2 plants were cut as tissue samples for DNA extraction from the greenhouse. An equal amount of tissue was taken from each single plant. Only one replication was sampled for DNA extraction. The tissues were transported the same day to the laboratory on liquid nitrogen and stored at –80 °C.

2.3.3.2. Genomic DNA extraction for mapping

Total genomic DNA was isolated according to the protocol described previously by Anderson *et al.* (1992). Briefly, 3-5 g of leaf tissue per sample (each sample was collected from each F_2 seedling 8 weeks after sowing, 81 plants in total) were ground in liquid nitrogen and incubated at 60 °C for 45 min with 15 ml of extraction buffer, (100 mM Tris-HCl, 500 M NaCl, 50 mM EDTA, 1.25 % SDS) in 50 ml polypropylene tubes. After cell disruption and incubation with hot isolation buffer, proteins were removed by chloroform: iso-amyl alcohol (24:1, *v:v*). Samples were incubated for 30 min by shaking and then centrifuged at 3000 rpm for 30 min. The aqueous layer was transferred to a new tube and 20 µl RNAse A (10 mg/ml) was added. Samples were incubated for 30 min at room temperature. One volume of cold ethanol was added to precipitate DNA. After 30 min incubation at 4 °C, precipitated DNA was hooked out and placed in a 2 ml reaction tube containing 1 ml of 75% ethanol. After washing twice with 75% ethanol, the washing solution was removed and the DNA pellet was dried thoroughly and dissolved in TE buffer. The DNA samples were diluted and stored at -20 °C. The DNA was diluted to a concentration of 50 ng/µl before used in SSR experiment.

2.3.3.3. Concentration measurement of DNA

This step is essential for checking that the isolated DNA is of high molecular weight. For that, uncut DNA was run on 1% agarose gel. The quality and quantity of DNA were measured by comparison of band-intensity on ethidium bromide stained agarose gels with a DNA molecular weight standard.

2.3.4. Simple sequence repeats (SSRs) or microsatellite analysis

Wheat microsatellite (WMS) primer pairs were developed by Röder *et al*. (1995; 1998; unpublished results). One primer of each WMS pair was labelled by florescent agent. The primer taglgap was described by Devos *et al*. (1995). All Gatersleben Wheat Microsatellite (*gwm*) used were di-nucleotide repeats (Appendix Table 2), whereas taglgap has a tri-nucleotide motif.

2.3.4.1. Polymerase chain reaction analysis (PCR)

SSR procedures were as described by Röder *et al*. (1995; 1998) and Devos *et al*. (1995), respectively. Briefly, each polymerase chain reaction (PCR) was performed in a volume of 25 µl in Perkin-Elmer (Norwalk, Ct.) thermocycles. The reaction mixture contained the following:

Stock	PCR reaction	25 µl (1x)	50x	100x
10x PCR buffer	1 M Tris-HCl 1 M KCl 1.5 mM $MgCl_2$	2.5 µl	125 µl	250 µl
Left primer	250 nM	0.65 µl	32.5 µl	65 µl
Right primer	250 nM	0.65 µl	32.5 µl	65 µl
Taq DNA polymerase	1 U	0.1 µl	5 µl	10 µl
dNTPs	0.2 nM	50 µl	100 µl	200 µl
Wheat genomic DNA	50-100 ng	5 µl	--	--
dd H_2O	Variable	14.1 µl	705 µl	1410 µl

Amplification for all Gatersleben wheat microsatellites should be carried out according to the following program conditions:

	Temperature	Time	Number of cycles
Initial denaturation	94 °C	3 min	1 (first)
Denaturation	94 °C	1 min	45 Cycles
Annealing (depending on individual microsatellite)	50, 55 or 60 °C	1 min	
Elongation	72 °C	2 min	
Final elongation	72 °C	8 min	1 Cycle
	4 °C	until turn off	

After the final extension (polymerization) step, the samples were transferred to 4 °C or to -20 °C if they were not going to be used immediately.

2.3.4.2. Fragment analysis

The technique involves labeling of one of the two primers of a PCR reaction with one of the two coloured fluorescent tags (blue or yellow). The samples were mixed with 2µl internal size standard, denatured at 90°C for 2 min and chilled on ice. The resulting PCR product(s) are separated on polacrylamide gels with the help of the automated laser fluorescence (ALF) express DNA sequencer. Fragment analysis was carried out on (ALF) express sequencers (Amersham Biosciences, Freiburg, Germany) using short gel cassettes. Each sample was loaded on a polyacrylamid gel. Denaturing 6% polyacrylamide gels, 0.35 mm thick, were prepared. The gels were run in 1 X Tris-borate-EDTA (TBE) buffer (pH 8.0) with 600 V, 50 mA and 50 W with 2 mW laser power and a sampling interval of 1,00 sec. The gels were reused four to five times. In

each laser, fragments with known size were included as standards. Microsatellite fragment sizes were calculated using the computer program Fragment Analyser Version 1.02 'Amersham Bioscience, Freiburg, Germany', which was added to each lane in the loading buffer by comparison with the internal size standards (Röder *et al*., 1998). (Appendix Fig. 1).

2.3.5. Marker nomenclature

Wheat microsatellite loci were designated '*Xgwm*' for 'Gatersleben Wheat Microsatellite' followed by a primer number, according to Röder *et al.* (1998). Detected loci were marked with an '*X'*, the basic symbol for molecular marker loci of unknown function in wheat. The information of mapped *gwm* primer pairs in this study can be found in Appendix Table 2.

2.4. Statistical methods

2.4.1. Analysis of variance

Analysis of variance was performed using the program Minitab. The ANOVA was estimated for 1000-grain weight stress tolerance index. The calculation tables were as follows:

ANOVA for 1000-grain weight stress tolerance index

S.O.V	DF	MS	Expected MS
Block	r-1		
Genoypes (G)	g-1		$\sigma^2 e + r \sigma^2 g$
Error (e)	(r-1) (g-1)		$\sigma^2 e$
Total	(rg-1)		

2.4.2. Phenotypic frequency distribution

Phenotypic frequency distribution was performed using the program Minitab.

2.4.3. Map construction

Linkage of all marker loci analysis was performed with the computer program MAPMAKER (Lander *et al.*, 1987). Kosambi function (Kosambi, 1944) was used to convert the recombination frequency to genetic distances in centimorgans (cM). This analysis was carried out by evaluating the mapping populations as an F_2 using two-point analysis to identify linkage group at a LOD score of 3.0. Data was put in as A, B and H to mark genotypes of parent A; parent B, and heterozygotes, respectively, for co-dominant marker. Other situations were coded by C = not A; i. e. H or B (for dominant markers), D = not B; i. e. H or A (for dominant markers), '-' = missing data for the individual at a locus.

Any marker of one group has to any marker of the other group and LOD score < 3.0 or recombination ratio > 0.40. The formed groups were afterwards ordered using the 'First Order' command whenever possible. Usually, the first order was aided with LOD table correlations between markers, to figure out the most-linked markers. The 'Compare' command calculated the maximum likelihood map for each specified order of markers and to report the orders stored by likelihood of their maps. One sequence can specify more than one order of loci. For example, the sequence '{1 2 3}' specifies the three orders '1 2 3', '1 3 2' and '2 1 3'. Only the 20 most likely orders were reported by MAPMAKER. The best order was indicated as having a relative *log-likelihood* of 0.0. The obtained order was then analyzed further using a three-Point linkage analysis 'Ripple' command. Other markers were added using the 'Try' command and fine-tuned using again the 'Ripple' command. The 'Ripple' command was conducted to assign exact positions to markers. Both chromosome assignment and centromere localization were determined by comparing the map to the previously published wheat maps, especially to the Röder *et al.* (1998) wheat SSR map. Marker loci and linkage group that were more than 50 cM apart were considered to be not significantly linked.

2.4.4. Quantitative trait loci analysis

The QTL analysis was performed as a composite interval mapping analysis (CIM) to identify genomic regions associated with the traits evaluated using *QGENE* (Nelson, 1997). The association between phenotype and marker genotype was investigated using single-marker regression. The program performs a multiple regression on evenly distributed positions of the linkage map. It calculates the test statistics (LOD) based on the sum of squares of the regression in a model with QTLs versus the sum of squares of the regression in a model without QTLs. Also, the proportion of phenotypic variance explained by each QTL marker was estimated using the coefficient of determination (PV), which is based on the partial correlation of a putative QTL with the trait adjusted for cofactors in the multi locus model. For each QTL, the regression coefficient from the multi-locus model was used to estimate the additive effect of the 'A' or 'B' allele. Additive effect was positive if the allele of 'A' increase the post-anthesis drought tolerance score, plant height, heading date or grain characters measurements and negative if the 'B' increased the post-anthesis drought tolerance score, plant height, heading date or grain characters measurements. In the *QGENE* program, the parameters for the QTL data were included in data files. These parameters were marker data, linkage groups and the phenotypic observation values.

3. RESULTS

For better representation and discussion of the results obtained, herein, it is preferred to outline these results into three main parts; i.e. (i) screening wheat genotypes for post-anthesis drought tolerance, (ii) Analysis of post-anthesis drought tolerance in F_3 families and (iii) Analysis of post-anthesis drought tolerance in RILs mapping population.

3.1. Screening wheat genotypes for post-anthesis drought tolerance

The main purpose of this part of study was to determine whether there were any genetic differences among lines resulting from spraying the wheat canopy with potassium iodide (KI, 0.5% *w:v*) 14 days after anthesis. Spraying of leaves and ears with KI induced a gradual loss of chlorophyll in the leaves and ears though in water stressed plants. The effect of KI spray was observed from one week after the treatment in yellowing of the awns, glumes, leaf lamines, parts of the spike peduncles, leaf sheaths and spikes. Within one week after the chemical desiccant spray application, most of the green plant tissues were dead, as judged by the complete disappearance of chlorophyll and brittleness of affected tissues (Fig 4). The desiccation treatment for all wheat species affected grain weight.

Figure (4): Chemically desiccated (left) and control (right) spikes. Photographs were taken 14 days after spraying.

Table 4 shows the results of the analysis of variance based on stress tolerance index indicated significant differences ($P \leq 0.01$) for 1000-grain weight stress tolerance index between the wheat genotypes. Genotypes were found to be highly significant for stress tolerance index, indicating that there was genetic diversity in post-anthesis drought tolerance within the wheat germplasm.

Table (4): Mean square estimates of analysis of variance for 1000-grain weight stress tolerance index

Source of variance	df	Mean square	F
Genotypes	76	471.6	5.41**
Blocks	1	581.4	6.67*
Error	76	87.2	
Total	153		

* and ** significant at 0.05 and 0.01 levels of probability, respectively.

The drought stress tolerance index based on grain yield i.e., 1000-grain weight under KI spray treatment (S) and 1000-grain weight under control (C) for the genotypes analysed is reported in Appendix Table 3. Among the seventy-seven wheat genotypes tested in the wheat growing season 2001/2002, the stress tolerance index, ranged from 22.26% to 87.78%. The wheat genotypes ATRI 1896, ATRI 5283, ATRI 17620, Synthetic/N, ATRI 9882, ATRI 5951, W7984 and ATRI 7099 exhibited the highest stress tolerance index values (87.78%, 82.41%, 80.23%, 78.46%, 77.71%, 74.33%, 70.80% and 70.06%, respectively). On the other hand, the wheat genotypes ATRI 11457, ATRI 11445, ATRI 6931, ATRI 10213, Capelle-Desprez, ATRI 10197, ATRI 1634 and Bezostaya exhibited the lowest stress tolerance index values (22.26%, 25.72%, 26.60%, 26.88%, 30.29%, 30.37%, 30.55% and 31.13%, respectively).

3.2. Analysis of post-anthesis drought tolerance in F_3 families

3.2.1. Analysis of field experiments

3.2.1.1. Phenotypic analysis and inheritance of stem reserve mobilization

In two experiments in Gatersleben, a set of 81 F_3 families plus the two parental accession lines, 'ATRI 5283' and 'ATRI 15010' were grown in the field for the purpose of phenotyping stem reserve mobilization. Plants were tested using potassium iodide (KI, 0.5 % *w/v*) after 14 days and stress tolerance index (STI) for 1000-grain weight was measured. In

this study, mean responses of the parents were recorded as percent of 1000-grain weight injury after treated by KI in Gatersleben location for the years 2002 and 2003. The two parental lines differed in post-anthesis drought tolerance. The stress tolerance index for 'ATRI 5283' (80.42%-77.60%) was higher than that of 'ATRI 15010' (46.15%-57.72%). These results confirmed that the 'ATRI 5283' have more stem reserve mobilized and a high translocation ability for kernel weight compared with the 'ATRI 15010'. Using the data of 1000-grain weight stress tolerance index of F_3 families, a frequency distribution curve was prepared (Fig. 5). A wide or continuous frequency distributions with transgressive segregants was observed, as one would expect for a quantitative trait. The continuous distribution of stem reserve indicated that stem reserve mobilization is polygenic in nature and quantitatively inherited.

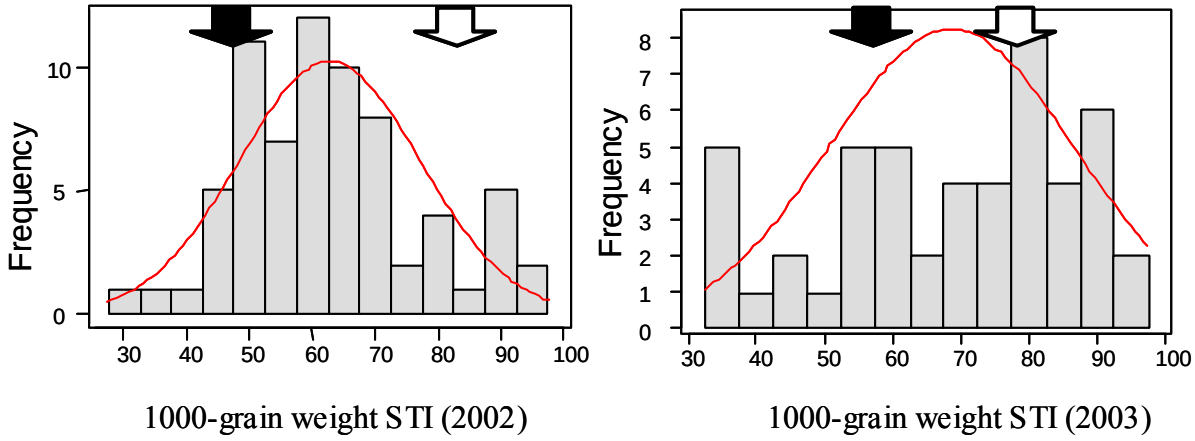


Figure (5): Phenotypic distribution of stress tolerance index (STI%) for 1000-grain weight means of F_3 families derived from a cross between 'ATRI 5283' and 'ATRI 15010' measured for the two environments (Gatersleben 2002 and Gatersleben 2003). (Empty arrows = means of 'ATRI 5283'; filled arrows = means of 'ATRI 15010').

3.2.1.2. Phenotypic analysis and inheritance of vegetative traits

Plant height (*Ht*) was measured at Gatersleben in 2002 and 2003 as the distance from the ground to the top of the spike (excluding awns) in centimeters. Also, flowering time (*Flt*) was quantified as the number of days from planting to flowering of 50% of plants of each genotype. Significant differences were noticed between the two parents means for the two traits, where, the 'ATRI 15010' parent line was earlier in flowering time and shorter in plant length than 'ATRI 5283'. Using the data on plant height and flowering time of F_3 families, frequency distribution curves were obtained (Fig. 6). Wide or continuous frequency distributions with transgressive segregants were observed, as one would expect for QTLs. The

continuous distributions of plant height and flowering time indicated that plant height and flowering time are polygenic in nature and quantitatively inherited.

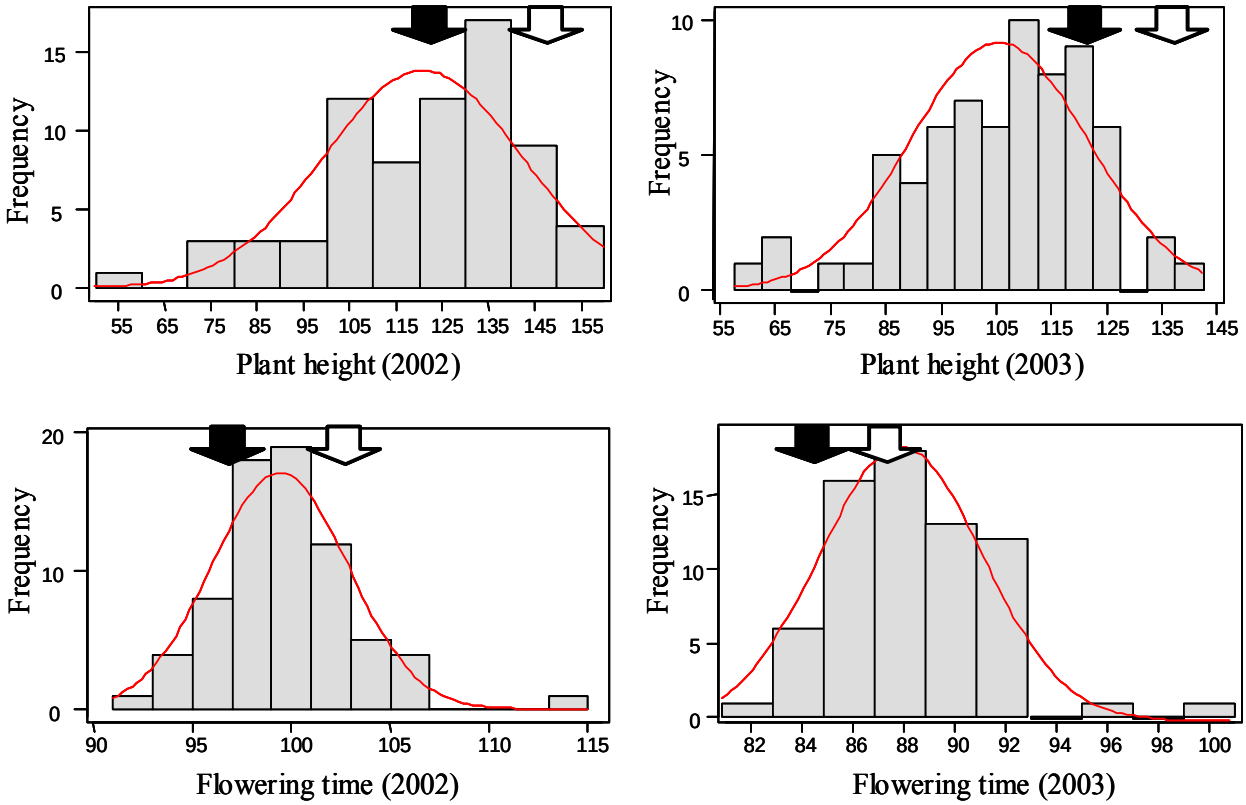


Figure (6): Phenotypic distribution of the vegetative traits (plant height in cm and flowering time in days) means of F_3 families derived from a cross between 'ATRI 5283' and 'ATRI 15010' measured for the two environments (Gatersleben 2002 and Gatersleben 2003). (Empty arrows = means of 'ATRI 5283'; filled arrows = means of 'ATRI 15010').

3.2.1.3. Phenotypic analysis and inheritance of grain characters

Stress tolerance index (STI%) for all grain characters was measured. The parental means for the two environments Gatersleben field season 2002 and 2003 are given in Appendix Table 4. Using the STI for the grain characters data of F_3 families, frequency distribution curves were prepared (Fig. 7). Wide or continuous frequency distributions with transgressive segregants were observed, as one would expect for QTLs. The presence of transgressive segregants for all the grain traits suggested that the parents selected for this analysis had alleles associated with low and high values of these traits. The continuous distributions indicated that the characters are polygenic in nature and quantitatively inherited.

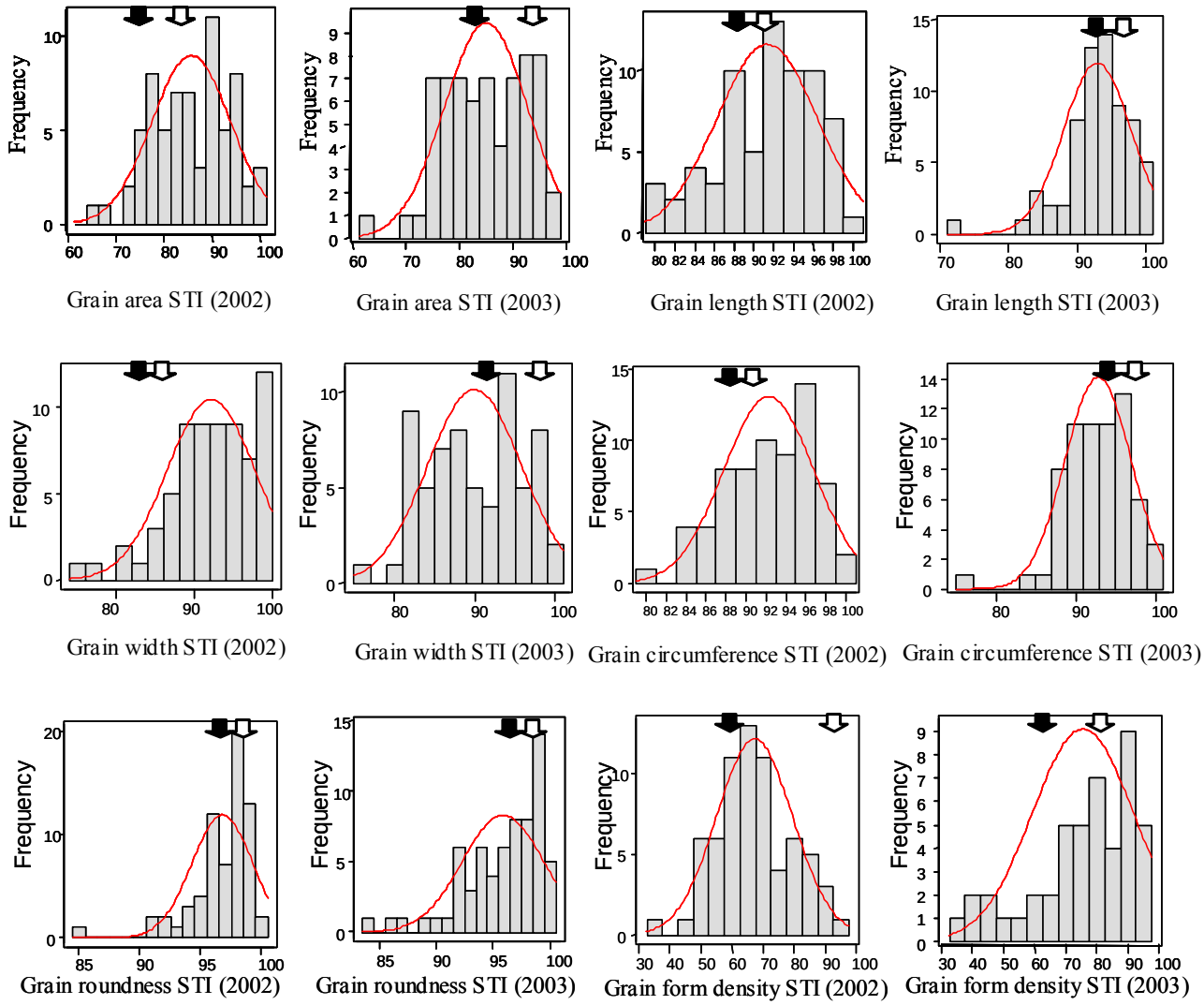


Figure (7): Phenotypic distribution of stress tolerance index (STI%) for grain characters (grain area, grain length, grain width, grain circumference; grain roundness and grain form density factor) means of F_3 families derived from a cross between 'ATRI 5283' and 'ATRI 15010' measured for the two environments (Gatersleben 2002 and Gatersleben 2003). (Empty arrows = means of 'ATRI 5283'; filled arrows = means of 'ATRI 15010').

3.2.2. Genetic mapping

3.2.2.1. Polymorphism rate detected by microsatellite markers

In this part of the study the genetic variation on the DNA level between the two parental lines 'ATRI 5283' and 'ATRI 15010' was estimated using DNA molecular markers. The markers used were microsatellites, which offer great potential for generating large numbers of markers evenly distributed throughout the genome and have efficiently been used to give reliable and reproducible genetic markers. A total of 442 Gatersleben Wheat

Microsatellites (GWM) with known map positions were analysed using the DNA of the two parents in a polymerase chain reaction (PCR) for polymorphism. of the 442 GWM primer pairs tested, a total of 184 GWM assigned to the A and B genomes showed polymorphisms (41.63%) and were used for mapping in F_2 generation.

3.2.2.2. Linkage map construction

The distribution of the mapped SSR markers for A and B genomes, the distribution per each homoeologous group (H. G.), percent of covering per each chromosome, percent of covering per each homoeologous group (H. G.), chromosome length (cM) and average distance between markers in each chromosome (cM), are shown in Table 5. The map was constructed using the data of 184 SSR markers on the 81 F_2 plants applying the F_2 model in the Mapmaker program. The loci are fairly evenly distributed between the A and B genomes. However, in all homoeologous groups with the exception of group 1, 2 and 7, the B genome shows a slightly higher percentage of markers (Table 5). The basic map having a length of 2,603.34 cM is shown in (Figure 8). Consequently, 184 loci were mapped on A and B genomes. The number of mapped loci was higher for B genome (103) compared to the A genome (81). In both genomes the loci were distributed across all 7 chromosomes. As for the mapping frequency of SSR markers in relation to chromosomes, the highest numbers of SSRs were found on 6B (20 markers) and 4B (19 markers). The chromosomes with the fewest markers are 5A (7 markers), 4A (8 markers), 3A (9 markers) and 1B (10 markers). The homoeologous groups having the most markers are groups 2 and 6 (31 markers = 16.85% of the total markers mapped) followed by group 7 (29 markers). Group 5 has the fewest number of markers (18 markers = 9.78%). The 184 SSR markers cover a total length of 2,603.34 cM, almost comparable with the linkage map reported by Röder *et al.* (1998; unpublished) for the cross *T. aestivum* x *T. aestivum* considering the A and B genomes of that cross only. The average distance between marker pairs is 15.17 cM, ranging from 8.43 cM for chromosome 4B to 22.49 cM for 5A (Table 5), however, there were some gaps wider than 50 cM on chromosomes 1A, 2A, 3A, 4A, 5A, 5B and 7A (Fig. 8). Chromosomes 2A, 4B, 6B and 7A showed marker clustering around the centromeric region. Marker clusters are usually associated with reduced recombination in the proximal region of chromosome arms. However, in this mapping population the marker distribution was relatively adequate and few clusters of tightly linked loci were revealed, as all SSR marker locations were known and the markers were selected to avoid closely linked multiple loci. Map locations of all markers were comparable to that reported for the ITMI population (Röder *et al*., 1998).

Table (5): Distribution of polymorphic microsatellite markers and centiMorgan (cM) coverage across the A and B genomes

Chromosome	SSRs markers				Size (cM)	cM/ Marker
	Number	% of total number of SSRs	H. G.	% of total number of SSRs		
1A	12	6.52	22	11.95	199.13	16.59
1B	10	5.43			179.17	17.92
2A	18	9.78	31	16.85	184.74	10.26
2B	13	7.07			187.62	14.43
3A	9	4.89	26	14.12	197.00	21.89
3B	17	9.23			282.18	16.59
4A	8	4.35	27	14.68	120.96	15.12
4B	19	10.33			160.25	8.43
5A	7	3.80	18	9.78	157.49	22.49
5B	11	5.98			199.79	18.16
6A	11	5.98	31	16.85	156.85	14.26
6B	20	10.87			190.23	9.51
7A	16	8.70	29	15.77	216.66	13.54
7B	13	7.07			171.27	13.17
Total	184	100	184	100	2,603.34	15.17

H. G. = Homoeologous Group

Chromosomes 1A and 1B: The number of polymorphic loci for chromosomes 1A and 1B was 6.52% and 5.43% of the total markers mapped, respectively (Table 5). No clustering of markers was shown for both chromosomes. The linkage map for group 1 chromosomes (Fig. 8) comprises 22 markers. Chromosomes 1A and 1B consist of 12 and 10 markers, respectively. The centromere was placed on 1A between *Xgwm1111* and *Xgwm164* (Röder *et al.* 1998). As for 1B, the centromere was positioned between *Xgwm413* and *Xgwm18*.

Chromosomes 2A and 2B: The linkage map of the group 2 chromosomes (Fig. 8) comprises 31 SSR markers. With respect to 2A, 18 SSRs were mapped. For 2B, the mapped SSRs were 13 markers. The centromeres were drawn according to Röder *et al.* (1998). Chromosome 2B is relatively well covered with markers; however, for 2A, additional markers are required for the short arm.

Chromosomes 3A and 3B: Nine and seventeen markers were mapped on chromosomes 3A and 3B, respectively. The centromere of 3A was positioned between the microsatellites *Xgwm30b* and *Xgwm1063*. The centromere of chromosome 3B was located between *Xgwm376* and *Xgwm1015*.

Chromosomes 4A and 4B: Homoeologous group 4 had a total 27 markers mapped. 8 and 19 markers for chromosomes 4A and 4B, respectively, were mapped. The suggested centromere position of chromosome 4A is between *Xgwm929 and Xgwm610*, while for 4B it is between *Xgwm925* and *Xgwm946*.

Chromosomes 5A and 5B: On chromosome 5A, 7 markers were mapped, 5 of which were located on the long arm. However on 5B, 11 *gwm* were mapped, 9 of which were located on the long arm. The centromere of 5A was positioned between *Xgwm415* and *Xgwm186* based on previously published maps (Röder *et al.,* 1998). For chromosome 5B the centromere was positioned between *Xgwm810* and *Xgwm1165*.

Chromosomes 6A and 6B: The homoeologous group 6 consists of 31 markers (11 on 6A and 20 on 6B). The centromere for 6A was positioned between *Xgwm1011a* and *Xgwm786*. The centromere of chromosome 6B was located between *Xgwm1233* and *Xgwm644a*.

Chromosomes 7A and 7B: Chromosome group 7 contains 29 markers, 16 and 13 on chromosomes 7A and 7B, respectively. On chromosome 7A, the centromere was positioned between *Xgwm890* and *Xgwm631*. The centromere of chromosome 7B was located between *Xgwm1184* and *Xgwm297*.

3.2.3. Mapping QTLs for post-anthesis drought tolerance in F_3 families

Mapping of quantitative trait loci (QTLs) was carried out in a set of 81 F_3 families derived from a cross between the two accessions 'ATRI 5283' and 'ATRI 15010'.

Individual putative QTLs were detected for stem reserve mobilization character, vegetative traits and grain characters. All traits were recorded in two years. The QTL analysis was carried out for each year separately. Putative QTLs for each trait and their map positions are shown in Fig. 8. According to Fulton *et al.* (1997, 2000) and Tanksley *et al.* (1996), regions of the genomes were identified as putatively containing 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 environment with $P<0.001$; significant effects were observed in the same direction (i.e. either all positive effects or all negative effects) for a single marker/trait combination at one or two environments with $P<0.01$; significant effects were observed in the same direction for a single marker/trait combination at one or two environments with $P<0.1$.

Based on this criteria, a total of 53 putative QTLs were identified, ranging from 3 to 9 QTLs covering the 9 studied characters.

3.2.3.1 Mapping QTL for stem reserve mobilization (*Srm*)

The individual QTLs for stem reserve mobilization as identified by the single-marker regression analysis using the *QGENE* program are presented in Figure 8 and Appendix Table 5. Six QTLs were detected on chromosomes 1A, 3A, 3B, 4B, 6A and 7B, explaining from 13.41% to 24.74% of the phenotypic variance (PV%) with a LOD score of 2.16 to 3.47. Positive additive effect indicated that the score was higher for the parental allele of 'ATRI 5283' i.e. tolerance is inherited by the 'ATRI 5283' allele and sensitivity (smaller score) by the 'ATRI 15010'. For four QTLs, (designated *QSrm.ipk-3B*, *QSrm.ipk-4B, QSrm.ipk-6A* and *QSrm.ipk-7B*) 'ATRI 5283' increased the stem reserve mobilization. For two QTLs, (designated *QSrm.ipk-1A* and *QSrm.ipk-3A*) the 'ATRI 15010' alleles increased stem reserve mobilization by 22.60% and 13.93%, respectively (Appendix Table 5). The loci *QSrm.ipk-1A, QSrm.ipk-3B* and *QSrm.ipk-6A*, however, were detected in one environment only.

3.2.3.2. Mapping QTL for vegetative traits

3.2.3.2.1. Plant height (*Ht*)

Under non-stress conditions, eight putative QTLs significantly associated with plant height were detected (Appendix Table 6). These eight QTLs were located on chromosomes 1A, 2A, 2B, 3A, 3B, 4A, 5A and 7A (Fig. 8), where individual QTLs explained between 12.08% and 22.96% of the phenotypic variance. For six QTLs (designated *QHt.ipk-2A*, *QHt.ipk-2B, QHt.ipk-3A, QHt.ipk-3B, QHt.ipk-5A* and *QHt.ipk-7A*), the 'ATRI 15010' alleles decreased the plant height. For two QTLs (designated *QHt.ipk-1A* and *QHt.ipk-4A*), the 'ATRI 5283' alleles had an effect that increased plant height (Appendix Table 6). The *QHt.ipk-1A, QHt.ipk-2B, QHt.ipk-3B* and *QHt.ipk-4A* were only detected in one environment.

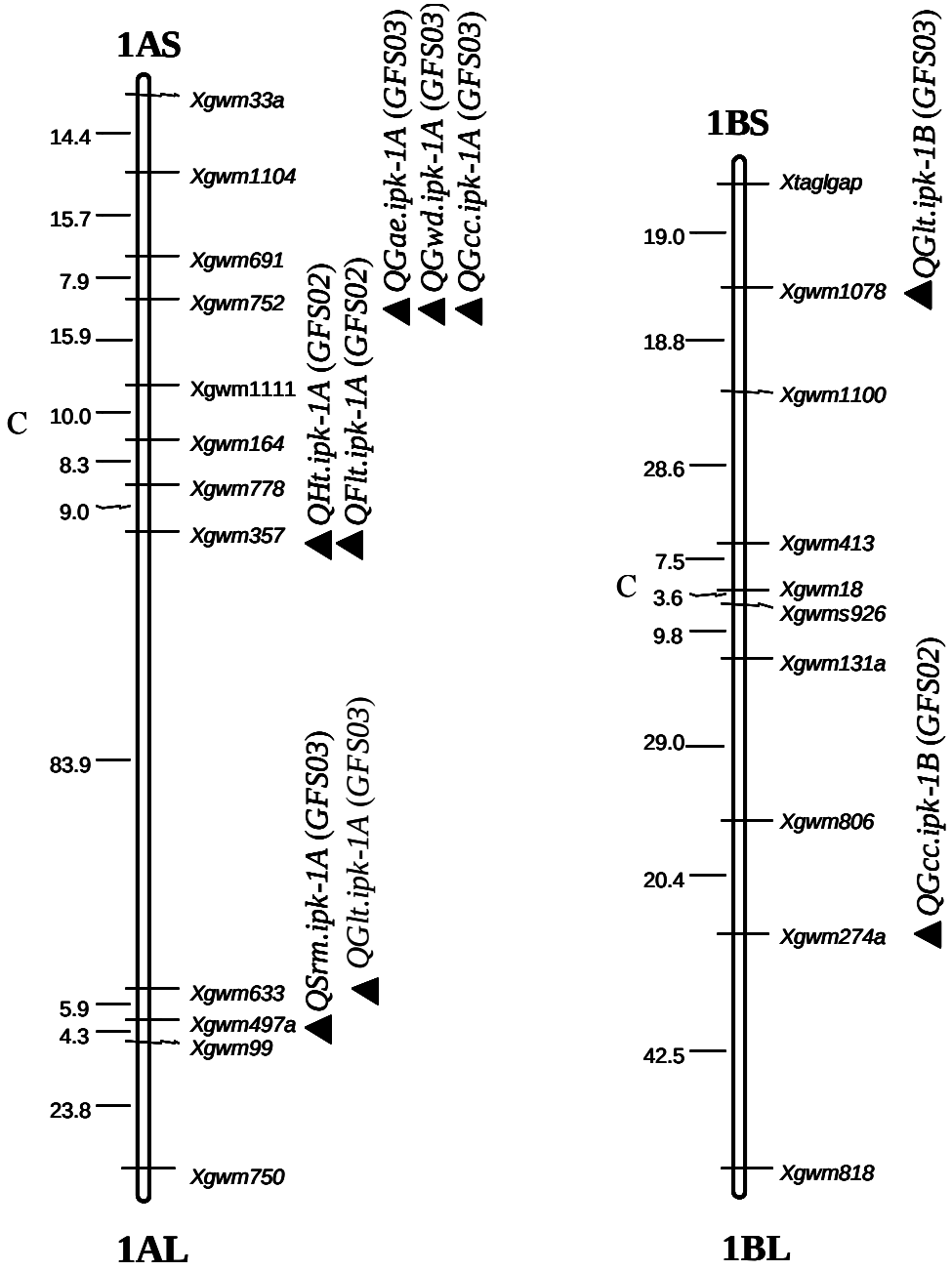


Figure (8): Microsatellite genetic linkage map of the 'ATRI 5283' x 'ATRI 15010' cross. Markers used for base map construction are shown on the right-hand side of each linkage group and centiMorgan (cM) on the left. QTLs are indicated by triangles. Symbols for QTLs are presented in Table 3 see section 2.2.5. in materials and methods. C = estimated centromere position. GFS02 = Gatersleben field season 2002. GFS03 = Gatersleben field season 2003.

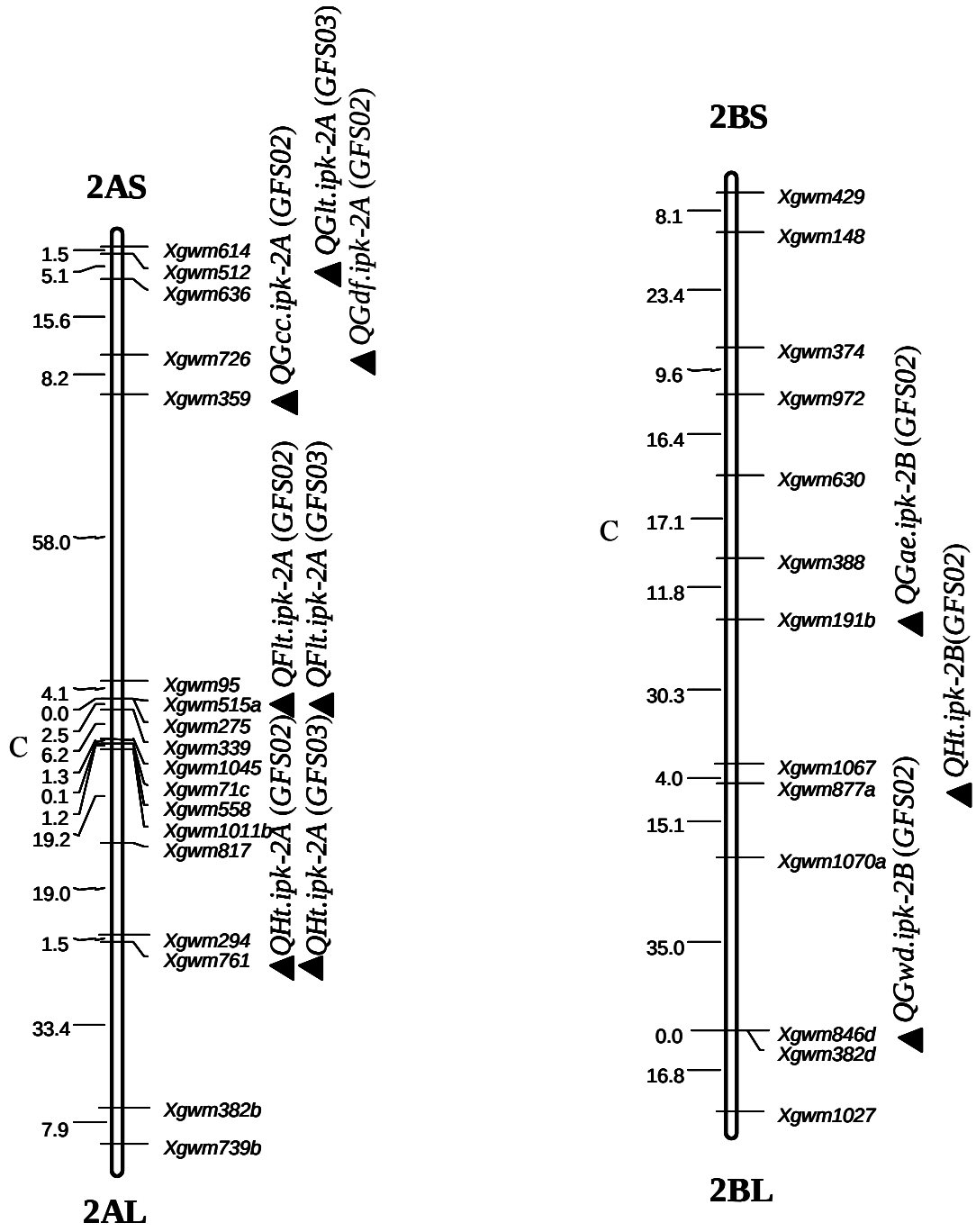
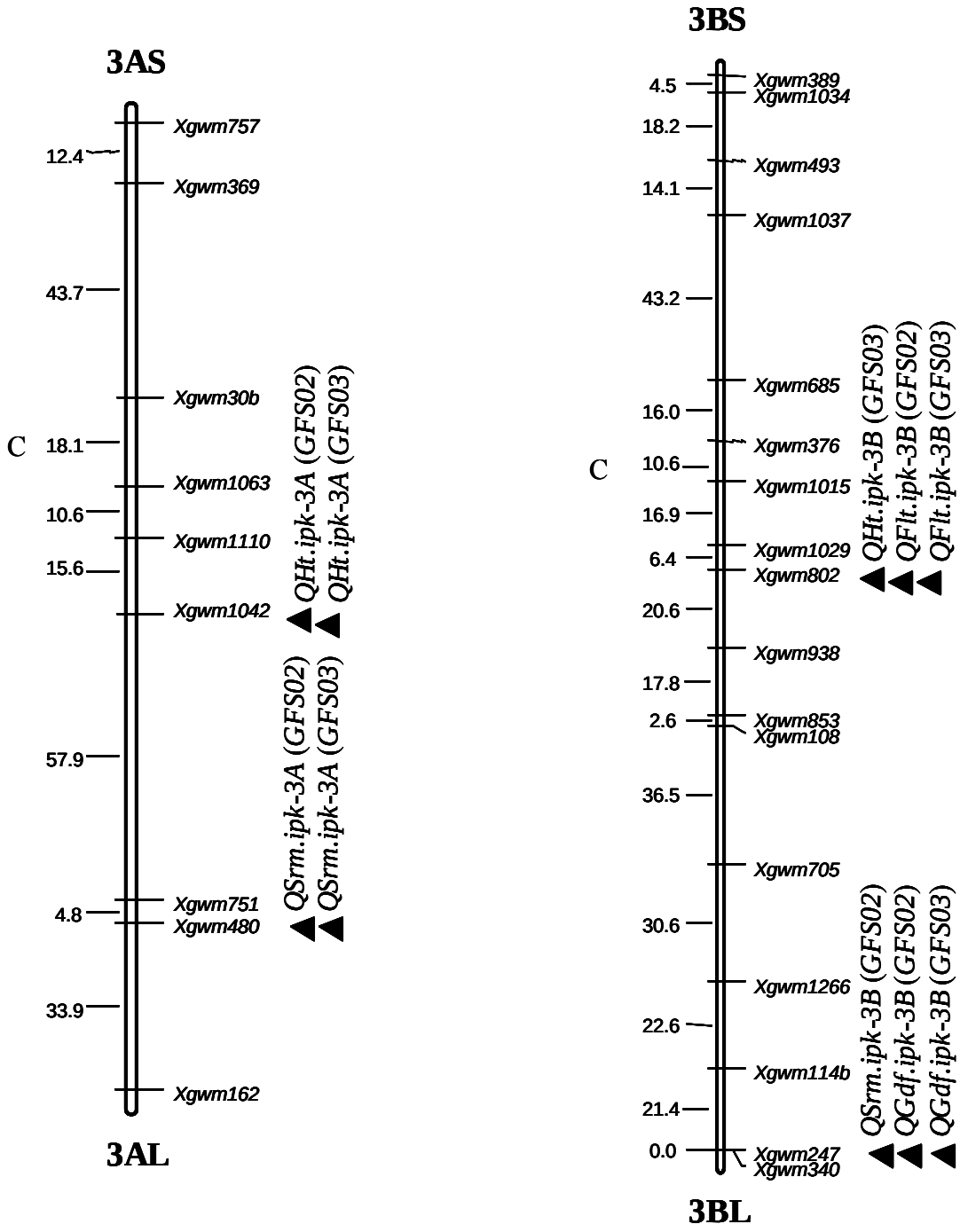


Figure (8): continued



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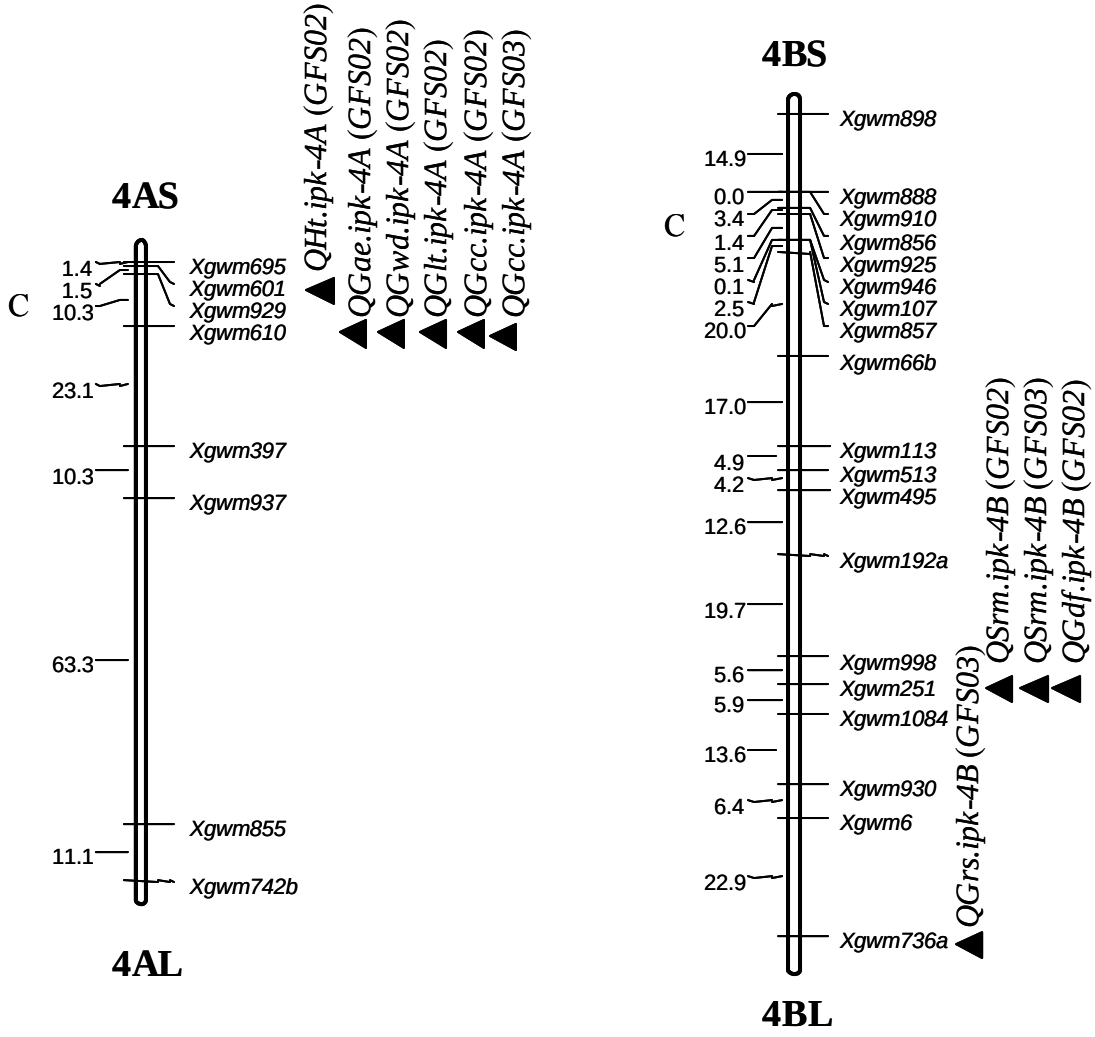

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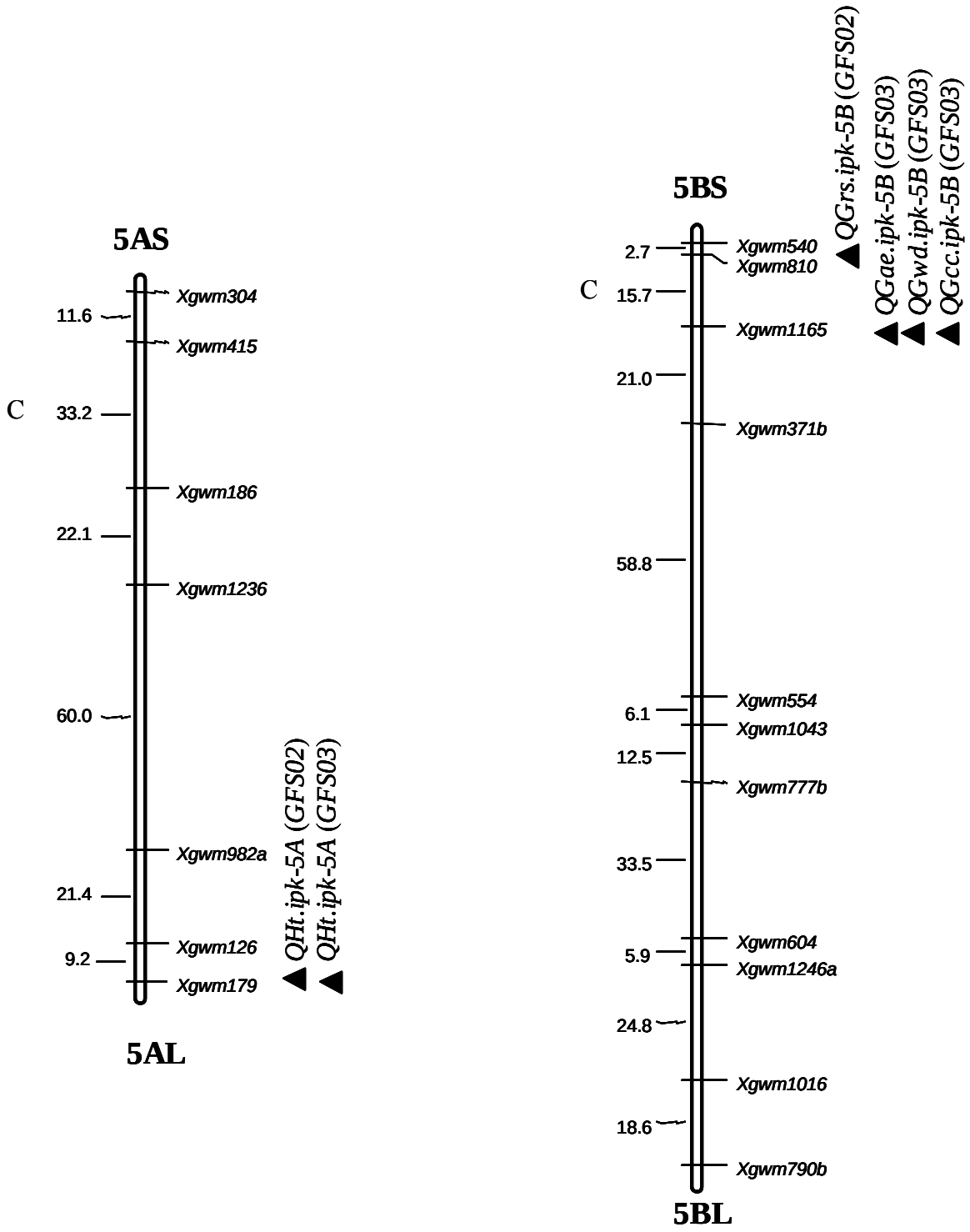

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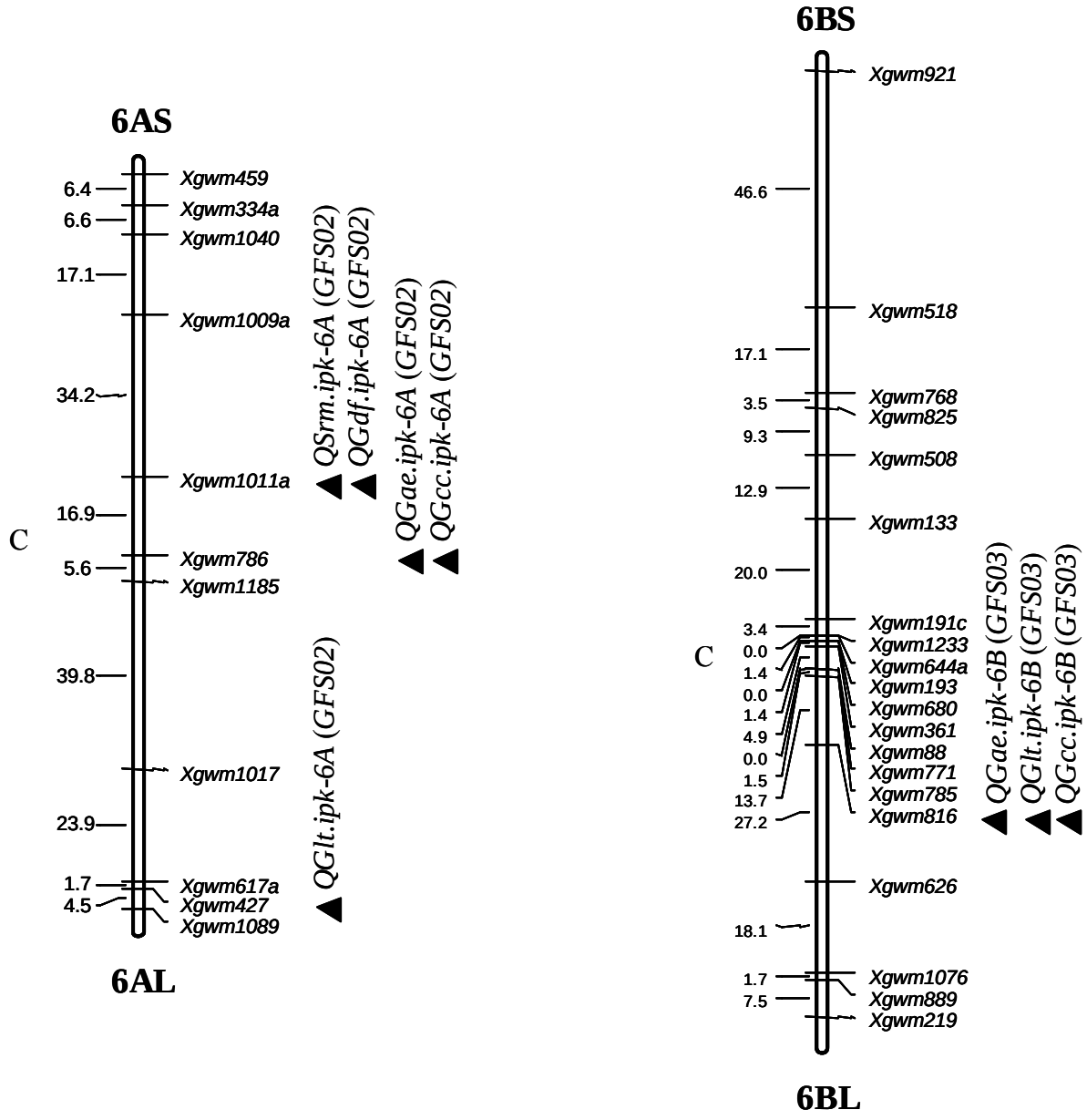

Figure (8): continued

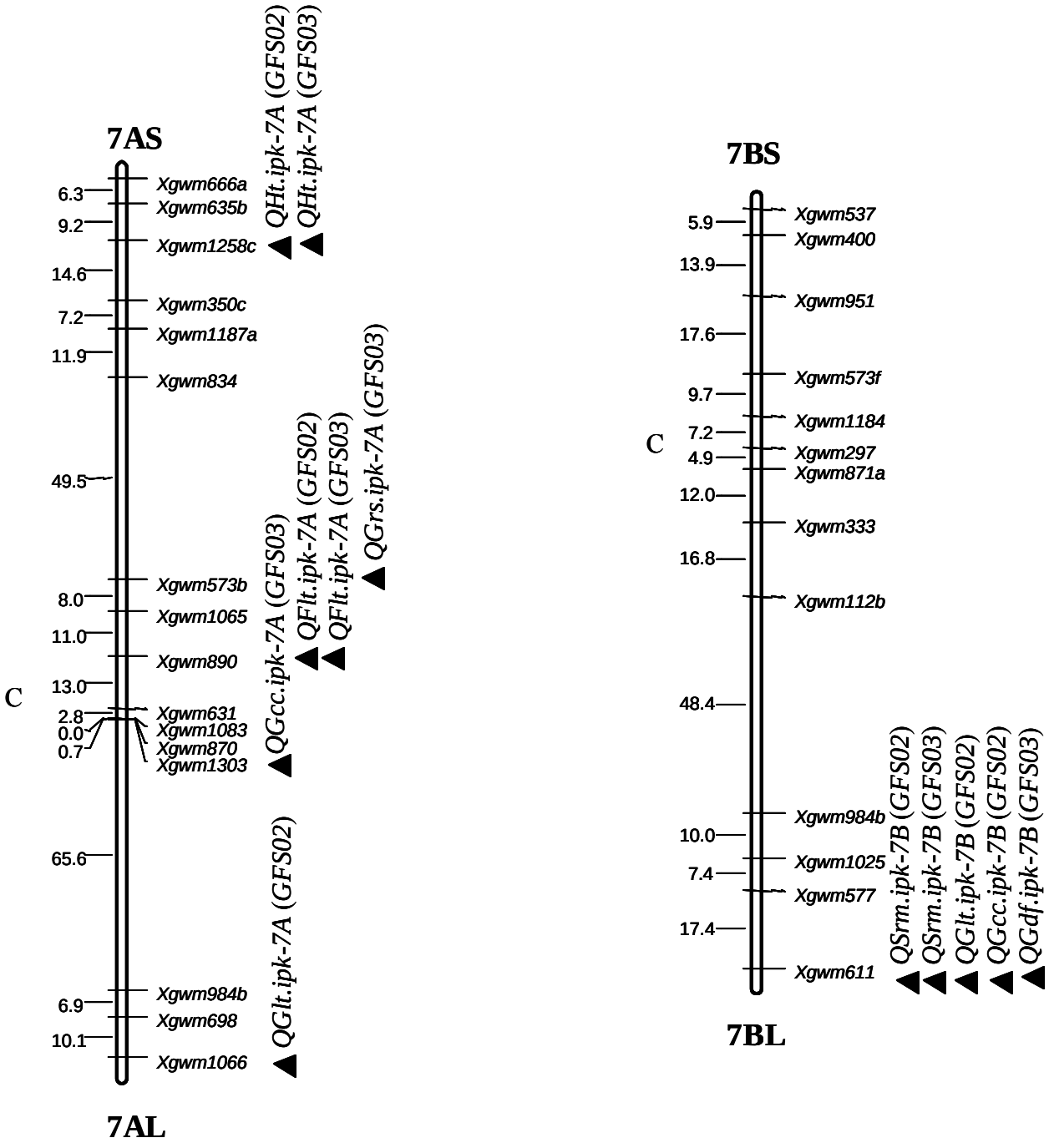

Figure (8): continued

3.2.3.2.2. Flowering time (*Flt*)

Under non-stress conditions, four QTLs significantly associated with flowering time (*Flt*) were located on chromosomes 1A, 2A, 3B and 7A (Fig. 8). For two loci (designated *QFlt.ipk-1A* and *QFlt.ipk-2A*), the alleles for early flowering time were contributed from the parent 'ATRI 15010' (the additive effect scores were -1.36 and –1.45), while for two QTLs (designated *QFlt.ipk-3B* and *QFlt.ipk-7A*), late flowering time alleles were derived from the parent 'ATRI 5283' (additive effect score was +2.48 and +1.60). The variation explained by these individual QTLs ranged from 12.37% to 23.33% (Appendix Table 6). Three QTLs were detected for both seasons, whereas one QTL was identified for season 2002 only.

3.2.3.3 Mapping QTL for grain characters

3.2.3.3.1. Grain area (*Gae*)

Six significant QTLs for grain area STI were found on chromosomes 1A, 2B, 4A, 5B, 6A and 6B as shown in Fig. 8 and Appendix Table 7. At two QTLs (designated *QGae.ipk-1A* and *QGae.ipk-5B*), the trait was positively influenced by 'ATRI 5283' alleles, while at the other four loci (designated *QGae.ipk-2B, QGae.ipk-4A, QGae.ipk-6A* and *QGae.ipk-6B*), the positive effect comes from 'ATRI 15010' alleles. The variation explained by these individual QTLs ranged from 13.40% to 24.93%. The LOD scores ranged from 2.12 to 4.11.

3.2.3.3.2. Grain width (*Gwd*)

Four QTLs significantly associated with grain width STI were found on chromosomes 1A, 2B, 4A and 5B as presented in Fig. 8 and Appendix Table 7. At two QTLs (designated *QGwd.ipk-1A* and *QGwd.ipk-5B*), the trait was positively influenced by 'ATRI 5283' alleles, while at the other two loci (designated *QGwd.ipk-2B* and *QGwd.ipk-4A*), the positive effect comes from 'ATRI 15010'. The variation explained by these individual QTLs ranged from 13.91% to 25.16%. The LOD score ranged from 2.12 to 4.15.

3.2.3.3.3. Grain length (*Glt*)

Eight QTLs were detected for grain length STI was found on chromosomes 1A, 1B, 2A, 4A, 6A, 6B, 7A and 7B as shown in Fig. 8 and Appendix Table 7. At three QTLs (designated *QGlt.ipk-1A*, *QGlt.ipk-2A* and *QGlt.ipk-6A*), the trait was positively influenced by 'ATRI 5283' alleles, while at the other five loci (designated *QGlt.ipk-1B, QGlt.ipk-4A, QGlt.ipk-6B, QGlt.ipk-7A* and *QGlt.ipk-7B*), the positive effect come from 'ATRI 15010'

alleles. The phenotypic variance explained by these individual QTLs ranged from 15.12% to 25.39%. The LOD score ranged from 2.20 to 4.20.

3.2.3.3.4. Grain circumference (*Gcc*)

Nine QTLs detected for grain circumference STI were found on chromosomes 1A, 1B, 2A, 4A, 5B, 6A, 6B, 7A and 7B (Fig. 8, Appendix Table 8). At two QTLs, (designated *QGcc.ipk-1A* and *QGcc.ipk-5B*), the trait was positively influenced by 'ATRI 5283' alleles, while at the other seven loci (designated as, *QGcc.ipk-1B, QGcc.ipk-2A, QGcc.ipk-4A, QGcc.ipk-6A, QGcc.ipk-6B, QGcc.ipk-7A* and *QGcc.ipk-7B*), the positive effect comes from 'ATRI 15010'. The phenotypic variance explained by these individual QTLs ranged from 13.04% to 29.92%. The LOD score ranged from 2.03 to 5.10.

3.2.3.3.5. Grain roundness (*Grs*)

Three QTLs detected for grain roundness STI were found on chromosomes 4B, 5B and 7A as presented in Fig. 8 and Appendix Table 8. At two QTLs (designated *QGrs.ipk-4B* and *QGrs.ipk-7A*), the trait was positively influenced by 'ATRI 5283' alleles, while at one QTL (designated *QGrs.ipk-5B*), the positive effect come from 'ATRI 15010' alleles. The phenotypic variance explained by these individual QTLs ranged from 13.72% to 18.14%. The LOD score ranged from 2.08 to 2.87.

3.2.3.3.6. Grain form-density factor (*Gdf*)

Five QTLs were detected for grain form-density factor STI located on chromosomes 2A, 3B, 4B, 6A and 7B (Fig. 8, Appendix Table 8). At all QTLs (designated *QGdf.ipk-2A*, *QGdf.ipk-3B, QGdf.ipk-4B, QGdf.ipk-6A* and *QGdf.ipk-7B*) the trait was positively influenced by 'ATRI 5283' alleles. The phenotypic variance explained by these individual QTLs ranged from 15.01% to 23.02%. The LOD score ranged from 2.40 to 3.77.

3.3. Analysis of post-anthesis drought tolerance in RILs mapping population

3.3.1 Analysis of field experiments

3.3.1.1 Phenotypic analysis and inheritance of stem reserve mobilization

A set of 114 RILs plus the two parental lines 'W 7984' and 'Opata 85' were grown in the field for the purpose of phenotyping stem reserve mobilization in two experiments in Gatersleben. Plants were treated with potassium iodide (KI, 0.5 % *w/v*) after 14 days and stress tolerance index (STI) for 1000-grain weight was measured. The two parental lines

differed in post-anthesis drought tolerance. The stress tolerance index for 'W 7984' (97.96%-75.26%) was higher than that of 'Opata 85' (35.07%-50.32%). These results confirmed that the synthetic spring wheat 'W 7984' have a higher stem reserve mobilization ability compared to 'Opata 85'. Using the data of 1000-grain weight stress tolerance index of RILs population, a frequency distribution curve for Gatersleben location in two years was prepared (Fig. 9).

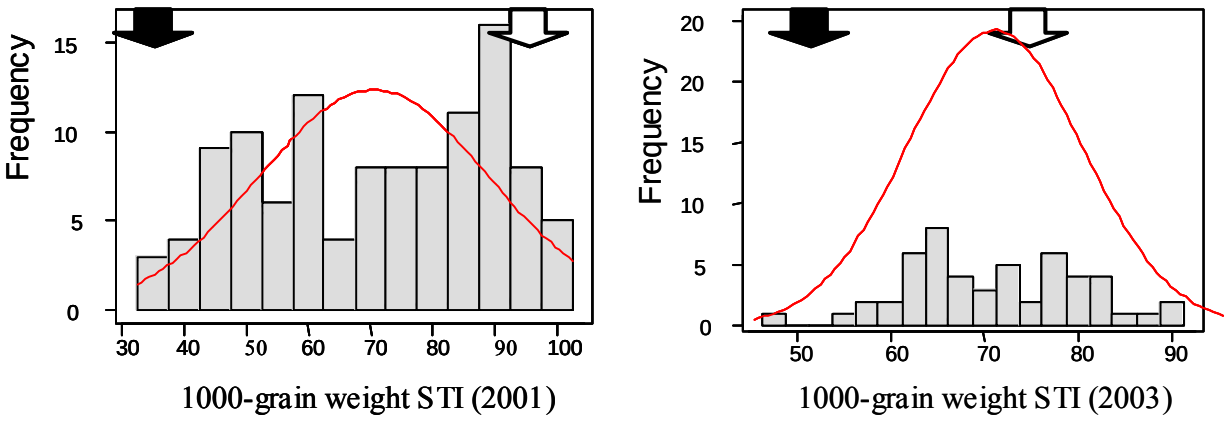

Figure (9): Phenotypic distribution of stress tolerance index (STI%) for 1000-grain weight means of RILs population derived from a cross between 'W 7984' and 'Opata 85' measured for the two environments (Gatersleben 2001 and Gatersleben 2003). (Empty arrows = means of 'W 7984'; filled arrows = means of 'Opata 85').

Wide or continuous frequency distributions with transgressive segregants were observed, as one would expect for QTLs. The continuous distribution of 1000-grain weight stress tolerance index (STI) indicated that post-anthesis drought tolerance is polygenic in nature and quantitatively inherited.

3.3.1.2. Phenotypic analysis and inheritance of vegetative traits

Plant height (*Ht*) was measured at Gatersleben in 2003. However, flowering time (*Flt*) was quantified as the number of days from planting to flowering of 50% of plants of a genotype at Gatersleben in 2001 and 2003. Significant differences were measured between the parental means for the two traits, where 'Opata 85' was earlier in flowering time and shorter in plant length than the synthetic spring wheat genotype 'W 7984'. Using the data on plant height and flowering time of RILs population, frequency distribution curves were prepared (Fig. 10). Wide or continuous frequency distributions with transgressive segregants were

observed. The continuous distribution of plant height and flowering time indicated that plant height and flowering time are polygenic in nature and quantitatively inherited.

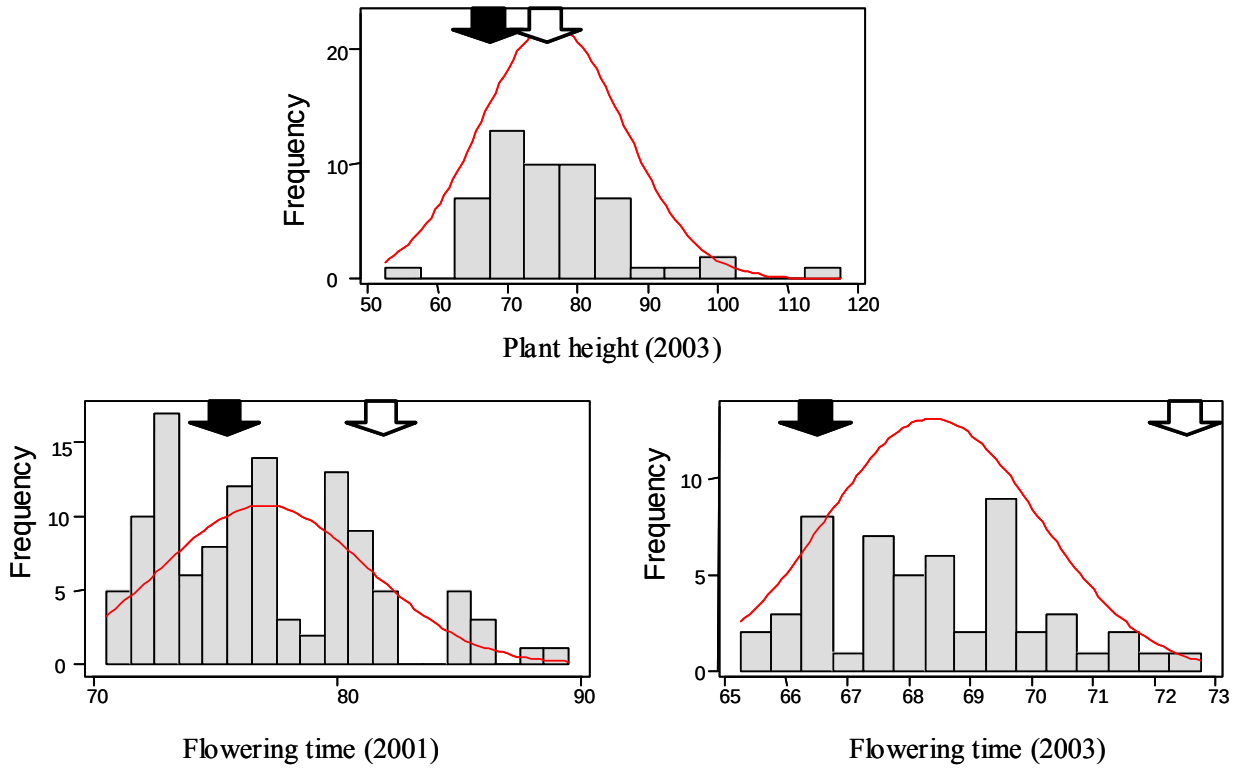

Figure (10): Phenotypic distribution of vegetative traits (plant height in cm and flowering time in days) means of RILs population derived from a cross between 'W 7984' and 'Opata 85' measured for the two environments (Gatersleben 2001 and Gatersleben 2003). (Empty arrows = means of 'W 7984'; filled arrows = means of 'Opata 85').

3.3.1.3. Phenotypic analysis and inheritance of grain characters

Stress tolerance index (STI) for all grain characters was measured. The parental data for grain characters for the two environments Gatersleben field season 2001 and 2003 are given in Appendix Table 9. Using the data on RILs, a frequency distribution curve was prepared (Fig. 11). The continuous distribution of STIs for grain traits indicated that these traits are polygenic in nature and quantitatively inherited. Transgressive segregation occurred in both directions for all traits. The presence of transgressive segregants for all the grain traits suggested that the parents selected for this analysis had alleles associated with both low and high values.

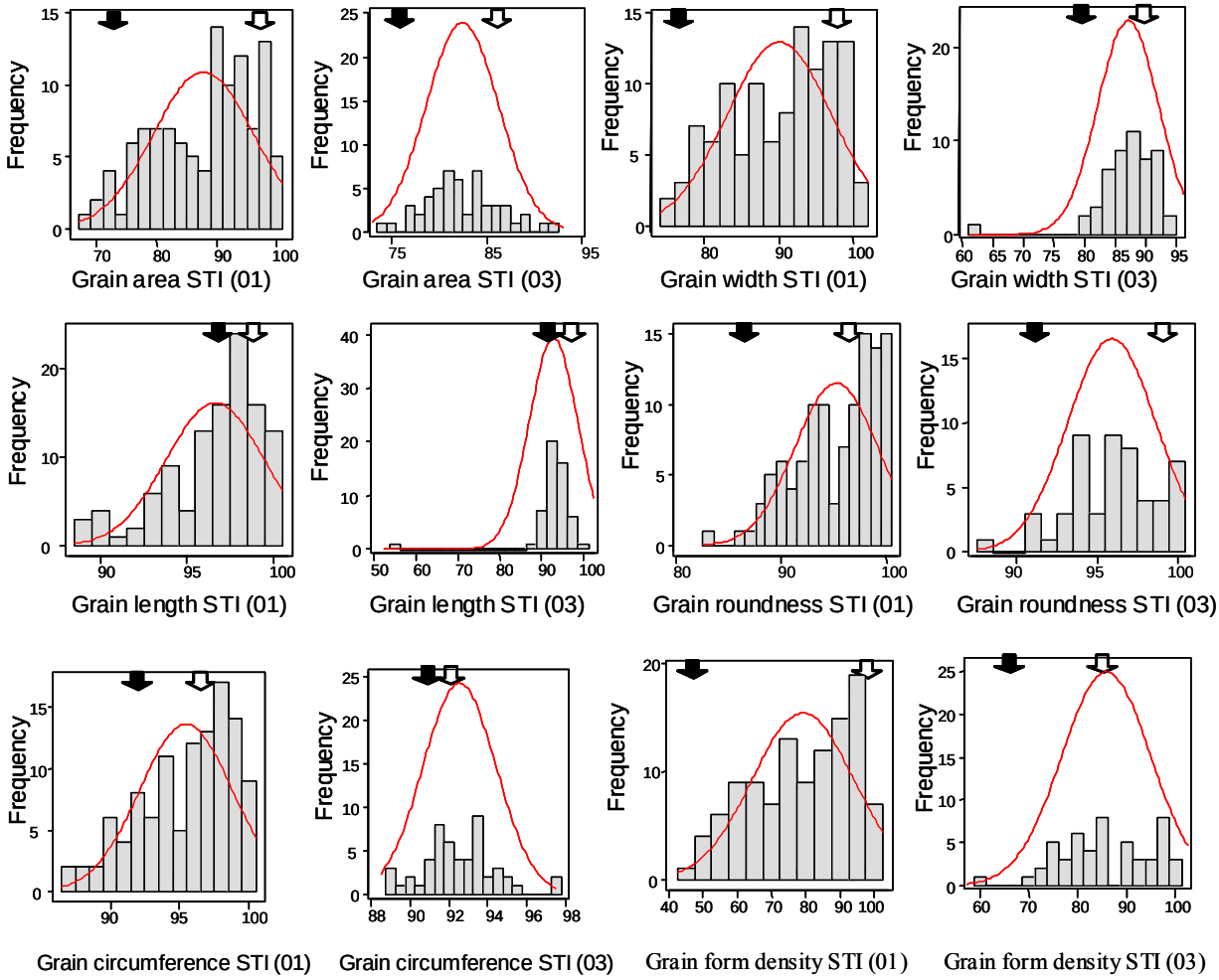

Figure (11): Phenotypic distribution of stress tolerance index (STI%) for grain characters (grain area, grain length, grain width, grain circumference; grain roundness and grain form density factor) means of RILs population derived from a cross between 'W 7984' and 'Opata 85' measured for the two environments (Gatersleben 2001 and Gatersleben 2003). (Empty arrows = means of 'W 7984'; filled arrows = means of 'Opata 85').

3.3.2. Mapping QTLs for post-anthesis drought tolerance in RILs

Based on the RILs, a genetic linkage map was constructed consisting of 654 RFLP and SSRs markers (Röder *et al*., 1998, unpublished). The map covered a distance of 4,329.64 cM of the wheat genome comprising 21 chromosomes. All traits were recorded in two years except plant height for one year. Individual putative QTLs were detected for the stem reserve mobilization character, vegetative traits and grain characters. Putative QTLs for each trait and their map positions are shown in Fig. 12. As described before in section 3.2.3., criteria for definition of a QTL were set in accordance to Fulton *et al*. (1997, 2000) and Tanksley *et al*.

(1996). Based on this criteria, a total of 57 putative QTLs were identified, ranging from 4 to 8 QTLs covering the 9 studied characters.

3.3.2.1. Mapping QTLs for stem reserve mobilization (*Srm*)

Putative QTLs for stem reserve trait are listed in Appendix Table 10 and their map positions are shown in Fig. 12. Eight QTLs were detected on chromosomes 1A, 1B, 2D, 5B, 5D, 6A, 7B and 7D for stem reserve mobilization, explaining from 10.17% to 42.22% of the phenotypic variance (PV%) with a LOD score of 1.52 to 3.15. For four QTLs (designated *QSrm.ipk-2D*, *QSrm.ipk-5B, QSrm.ipk-5D* and *QSrm.ipk-7D*), the 'W 7984' alleles increased the post-anthesis drought tolerance. For the other four QTLs (*QSrm.ipk-1A, QSrm.ipk-1B, QSrm.ipk-6A* and *QSrm.ipk-7B*), the 'Opata 85' alleles had an effect that increased stem reserve mobilization by 10.17% and 24.75%, respectively (Appendix Table 10).

3.3.2.2. Mapping QTLs for vegetative traits

3.3.2.2.1. Plant height (*Ht*)

Under non-stress conditions, four putative QTLs were significantly associated with plant height (Appendix Table 11). These four QTLs were located on chromosomes 3B, 4D, 5A and 6D (Fig. 12), where individual QTLs explained between 14.62% and 30.01% of the phenotypic variance. For two QTLs (*QHt.ipk-4D* and *QHt.ipk-6D*), the 'Opata 85' alleles decreased the plant height. For the other two QTLs (*QHt.ipk-3B* and *QHt.ipk-5A*) the synthetic wheat alleles had an effect that increased plant height (Appendix Table 11).

3.3.2.2.2. Flowering time (*Flt*)

Under non-stress conditions, seven QTLs significantly associated with flowering time were identified on chromosomes 1A, 2B, 3D, 5B, 5D, 7B and 7D (Fig. 12, Appendix Table 11). For four loci (*QFlt.ipk-2B, QFlt.ipk-3D, QFlt.ipk-5B* and *QFlt.ipk-7D*), the alleles for early flowering time were contributed by the parent 'Opata 85' (the additive effect scores were –0.63 and –1.47), while for the other three QTLs (*QFlt.ipk-1A, QFlt.ipk-5D* and *QFlt.ipk-7B*) the alleles was derived from the synthetic wheat parent 'W 7984' (additive effect score was +0.79 and +1.87). The variation explained by these individual QTLs ranged from 12.91% to 22.61%.

3.3.2.3. Mapping QTLs for grain characters

3.3.2.3.1. Grain area (*Gae*)

Six significant QTLs determining for grain area STI were found on chromosomes 1A, 1B, 2D, 4D, 6B and 7D (Fig. 12, Appendix Table 12). At three QTLs (designated *QGae.ipk-2D, QGae.ipk-4D* and *QGae.ipk-7D*), the trait was positively influenced by the tolerance parent 'W 7984' alleles, while at the other three loci (designated *QGae.ipk-1A, QGae.ipk-1B* and *QGae.ipk-6B*), the positive effect came from 'Opata 85'. The variation explained by these individual QTLs ranged from 7.57% to 19.04%. The LOD scores ranged from 1.54 to 1.94.

3.3.2.3.2. Grain width (*Gwd*)

Eight QTLs significantly associated with grain width STI were found on chromosomes 1B, 1D, 3D, 5A, 5B, 5D, 6D and 7D (Fig. 12, Appendix Table 12). At five QTLs (designated *QGwd.ipk-3D, QGwd.ipk-5B, QGwd.ipk-5D, QGwd.ipk-6D* and *QGwd.ipk-7D*), the trait was positively influenced by 'W 7984' alleles, while at the other three loci (designated *QGwd.ipk-1B, QGwd.ipk-1D* and *QGwd.ipk-5A*), the positive effect came from 'Opata 85'. The variation explained by these individual QTLs ranged from 6.15% to 17.48%. The LOD score ranged from 1.52 to 2.40.

3.3.2.3.3. Grain length (*Glt*)

Six QTLs detected for grain length STI were found on chromosomes 2D, 3D, 4D, 5A, 7A, and 7D (Fig. 12, Appendix Table 12). At four QTLs (designated *QGlt.ipk-2D*, *QGlt.ipk-4D, QGlt.ipk-7A* and *QGlt.ipk-7D*), the trait was positively influenced by 'W 7984' alleles, while at the other two loci (designated *QGlt.ipk-3D* and *QGlt.ipk-5A*) the positive effect came from 'Opata 85'. The phenotypic variance explained by these individual QTLs ranged from 6.35% to 17.37%. The LOD score ranged from 1.50 to 2.78.

3.3.2.3.4. Grain circumference (*Gcc*)

Seven QTLs detected for grain circumference STI were found on chromosomes 1A, 2B, 2D, 5B, 5D, 6B and 7D (Fig. 12, Appendix Table 13). At two QTLs (designated *QGcc.ipk-2D* and *QGcc.ipk-7D*), the trait was positively influenced by 'W 7984' alleles, while at the other five loci (designated *QGcc.ipk-1A, QGcc.ipk-2B, QGcc.ipk-5B, QGcc.ipk-5D* and *QGcc.ipk-6B*), the positive effect came from 'Opata 85'. The phenotypic variance explained by these individual QTLs ranged from 10.10% to 19.24%. The LOD score ranged from 1.68 to 2.57.

3.3.2.3.5. Grain roundness (*Grs*)

Five QTLs detected for grain roundness STI were found on chromosomes 1B, 3D, 5A, 5D and 7D (Fig. 12, Appendix Table 13). At two QTLs (designated *QGrs.ipk-1B* and *QGrs.ipk-5A*), the trait was positively influenced by 'W 7984' alleles, while at three loci (designated *QGrs.ipk-3D, QGrs.ipk-5D* and *QGrs.ipk-7D*), the positive effect came from 'Opata 85'. The phenotypic variance explained by these individual QTLs ranged from 6.92% to 19.87%. The LOD score ranged from 1.71 to 3.61.

3.3.2.3.6. Grain form-density factor (*Gdf*)

Six QTLs were detected for grain form-density factor STI were found on chromosomes 1B, 2D, 5D, 6A, 7B and 7D (Fig. 12, Appendix Table 13). At three QTLs (designated *QGdf.ipk-2D*, *QGdf.ipk-5D* and *QGdf.ipk-7D*), the trait was positively influenced by 'W 7984' alleles, while at the other three QTLs (designated *QGdf.ipk-1B, QGdf.ipk-6A* and *QGdf.ipk-7B*), the positive effect came from 'Opata 85'. The phenotypic variance explained by these individual QTLs ranged from 9.12% to 42.99%. The LOD score ranged from 1.76 to 3.17.

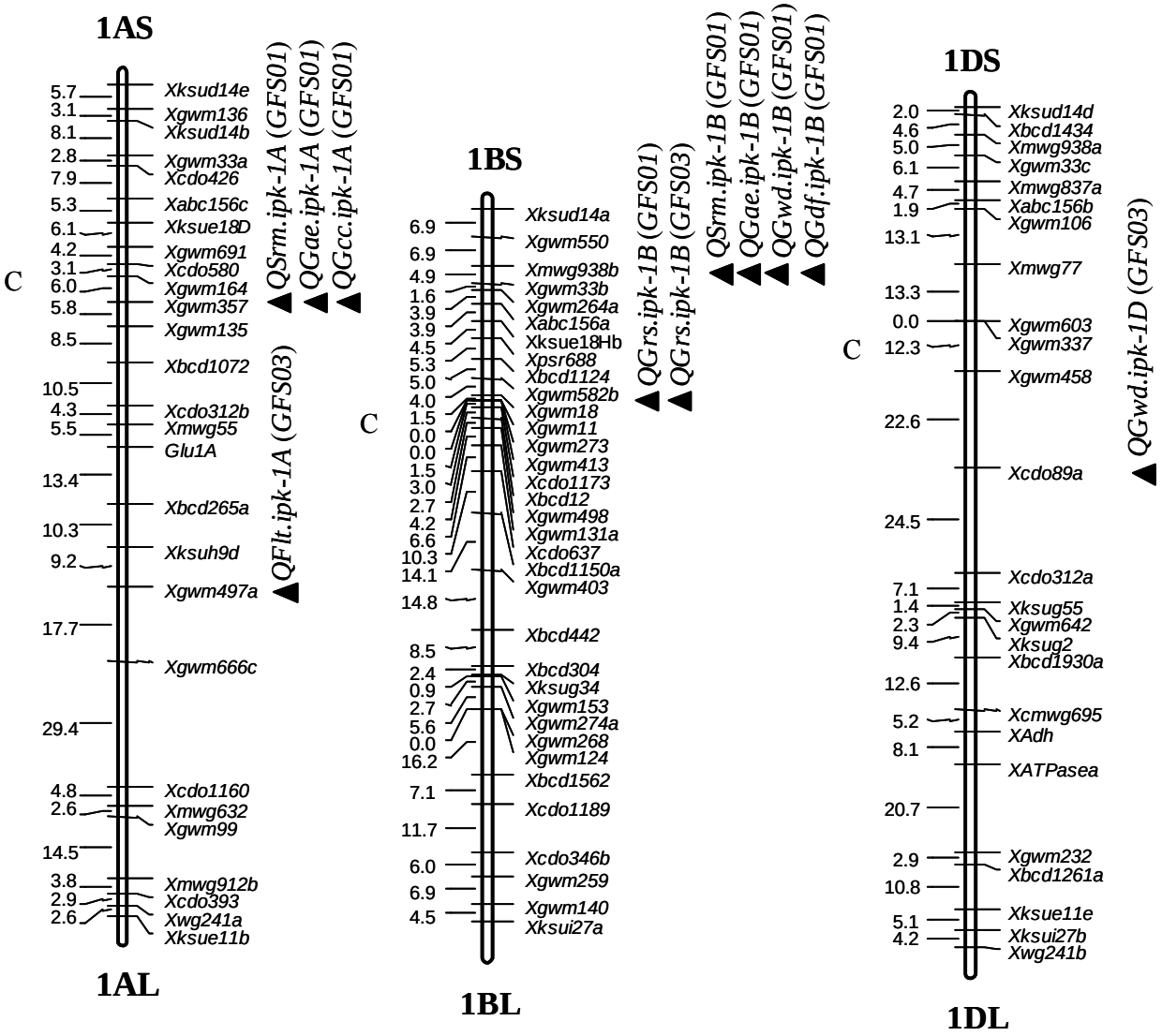

Figure (12): RFLP and microsatellite genetic linkage map of the RILs from the cross 'W 7984' x 'Opata 85'. Markers used for base map construction are shown on the right-hand side of each linkage group and centiMorgans (cM) on the left (Röder *et al.*, 1998, unpublished). QTLs are indicated by triangles. Symbols for QTLs are presented in Table 3 see section 2.2.5. in materials and methods. C = estimated centromere position. GFS01 = Gatersleben field season 2001. GFS03 = Gatersleben field season 2003.

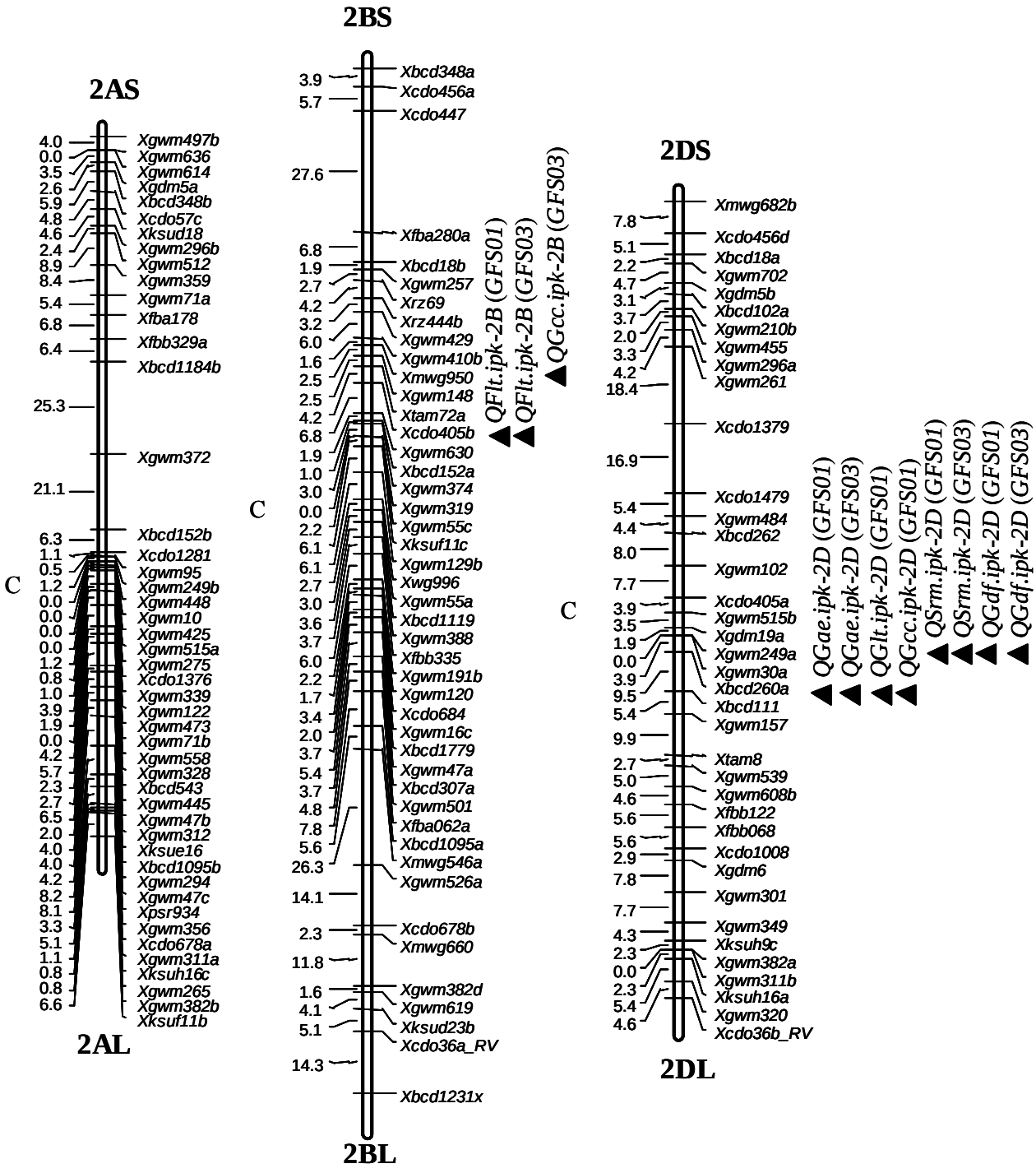

Figure (12): continued.

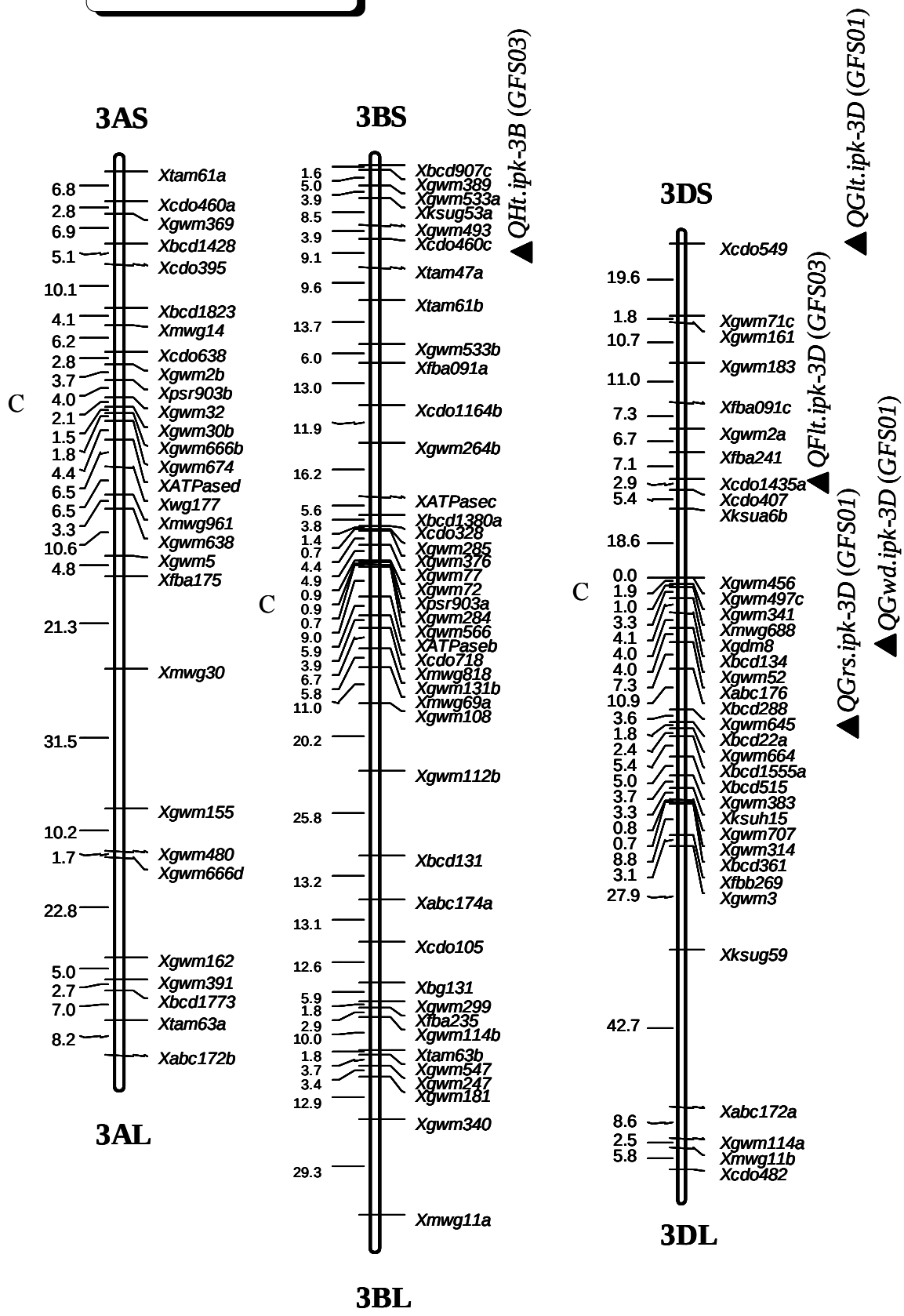

Figure (12): continued.

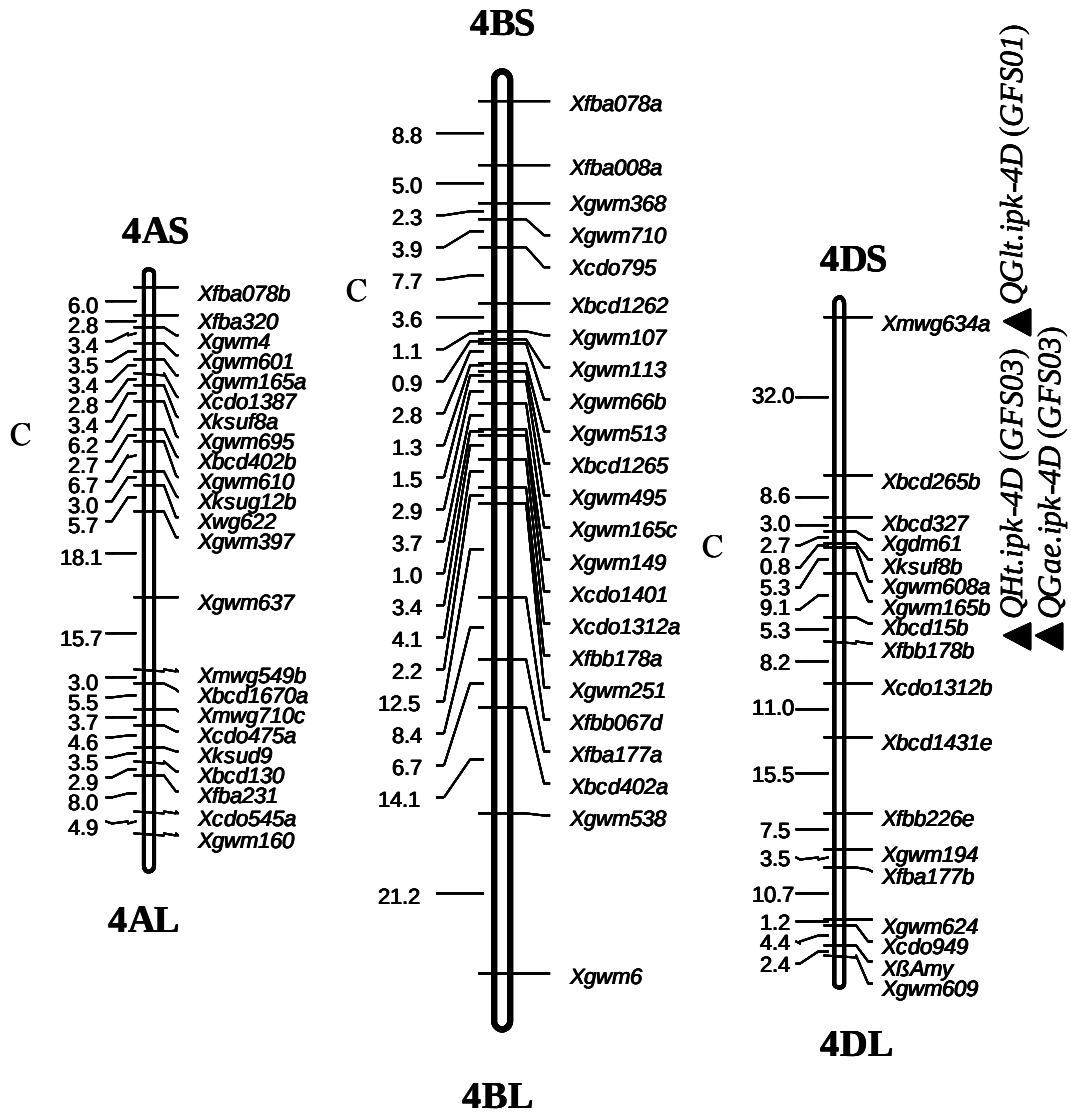

Figure (12): continued.

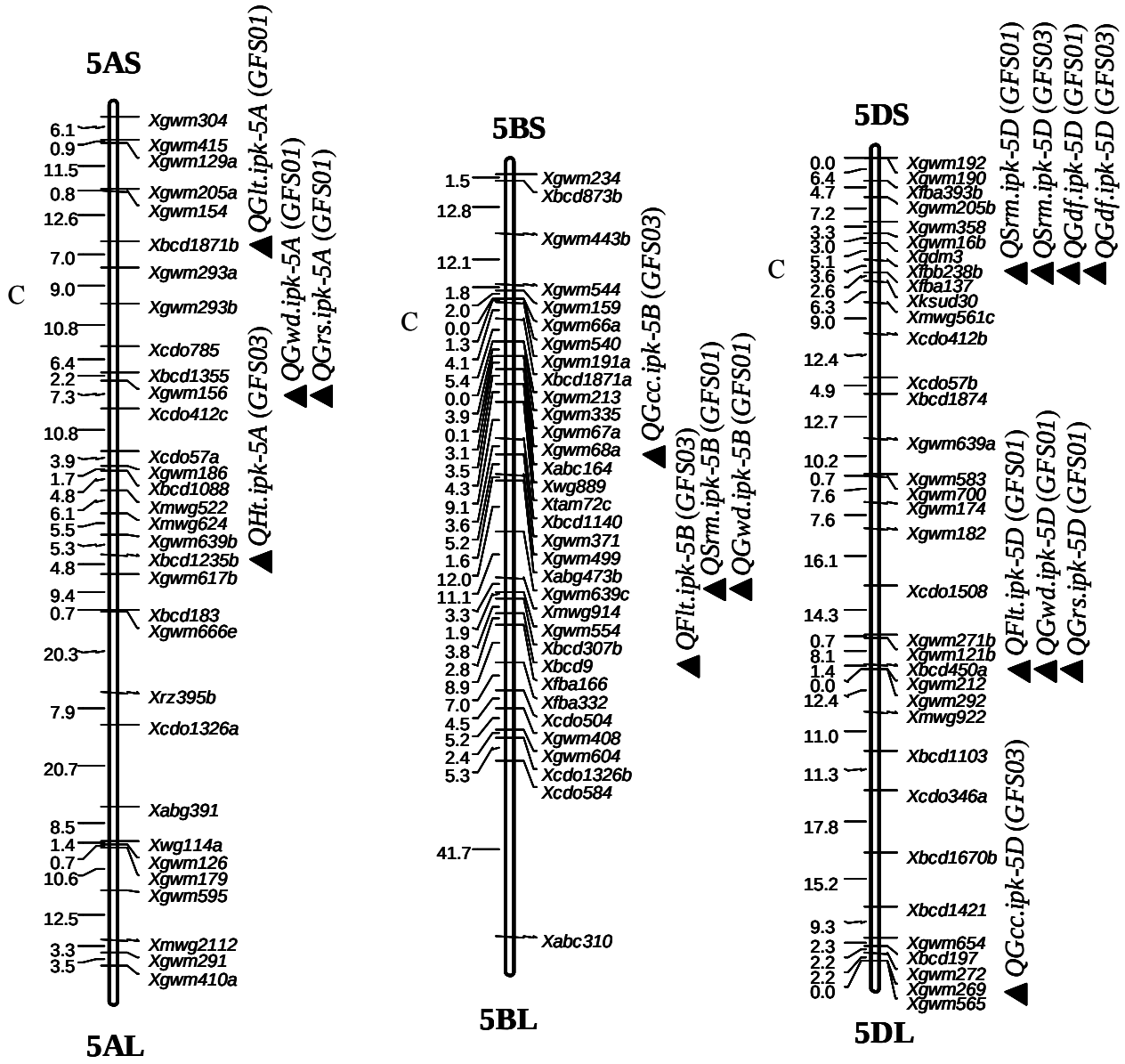

Figure (12): continued.

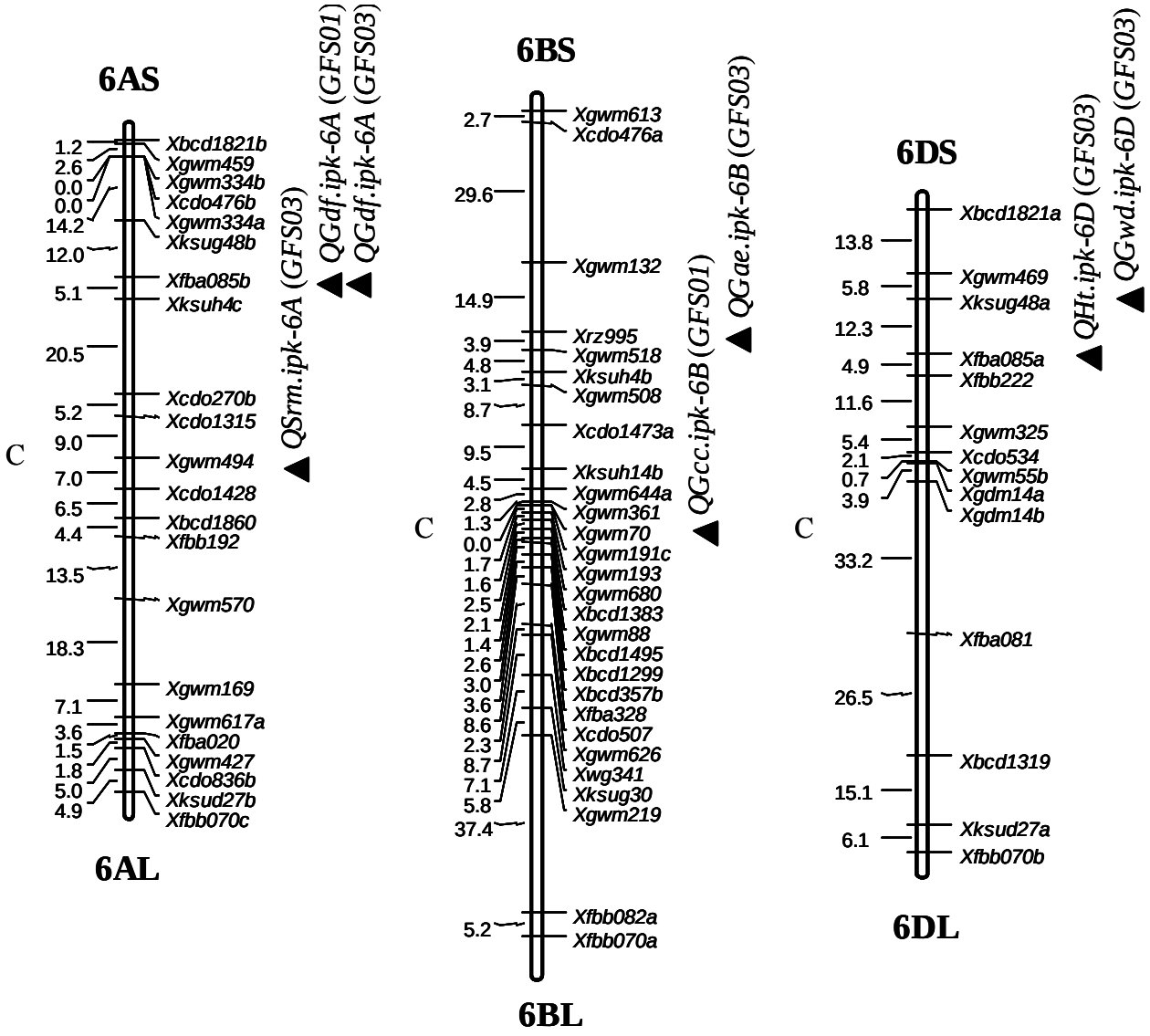

Figure (12): continued.

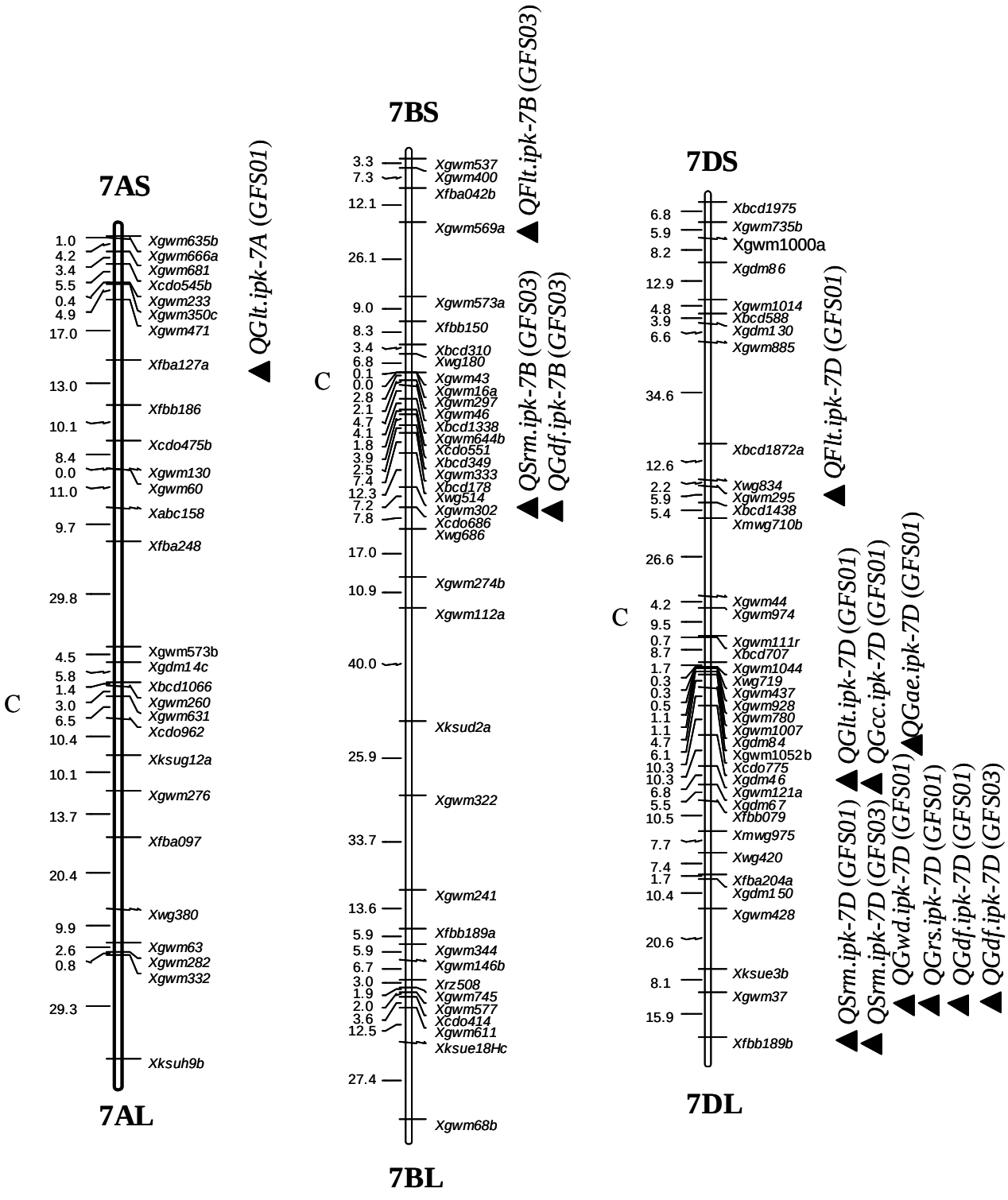

Figure (12): continued.

4. DISCUSSION

4.1. Screening wheat genotypes for post-anthesis drought tolerance

The improvement of drought tolerance is suggested as a desirable breeding objective in crops such as wheat (Keim and Kronstad, 1979; Blum, 1983b). When sever drought stress occurs during grain filling, leaves desiccate and transient photosynthesis is sharply reduced. Under such conditions, grain filling and consequently yield are highly dependent on mobilized stem reserves (Bidinger *et al*., 1977; Davidson and Birch, 1978; Hunt, 1979; Blum, 1988). Chemical desiccation of plant canopies at the onset of grain filling was developed as a tool for revealing genotypic differences in grain filling from stem reserves in the absence of current photosynthesis (Blum *et al*., 1983a, 1983b, 1990). Potassium iodide (KI), a chemical contact-desiccant, has been endorsed as useful for assessing genotypic diversity in grain filling under drought stress (Blum *et al*., 1983a, 1983b, 1990; Hossain *et al*., 1990; Nicholas and Turner, 1993; Tyagi *et al*., 2000). One of the advantage of this technique is that water stress situation can artificially be created in field grown crops under irrigated conditions. As has been documented for water stress (Farquhar and Sharkey, 1982), potassium iodide induced desiccation at the post-anthesis stage, lowered chlorophyll content, stomatal conductance and rates of photosynthesis and transpiration of flag leaves of the treated plants. The observed effects of potassium iodide treatment are qualitatively identical to those documented in plants under water stress see also section 1.2.4.4.

The purpose of the present study was to determine whether there were any genetic differences among different wheat germplasm resulting from spraying the wheat canopy with potassium iodide (KI, 0.5% *w:v*), 14 days after anthesis. In the present investigation, means for 1000-grain weight stress tolerance index (STI) after desiccation ranged from 22.26% to 87.78%. The observed magnitude of effect of potassium iodide treatment on 1000-grain weight in drought sensitive genotypes (i.e., ATRI 11457, ATRI 11445, ATRI 6931, ATRI 10213, Cappelle-Desprez, ATRI 10197, ATRI 1634 and Bezostaya) was higher than in tolerant genotypes (i.e., ATRI 1896, ATRI 5283, ATRI 17620, Synthetic/N, ATRI 9882, ATRI 5951, W 7984 and ATRI 7099). This indicated that the tolerant wheat genotypes had more stem reserves mobilized and high translocation ability for grain weight while the sensitive wheat genotypes showed low stem reserve mobilization and poor translocation ability. Wheat varieties were found to differ in their contributions of stem reserves to support grain filling from mobilized stem reserves. The relative contribution of stem reserve was estimated by Blum *et al*. (1983a, 1983b). These contributions were estimated to be anywhere

between 6% and 100% (Austin *et al.,* 1980; Papakosta and Gagiannas, 1991; Pheloung and Siddique, 1991; Davidson and Chevalier, 1992; Borrell *et al*., 1993; Blum *et al*., 1994; Gent, 1994; Palta *et al*., 1994; Khlestkina *et al*., 2001; Börner *et al*., 2002a, 2003; Salem and Börner, 2003).

Translocation capacity of the plant in the absence of transient photosynthesis is generally estimated as variation in grain weight because, when the treatment is applied (generally 14 days after anthesis), all yield components except grain weight have already been determined (Blum *et al*., 1983a; b; 1991). The analysis of variance (ANOVA) based on stress tolerance index indicated that significant differences ($P \leq 0.01$) for 1000-grain weight stress tolerance were noticed between the wheat genotypes. These observations demonstrated that reduction in 1000-grain weight caused by KI treatment differs from genotype to genotype. This result was to be expected because of the genetic diversity in post-anthesis drought tolerance within the wheat germplasm. There is, therefore, potential for improving post-anthesis drought tolerance in wheat through breeding programs. From the present study, stem reserve offers a powerful resource for grain filling under post-anthesis drought stress, which inhibits current assimilation. It thus appears that KI treatment can be employed to create water-limiting conditions in irrigated environment for screening of wheat genotypes for post-anthesis drought tolerance.

4.2. Genetic analysis of post-anthesis drought tolerance

4.2.1. Phenotypic analysis and inheritance of stem reserve mobilization character

One of the objectives of this research was to elucidate the genetic basis of the stem reserve mobilization under post-anthesis drought stress using $F_{2:3}$ and RILs mapping populations. The phenotypic frequency distributions of 1000-grain weight STI for different environments and different populations among the $F_{2:3}$ families and RILs suggested polygenic inheritance of this trait. The genetic control is complex. The parents differed at several QTLs controlling stem reserve mobilization. Therefore, it would be difficult to improve this trait by traditional breeding methods. However, the transgressive segregation for 1000-grain weight STI observed in our study indicated that it would be possible to select lines with high stem reserve mobilization ability within these two populations. The recovery of progenies having a 1000-grain weight STI as high or low as the parents supported that the two populations were useful for the molecular tagging. In the present study loci were detected, comparable to earlier studies investigating 1000-grain weight under non-stressed conditions (Halloran, 1976; Bannier, 1979; Chojecki *et al.*, 1983; Petrovic and Worland, 1988; Giura and Saulescu, 1996;

Campbell *et al*., 1999; Varshney *et al*., 2000; Ammiraju *et al*., 2001; Börner *et al*., 2002b; Huang *et al*., 2003a; Dholakia *et al*., 2003; Elouafi and Nachit, 2004).

4.2.2. Phenotypic analysis and inheritance of vegetative traits

Although the prime purpose of this study was to discover new genes for drought tolerance, the opportunity was also taken to evaluate the genetics of the vegetative traits, plant height and flowering time, using $F_{2:3}$ and RILs mapping populations. Plant height and flowering time for the different environments and the two different populations showed continuous distributions suggesting that these traits were not simply inherited. Transgressive segregants occurred towards a low or a high plant height and early or late flowering time. Our results are in conformity with the results of several earlier studies, where many loci located on several chromosomes were reported to control both traits (Cadalen *et al*., 1998; Keller *et al*., 1999a; Ahmed, *et al*., 2000; Börner *et al*., 2002b; Huang *et al*., 2003a).

4.2.3. Phenotypic analysis and inheritance of grain characters

One of the objectives of this study was to investigate the genetic basis of the grain morphology characters under post-anthesis drought stress i.e., grain area STI (*Gae*), grain length STI (*Glt*), grain width STI (*Gwd*), grain circumference STI (*Gcc*), grain roundness STI (*Grs*) and grain form density factor STI (*Gdf*) using $F_{2:3}$ and RILs mapping populations. Phenotypic frequency distributions of grain characters for different environments and different populations indicated that the inheritance of these traits is complex. The parents differed at several QTLs controlling grain characters. Transgressive segregants occurred towards low and high parental values for all characters. The present ressults are in conformity with several published studies performed under non-stressed conditions, which show linkage of seed size and shape traits to a number of different loci in wheat (Snape *et al*., 1985; Giura and Saulescu, 1996; Campbell *et al*., 1999; Ammiraju *et al*. 2001; Dholakia *et al*., 2003).

4.3. Genetic mapping of gene/s loci for post-anthesis drought tolerance

Microsatellites belong to an important class of molecular markers, since they are abundant in all animal and plant genomes and are hypervariable in nature (Gupta *et al*., 1996; Gupta and Varshney, 2000). In bread wheat also, where molecular markers like RFLPs and RAPDs failed to detect adequate polymorphism (Röder *et al.,* 1998; Gupta and Varshney, 2000), microsatellites have been found to be useful. They have been used in bread wheat for genome mapping (Röder *et al.,* 1998, Stephenson *et al.,* 1998), gene tagging and genetic

diversity studies (Gupta and Varshney, 2000); see also section 1.3.5. Keeping in view the importance of microsatellites, in the present study, they were utilized as PCR-based approaches for gene/s tagging.

4.3.1. Polymorphism rate detected by microsatellite markers

The use of tolerant cultivars is the best way to decrease the reduction in grain yield due to post-anthesis drought stress. Also, because post-anthesis drought stress is quantitatively inherited and screening for post-anthesis drought stress is complicated and requires special equipment, breeding for post-anthesis drought stress with traditional methods requires substantial time and effort. Therefore, molecular identification of QTL has become the method of choice for post-anthesis drought tolerance. After a linkage between a QTL and molecular markers has been determined, the QTL can be transferred selectively into different genetic backgrounds by marker-assisted selection because these markers are not influenced by the environment and can be scored at all stages of plant growth. Therefore, it is important to start mapping with a group of markers, which showed a high level of polymorphism in the organism under study. In the present study, the large genetic distance between the two parental lines 'ATRI 5283' and 'ATRI 15010' provided a high degree of polymorphism and a sufficient number of offspring differing in their post-anthesis drought tolerance. Wheat is a segmental allopolyploid containing three distinct but genetically related homoeologous genomes, A, B and D. The haploid content of bread wheat genome is approximately 1.7 X 10^7 bp (Arumuganathan and Earle, 1991) with an average of 810 Mb per chromosome. Such a large genome of hexaploid wheat has resulted from polyploidy and extensive duplications, such that over 80% of the genome consists of repetitive DNA sequences (Gupta *et al*., 1999b). For these reasons, there have been problems in the preparation of molecular maps and in the development of markers for marker-assisted selection in wheat. The main problem has been the failure of a variety of molecular markers to detect adequate and useful polymorphism. However, despite these problems, success has been achieved in recent years and molecular maps have become available for chromosomes of all homoeologous groups in wheat by using different types of molecular markers. In the present study, one type of DNA molecular markers, microsatellites (PCR-based DNA markers), was used to construct a linkage map and to locate QTLs responsible for post-anthesis drought tolerance in wheat. The *gwm*-SSRs used have known chromosomal assignments and were previously mapped in several mapping populations, including the bread wheat populations '*T. aestivum;* W 7984' x '*T. aestivum*; Opata85' = ITMI population (Röder *et al.*, 1995, 1998), '*T. aestivum;* W 7984'

x '*T. aestivum;* Prinz' (Huang *et al.*, 2003a) and tetraploid populations, '*T. durum;* Messapia' x '*T. dicoccoides;* MG4343*'* (Korzun *et al*., 1999) or '*T. durum;* Jennah Khetifa' x '*T. durum;* Cham1' (Nachit *et al.,* 2001). Although, the SSRs indicated less polymorphism than AFLP, they were very informative, since they are co-dominant, locus specific and evenly distributed along chromosomes (Röder *et al.,* 1998). In addition, Plaschke *et al.* (1995), Röder *et al.* (1995), Ma *et al.* (1996) and Bryan *et al.* (1997) agreed that SSRs showed a much higher polymorphism and informativeness in hexaploid wheat than any other marker systems. However, due to the large genome size, the development of microsatellite markers in wheat is extremely time-consuming and expensive (Röder *et al*., 1998). The percentage of polymorphic SSRs used in this study was 41.63% of the total number of tested SSRs. This high rate of polymorphism found in the present population confirms the transferability of SSRs between bread and durum wheat as has been shown in *T. durum x T. dicoccoides* (Korzun *et al*., 1999) and *T. durum* x *T. durum* (Nachit *et al.,* 2001) mapping populations. The percentage of polymorphism of the $F_{2:3}$ mapping population used in the present study was higher than the numbers showed by Röder *et al.* (1995) or Ma *et al.* (1996) who found that the percentage of polymorphic microsatellites was about 22% and 36% in common wheat, respectively. This was expected because an interspecific '*T. durum;* ATRI 5283' x '*T. aestivum*; ATRI 15010' cross was used. Using the synthetic wheat 'W 7984' for creating the ITMI mapping population Röder *et al*., (1998), showed that 80% of 294 SSRs primer pairs detected polymorphism between the two parents. These results, along with others (Prasad *et al*., 1999, 2000; Roy *et al*., 1999) suggested that the microsatellite markers can be successfully utilized for various types of investigation e.g., genome mapping, gene tagging, evolutionary studies and germplasm characterization (see also section 1.3.5).

4.3.2. Linkage map construction

The population consisting of 81 $F_{2:3}$ families from an interspecific hybridization of the Chinese durum wheat landrace 'ATRI 5283' and the Ethiopian spring bread wheat landrace 'ATRI 15010' proved to be suitable for constructing a linkage map and for detecting QTL for post-anthesis drought tolerance. Because of the difficulties in finding polymorphisms between much more closely related varieties, an interspecific cross have been made. Many linkage maps involve interspecific crosses because of low polymorphism among cultivated varieties of wheat (Anderson *et al*., 1993; Devos *et al*., 1995). Since the numbers of loci controlling quantitative traits are large, the use of large mapping populations will give a higher chance in detecting these QTLs (Kicherer *et al.,* 2000). Large population sizes have been used by others

like Keller *et al.* (1999b); Messmer *et al.* (2000) and Sourdille *et al.* (2000) who used progenies of 226, 204 and 217 individuals, respectively, for constructing genetic maps. However, other researchers used mapping populations with smaller numbers such as Bai *et al.* (1999); de la Pena *et al.* (1999), Mingeot and Jacquemin (1999), Waldron *et al.* (1999), Toojinda *et al.* (2000) and Huang *et al.* (2003a). These differences in the size of the mapping populations may depend on the genome size of the organism, the generation of mapping population and the nature of the inheritance of the trait under study (Beavis, 1998). In the present study, 184 different polymorphic SSRs markers were used to construct the linkage map of $F_{2:3}$ families. A population of 81 F_2 plants is certainly at the lower end of the plant numbers that have been analysed in comparable studies. However, a larger population is a much higher burden for population generation (due to sterility in the material) and population analysis.

The 184 polymorphic marker loci covered the whole genome (A genome: 81; B genome: 103). According to extended linkage mapping data from integrated genetic maps of wheat (McGuire and Qualset, 1997) the average chromosome length varied between 150 and 200 cM, which would result in a total genome length of 3,200 to 4,200 cM. The map of this study spans 2,603.34 cM, covering the wheat A and B genomes. The distribution of the marker loci across the 14 chromosomes indicated that there are more markers identified on B genome than on A genome. This result is in harmony with genetic maps obtained by Röder *et al.* (1995, 1998, unpublished data) in bread wheat 'W 7984' x 'Opata 85' ITMI population; in 'W 7984' x 'Prinz' population (Huang *et al.*, 2003a) and in durum wheat populations, Messapia x MG4343 (Korzun *et al*., 1999) and 'Jennah Khetifa' x 'Cham1' (Nachit *et al.,* 2001). The percentage of markers assigned to the respective genomes in this research is in good agreement with the numbers obtained from other researchers. Comparable results were obtained by Röder *et al*. (1998) who found that out of 279 microsatellite markers, 93 mapped to the A genome, 115 to B genome and 71 to D genome. Thus it can be concluded, that the number of markers assigned to each genome is in part a reflection of the relative amount of genetic variation present among the different genomes of wheat. Therefore, in order to increase the number of A and D genome markers, they could be isolated from *T. monococcum* or *T. tauschii,* respectively. This idea of the potential of *Aegilops tauschii* the diploid progenitor of the D genome of wheat as a source of microsatellite markers for hexaploid bread wheat was investigated by Pestsova *et al.* (2000). Their data obtained, confirmed this idea. All primer pairs that were functional in *Aegilops tauschii* amplified well in hexaploid wheat and extended the existing wheat microsatellite map. Also, the use of new developed systems of

molecular markers like single nucleotide polymorphisms (SNPs, Gupta *et al.,* 1999b) may help in increasing the number of markers in different genomes including the A and D genomes. The use of SNPs system, which led to rapid advancement in developing human genetic map, would offer rapid and high-automated genotyping of wheat genome (Gupta *et al.,* 1999b).

4.4. Mapping QTLs for post-anthesis drought tolerance

The prime purpose of this study was to discover new genes for post-anthesis drought tolerance. Several new QTLs were discovered in the 'ATRI 5283' x 'ATRI 15010' and 'W 7984' x 'Opata 85' mapping populations and, overall, this indicates that there is quite a lot of genetic variation for the stem reserve mobilization trait.

4.4.1. Mapping QTL for stem reserve mobilization (*Srm*)

Abiotic stress such as drought, salinity and others generally reduce crop productivity. It has been estimated that crops attain only about 25% of their potential yield because of the detrimental effects of environmental stress (Boyer, 1982). Plant responses to water stress are clearly influenced by the timing and intensity of stress (Ludlow and Muchow, 1990), indicating a genotype x environment interaction, which makes the genetic analysis of such traits very complicated. Stem reserve mobilization was defined as the ratio of 1000-grain weight under chemical desiccation treatment to 1000-grain weight under control (Blum *et al*., 1983a, 1983b). In wheat, the stem reserve plays an important role in supplying carbohydrate to grains under post-anthesis drought stress (Blum *et al*., 1983a, 1983b; Reynolds, *et al*., 2000; see also section 1.2.4.).

For the mapping of QTL for tolerance to drought, consistent drought condition is critical for accurate assessment of the tolerance of plant genotypes and for determination of the magnitude of the genetic factors that contribute to drought tolerance. This is especially important for drought, since environment is one of the major determining factors for initiation and development of drought. The identification of markers associated with stem reserve QTLs would help breeders to construct beneficial allelic combinations and accelerate breeding programs for the development of drought tolerant cultivars. The markers linked to low seed size QTLs can also be used as indirect selection tools to eliminate the transfer of these alleles into elite breeding lines. Characterization of QTLs for drought tolerance in this study provides insight into an understanding of the mode of drought tolerance in wheat. The most-practical application of the identified QTLs for drought tolerance components is to perform marker-

assisted selection aimed at efficient pyramiding of favourable QTL alleles to improve drought tolerance in wheat. Further analysis of this population under different agroclimatic conditions to find out stable QTLs as well as to identify additional genes/QTLs for post-anthesis drought tolerance traits is our present effort. It is also possible to establish an ensemble of different QTLs linked to stem reserve mobilization for improved seed size in standard varieties in wheat.

Numerous QTL mapping studies examining drought tolerance and related traits in maize, rice, barley and wheat have demonstrated that this trait is affected by several loci, each of which have relatively small effects (Agrama and Moussa, 1996; McCouch and Doerge, 1995; Quarrie, 1996; Morgan and Tan, 1996). Polygenes controlling important metric traits such as seed size are usually distributed among several QTLs, which may not linked to one another (Law and Worland, 1973; Fatokun *et al*., 1992). The low level of contribution to phenotypic variation explained by individual markers in our data confirms the quantitative nature of seed-weight inheritance and implies that transfer of the grain size trait can not be approached by any easy way through conventional breeding programs. To our knowledge, no study has included the mapping of post-anthesis drought tolerance genes/QTLs in wheat.

In the present study, two wheat mapping populations, derived from the cross 'ATRI 5283' x 'ATRI 15010' and 'W 7984' x 'Opata 85' grown in two different environments (Gatersleben field season 2001 or 2002 and 2003), were used to detect QTLs for post-anthesis drought tolerance. In order to better understand the mechanisms of post-anthesis drought tolerance via stem reserve mobilization in wheat, a molecular dissection of QTLs for stem reserve in two different genetic backgrounds was studied. The parents were well studied at vegetative and grain yield levels and performed differently. The two populations segregated for 1000-grain weight stress tolerance index (STI). The contrasting features in the parents and the mapping populations made this germplasm ideal for studying drought tolerance in wheat. The consistent QTLs identified in this study could be useful in marker-assisted selection for high grain size in wheat drought tolerance breeding programs. Stem reserve is the only putative post-anthesis drought tolerance trait that has been associated with sustained grain yield in wheat plants under drought stress (Blum *et al*., 1983a, 1983b). For the first time, using two mapping population of $F_{2:3}$ families and RILs, QTLs were mapped for stem reserve mobilization in wheat.

The 81 $F_{2:3}$ families of the 'ATRI 5283' x 'ATRI 15010' cross were grown in two different environments. At the same time, 184 SSR markers were used to construct the genetic linkage map. It may be recalled that only 41.63% of *gwm* primers detected polymorphism

between the parental genotypes that differed for stem reserve mobilization. Six microsatellite markers (*Xgwm497a, Xgwm480, Xgwm247, Xgwm251, Xgwm1011a* and *Xgwm611*) showed an association with QTLs (designated *QSrm.ipk-1A*, *QSrm.ipk-3A, QSrm.ipk-3B, QSrm.ipk-4B, QSrm.ipk-6A* and *QSrm.ipk-7B*) for stem reserve mobilization, located on chromosomes 1A, 3A, 3B, 4B, 6A and 7B. Alleles derived from the tolerance parent 'ATRI 5283' were associated with a positive effect on stem reserve mobilization for four of the six QTLs detected for this trait in $F_{2:3}$ mapping population. The four QTLs for stem reserve mobilization increase were mapped on chromosomes 3B, 4B, 6A and 7B. The number and location of significant QTLs detected for stem reserve mobilization varied between the two environments. Since single environments differed in the plant development during vegetative stage and consequently in reproduction stage, different genes might be relevant for tolerance in different environments. Also, since the post-anthesis drought tolerance is controlled by group of QTLs, which affected by environment, gene expression of these QTLs would differ in different environments. This can be explained from the QTLs, which were identified in some environments at low LOD values. Two of these QTLs, which were identified on chromosomes 3A and 7B in both environments. Also, another QTL which was appointed in two different environments at Gatersleben 2002 and 2003 on chromosome 4B. Low values of LOD scores in one environment explained the low contribution of the QTL to the phenotypic variance in this environment. In other words, these QTLs are present at the specific loci and the different factors of environment pressure were not strong enough to let these QTLs to be expressed at the maximum level. In the proper environments, the same QTLs showed high level of gene expression (LOD more than 3.0).

Keeping in view the fact, that the F_3 families showed a distribution, it may be concluded that there may be other QTLs controlling the difference in post-anthesis drought tolerance between the parents. The presence of many QTLs for grain weight under non-stressed conditions was also suggested in recent studies (Campbell *et al*., 1999, Halloran, 1976; Bannier, 1979; Chojecki *et al*. 1983; Zheng *et al*. 1993, Börner *et al*., 2002b and Huang *et al*. 2003a).

Although the progress in preparation of wheat genetic maps has been steady, the use of RFLP markers in preparation of molecular maps has rather been slow because of the very limited level of RFLP polymorphism detected in wheat. Therefore, the preparation of molecular maps necessitated the use of populations derived from wide crosses. Consequently, at international level a mapping population was derived by single seed descent (SSD) F_8 from the cross of 'W 7984', an amphihexaploid wheat synthesized from *Aegilops tauschii* (DD)

and *Triticum durum* (AABB) variety 'Altar 84' with the Mexican variety 'Opata 85' from CIMMYT. The population has commonly been described as ITMI (International Triticeae Mapping Initiative) and map prepared on the basis of ITMI has been described as ITMI map. Using ITMI population for microsatellite markers, a detailed genetic map using 279 microsatellite loci has already been published (Röder *et al*., 1998). Keeping in view the importance of ITMI population, this population was also used for mapping the RFLP and the microsatellite markers that were linked with post-anthesis drought tolerance traits identified during the present study. Eight RFLP and microsatellite markers namely (*Xgwm357, Xmwg938b, Xgwm249a, Xgwm639c, Xfbb238b, Xgwm494, Xgwm302* and *Xfbb189b)* showed an association with QTLs (designated *QSrm.ipk-1A, QSrm.ipk-1B, QSrm.ipk-2D, QSrm.ipk-5B, QSrm.ipk-5D, QSrm.ipk-6A, QSrm.ipk-7B* and *QSrm.ipk-7D*) for stem reserve mobilization. They mapped to chromosomes 1A, 1B, 2D, 5B, 5D, 6A, 7B and 7D, respectively. For stem reserve mobilization, three QTLs were detected in the two environments. Those 'stable' QTLs were located on chromosomes 2D, 5D and 7D.

During the last two decades, several attempts have been made to understand the genetic basis of seed size in wheat. Halloran (1976) has reported that chromosome 4B is associated with seed size. Petrovic and Worland (1988) have identified that 1000-grain weight is associated with chromosome 5D. Giura and Saulescu (1996) have reported that chromosomes 6D and 4A are associated with a high 1000-grain weight while 5B and 5D are associated with a low 1000-grain weight. A QTL for 1000-grain weight on chromosome 3A was detected by Shah *et al*. (1999). Campbell *et al*. (1999) have shown that chromosomes 1A, 1B, 3B and 7A have loci which control 1000-grain weight, while Gupta *et al*. (1999a) have found chromosome 1AS to be associated with 1000-grain weight in the same cross. Ammiraju *et al.* (2001) identified QTLs for high and low seed size on chromosomes 6B, 2D and 1D. Börner *et al.* (2002b) mapped the QTLs for 1000-grain weight on chromosomes 1B, 2D, 3A, 3B, 5A, 6A, 6B, 7B and 7D. Groos *et al.* (2003) detected nine QTLs for 1000-grain weight on chromosomes 1D, 2B, 2D, 3A, 5B, 6A, 6D, 7A and 7D. Recently, Huang *et al*. (2003a) identified the chromosomal location for 1000-grain weight on chromosomes 2A, 2D, 4D, 5B, 7A, 7B and 7D. The QTLs detected in the present study on chromosomes 1B, 2D, 3A, 3B, 5B, 6A, 7B and 7D may be comparable to that found by Börner *et al*. (2002b) and Huang *et al*. (2003a). The chromosomes 1A, 4B and 7A identified during the present study, are three of the eight chromosomes (1A, 1D, 2B, 4B, 5B, 6B, 7A and 7D) that were earlier identified to carry the loci for high grain weight, using monosomic analysis (Varshney *et al*., 2000).

Concurrently, Jing *et al*. (2000) found that a drought tolerance gene in an ancient Chinese wheat landrace 'Pingyao Bai Mai' and its derived vareities was putatively linked to microsatellite loci *Xgwm11, Xgwm157, Xgwm5, Xgwm44* and *Xgwm111* on chromosomes 1B, 2D, 3A and 7D. This result fits well with the result of the present study.

Morgan (1991) suggested a genomic location for osmoregulation on chromosome 7A in wheat by studying chromosome substitution lines. Morgan and Tan (1996) have located a putative gene for osmoregulation on chromosome 7AS of wheat using RFLP analysis. The QTL on chromosome 7A found by Morgan (1991) and Morgan and Tan (1996) were not identified here.

Alleles derived from the synthetic wheat 'W 7984' were associated with a positive effect on stem reserve mobilization for four of the 8 QTLs detected for this trait in ITMI mapping population. The four QTLs for stem reserve mobilization increase were mapped on chromosomes 2D, 5B, 5D and 7D. The stem reserve mobilization increasing QTL*, QSrm.ipk-2D,* may be a pleiotropic effect of the gene *Ppd1* for day length insensitivity that is important for the adaptation to short days and increasing the yield in southern Europe (Börner *et al*., 1993; Worland *et al*., 1998a). Two loci, *QSrm.ipk.7B* and *QSrm.ipk.7D,* were located in the homoeologous positions of homoeologous group 7. Both are in comparable regions like the 1000-grain weight QTLs reported by Börner *et al*. (2002b) detected in the same population.

The results of the present study agree with other reports for the location of QTLs for 1000-grain weight except, the QTL on chromosomes 1D, 2A, 2B, 4A, 4D, 5A, 6B, 6D and 7A were not identified in the present study. Our results indicate that QTLs for stem reserve mobilization are spread over the genome. Also, genomes A and B play a great role in controlling this trait and genome D has little effects.

Finally, the few studies on the location of QTLs involved in drought tolerance showed the difficulty in finding general key regions for adaptation. The dissection of each adaptive trait enables major chromosomal regions to be located. The validity of the regions was strengthened when related to other studies or to results obtained for different adaptive traits. The co-location of the QTLs detected for the different traits allowed us to identify important genomic regions for stem reserve mobilization.

In conclusion, the key points revealed by our results are the stability of some QTLs for stem reserve mobilization and the existence of genetic factors specific for drought tolerance. This information can be useful in a breeding program aimed at improving yield stability.

4.4.2. Mapping QTL for vegetative traits

Although the prime purpose of this study was to discover new genes for post-anthesis drought tolerance, the opportunity was also taken to evaluate the genetics of vegetative traits under non-stress condition. Several new QTLs were discovered in the 'ATRI 5283' x 'ATRI 15010' and 'W 7984' x 'Opata 85' mapping population.

4.4.2.1. Plant height (*Ht*)

A reduction in plant height can improve lodging resistance and indirectly increase yield. The genetic control of plant height is known to be complex involving many genes (Börner *et al*., 1996). In the present study, eight and four QTLs were detected for plant height on chromosomes 2A, 2B, 3A, 3B, 5A and 7A in F_3 families and on chromosomes 3B, 4D, 5A and 6D in RILs population.

Law *et al.* (1976) mapped gene/s for plant height on chromosome 2B. Roberts (1990) found another locus on 5A. Hyne *et al.* (1994) located QTLs for plant height on chromosomes 6B and 7B. Cadalen *et al.* (1998) using RFLP markers found QTLs for plant height on 4A, 4D, 7A and 7B. Kato *et al.* (1999) identified 3 QTLs on 5AL chromosome. Keller *et al.*, (1999a) found 11 QTLs for plant height on chromosomes 1A, 2A, 4A, 5A, 6A, 1B, 4B, 5B and 7B. In addition, Shah *et al.* (1999) appointed a QTL on chromosome 3AL. Börner *et al*. (2002b) mapped 12 QTLs for plant height on chromosomes 1A, 1B, 2D, 3A, 3B, 3D, 4A, 4B, 4D, 5D, 6A and 6B using RILs. Finally, Huang *et al*. (2003a) identified 5 chromosome regions for plant height on chromosomes 2B, 4B, 4D, 6A and 7B using advance backcross mapping population.

The results of the present study agree with other reports for the location of QTLs for plant height except, the QTL on chromosome 6D, which was not identified by others. The QTLs controlling plant height identified by others on chromosomes 1A, 1B, 2D, 3D, 4A, 4B, 5B, 5D, 6A, 6B and 7B were not detected in the present study. Our results and those of other researchers indicate that QTLs for plant height are wide spread over the genome. Genomes A and B play an important role in controlling this trait compared to the D genome.

4.4.2.2. Flowering time (*Flt*)

Drought escape through early flowering and/or short growth duration is advantageous in environments with terminal drought stress and where root growth is inhibited by physical or chemical barriers (Turner, 1986; Blum, 1988; Blum *et al.,* 1989). On other hand, later flowering can be beneficial in escaping early-season drought, if drought is followed by rains

(Ludlow and Muchow, 1990). Under non-stress conditions, late-flowering varieties tend to yield higher than early-flowering ones (Turner, 1986; Ludlow and Muchow, 1990). This is because the early-flowering varieties are likely to leave the yield potential unutilized (Muchow and Sinclair, 1986).

Heading date is critical determinant of crop adaptation. Many genes are involved in fitting crop cultivars to prevailing environmental conditions; for example photoperiod and vernalization response genes that cause plants to change from vegetative growth to reproductive growth. Also, heading date is influenced by genes independent of environmental conditions (earliness *per se*) (Kato and Wada, 1999). Wheat cultivars are usually classified into two growth habits, namely, spring and winter types. The major physiological determinant of the difference between the two types is the requirement of winter wheats for certain period of growth at low temperature, called vernalization, before flora initiation. In hexaploid wheat, there are five genetic loci involved in response to vernalization requirement and the chromosomal locations of four have been identified; namely *Vrn-A1* on 5A (*Vrn1*), *Vrn-D1* on 5D (*Vrn3*), *Vrn-B1* on 5B (*Vrn2*) and *Vrn-B4* on 7B (*Vrn5*) (Law *et al.,* 1976; Snape *et al*., 1985; Galiba *et al*., 1995; Kato *et al.,* 1998; Snape *et al* 1998). Genes responding to photoperiod also affect heading date. They are designated *Ppd-D1* (formerly *Ppd1*), *Ppd-B1* (formerly *Ppd2*) and *Ppd-A1* (formerly *Ppd3*) on the short arms of chromosomes 2D, 2B and 2A, respectively, (Pirasteh and Welsh, 1975; Scarth and Law, 1983).

Stelmakh *et al*. (1998) compared different effect values of *Vrn-A1*, *Vrn-B1*, *Vrn-D1* genes in relation to heading date, plant height and yield components. He found that varieties possessed *Vrn-D1* could adapt to stress conditions such as high temperature and drought at grain filling stage and achieved high grain yield. Research of *wec* (wheat embryo cold) treatment genes associated with heading factors was also carried out by Shindo and Sasakuma (2002) using near isogenic lines of *Vrn-A*1. The only studies for *Vrn-D1* gene were just genetic mapping done by Snape *et al.* (2001) and Shindo *et al*. (2003).

Furthermore, Law and Wolfe (1966) located a genetic factor for ear emergence time on chromosome 7BS. Law *et al.* (1976) mapped the heading date on 5A. Hoogendoorn (1985) detected genes involved in earliness on chromosomes 3A, 4A, 4D, 6B and 7B. Miura and Worland (1994) found a QTL on chromosome 3A for heading date. Also, Hyne *et al.* (1994) identified two QTLs on 7A and 7D chromosomes for heading date. Kato *et al.* (1998) indicated two QTLs for heading date on chromosome 5A. Miura *et al.* (1999) identified two genes affecting earliness on chromosome 3A. In addition, Shah *et al*. (1999) appointed a QTL on 3A for heading date. Keller *et al.* (1999) detected 10 QTLs for heading date on

chromosomes 2A, 2B, 3A, 3B, 4A, 4B, 5A, 5B, 7A and 7B. There was a mapping report by Sourdille *et al*. (2000) who found three QTLs on 2BS, 5AL and 7BS chromosomes for heading date. Finally, Börner *et al*. (2002b) mapped QTLs for flowering time on chromosomes 2B, 2D, 3A and 5D.

In the present study, four and seven QTLs were identified for flowering time on chromosomes 1A, 2A, 3B and 7A in F_3 families and on chromosomes 1A, 2B, 3D, 5B, 5D, 7B and 7D in ITMI population. The QTLs on chromosome 2B and 5D, *QFlt.ipk-2B* and *QFlt.ipk-5D*, might be the same as that found in the ITMI population recently (Börner *et al*., 2002b). New QTLs on chromosomes 1A, 3D, 5B, 7B and 7D were detected here for the first time.

In this study two QTLs for flowering time and for plant height were found in the same intervals on chromosomes 1A and 3B in $F_{2:3}$ families. This observation may indicate that these traits are linked to each other. Our results and those of other researchers (Keller *et al*. 1999a) indicate that QTLs for these two traits are spread over the genome. As for flowering time and plant height, these QTLs most probably are at the same loci displaying, these QTLs are either tightly linked or have pleiotropic effects.

Early heading and short plants are desirable traits in wheat therefore, their association with drought tolerance is very useful in wheat improvement. One mechanism of drought tolerance is reducing the plant life cycle. Development of early maturing variety can help to escape from drought stress.

4.4.3. Mapping QTL for grain characters

The shape and size of wheat grains is a primary determinant in the value of the grain (Campbell *et al.,* 1999). It has an effect on many factors of the agronomy on end use of the crop and therefore is an important trait for genetic study. Millers obtain higher flour yields from larger grains (Wiersma *et al*., 2001; Giura and Saulescu, 1996) and therefore place pressure on breeders to ensure new varieties exhibit large grains. This has an effect on the specific weight of the grain sample, with large, full grains producing higher specific weights than small, shrivelled grains. As grain value is partly determined by specific weight values, again seed size and shape may be very important in increasing the premium on grain samples. It has been suggested in a number of studies that increasing grain size is an important factor in increasing yield from a crop. However, this may have some negative implications on the end use of the crop, with larger kernelled lines often showing a decrease in protein content due to the extra grain size being composed mainly of starch rather than protein. It has also been shown that large seeds may give a better start for plants

grown in the field, with greater seedling size and speed of growth coming from larger seeds (Bredemeier *et al.*, 2001).

The economic value of the wheat crop is determined by class, which depends in part on grain morphology and texture and by test weight. Colour, shape and length of the grain and shape of the germ are used to determine wheat grain classes (GIPSA, 1997).

Although the prime purpose of this study was to discover new genes for post-anthesis drought tolerance, the opportunity was also taken to evaluate the genetics of grain characters under post-anthesis drought stress condition. In fact this study has provided the first complete analysis of grain characters under post-anthesis drought stress in wheat. Using image analysis techniques, it was easy to measure a large number of grains and to process the results on a computer, avoiding laborious hand measurements. It was thus possible to measure variation in grain dimensions for the large number of samples needed for QTL mapping studies of such traits. All grain traits were measured by digital image analysis (DIA) (Symons and Fulcher, 1988), except grain form density factor. Grain form density factor was derived from DIA parameter and agronomic trait. Density factor, defined as grain weight/grain area, could be considered as a grain quality character. Grain density is traditionally measured using displacement assays with aqueous solutions (Peterson *et al*., 1986).

This study has shown that grain character STIs are under the genetic control of many genes. Interestingly, there are different 'types' of QTL. First, there are those that influence the components of grain area STI, width STI, length STI, circumference STI, Grain roundness STI, Grain form-density factor STI, independently. For example in F_3 mapping population, there are QTLs on chromosomes 6A and 6B that influences grain area STI, on chromosomes 7A and 7B that influences grain length STI and on chromosome 5B that influences grain width STI. The importance of such QTL is in the fact that they indicate that it should be possible to breed for different grain shapes, such as long thin grain, short thin grain etc., through utilizing such variation. Secondly, there are QTL, which influence more than one trait, for example, the grain area and grain width STIs on chromosome 1A. These imply that there are 'general' grain size factors, which influence all dimensions. Such variation means that it should be possible to increase grain size through simultaneously increasing all dimensions. By judicious selection of both types of QTL it should be possible to breed for larger grains and hence increase yield, with different grain shapes, as desired. Several QTL control grain area and these seemed to reflect the probable pleiotropic effect of QTL for grain width, grain length and grain circumference. Thus, the variation in grain area is due to grain shape and size differences. This indicates, not surprisingly, that to maximize grain area means breeding for many small grains. Thus, selection

has to be a compromise between 'good' grain shape and size. This could be achieved by directed plant breeding for the types of QTLs identified here.

It seems, from the differences in numbers and positions of the QTLs found in these studies, that different combinations of these genes may be responsible for producing the different phenotype of size and shape in different wheat varieties, although, of course, environment and genotype x environment interactions play a part.

Using monosomic analysis, Giura and Saulescu (1996) studied grain characters in an Italian local wheat population and indicated that kernel length was increased by chromosomes 1B, 2B, 3A, 4A and 4B; kernel width by chromosomes 1A and 1B and density by 6A and 6D. Campbell *et al*. (1999) detected QTLs for kernel traits on chromosomes 1A, 2A, 2B, 2D, 3B, 4A, 5A, 7A and 7B. Several researchers have mapped QTLs for seed size and shape in cereal grains. In wheat, Dholakia *et al*. (2003) discovered QTLs for kernel size and shape on wheat chromosomes 2B, 2D, 5B, 6B and 7B.

In our study, the main QTLs for grain morphology were located on chromosomes 1A, 1B, 1D, 2A, 2B, 2D, 3B, 3D, 4A, 4B, 4D, 5A, 5B, 5D, 6A, 6B, 6D, 7A, 7B and 7D. The homoeologous group 1, 2, 3, chromosomes were mentioned in several of the studies listed above. An interesting observation in this analysis was the identification of new loci associated with grain traits under post-anthesis drought stress which have not reported earlier on 1D, 3D, 5D and 7D, however no QTLs were detected on chromosome 3A in the present study. Like in other species QTLs are population specific (Melchinger *et al*., 1998).

4.5. Sources of alleles for post-anthesis drought tolerance

Post-anthesis drought tolerance genes are located throughout the genome and are genotype dependent. In this study, it was found that for stem reserve mobilization four putative QTLs were derived from 'ATRI 5283' in F_3 families and other four were derived from the synthetic wheat 'W 7984' in RILs population. However, some of the QTLs were also derived from sensitive parents of the two populations. Similar results for other traits of interest were found by Börner *et al*. (2002b) or Huang *et al*. (2003a). These findings further confirm that post-anthesis drought tolerance is a quantitative trait and that apparently sensitive parents may contain alleles for tolerance, which may not be found in the tolerant parents. It can be concluded that the sensitive parents 'ATRI 15010' and 'Opata 85' may contain some tolerance alleles that when combined with alleles from tolerant parents can result in increased level of tolerance.

4.6. Perspectives for marker-assisted selection

Early generation selection for drought in the field is difficult and unpredictable, and genotype screening requires replications and is resource intensive. Consequently, marker-assisted

selection could be used to facilitate the transfer of these genes for drought tolerance into well adapted genotypes. However, there are certain considerations need to be taken when deciding which QTL should be emphasized in MAS strategy. First of all it is necessary to decide which region(s) has enough evidence for the presence of a major QTL. This can be achieved by setting appropriate thresholds (LOD more than 3) for the identification of the QTLs and by detecting QTLs in the same region in different environments. In this study, three QTLs for stem reserve mobilization on chromosomes 3A, 4B and 7B in F_3 families and three QTLs on chromosomes 2D, 5D and 7D in ITMI population fulfilled these criteria. They showed high values of LOD scores and they were detected in two environments. Beside MAS for drought, selection can be done by plant height, flowering time and grain morphology. Finally, the selected QTL for MAS should indicate high levels of contribution to the phenotypic variance, which measured by PV. However, this consideration should be taken with caution because these values can be significantly influenced by population sizes and the number of markers used in the multi-locus model (Beavis, 1998). In simulation studies, QTL analyses using population sizes of 100 identified only a subset of the total number of simulated QTLs and often over-estimated their effects (de la Pena *et al*., 1999). It can be concluded that the three QTLs on chromosomes 3A, 4B and 7B in F_3 families and three QTLs on chromosomes 2D, 5D and 7D in ITMI population, which were constant under different environmental conditions, are promising candidates for MAS.

Molecular markers closely linked to genes of agronomic importance have been demonstrated to be useful tools for indirect selection in a barley breeding programmes (Jefferies *et al*. 1997). Marker-assisted selection is time-efficient, non-destructive and depending on linkage relationships, characterised by low selection error. Marker assisted selection should be done on a case by case basis. Further investigation for drought tolerance will be required to establish the importance of the identified genomic regions in other backgrounds. Also, field evaluation is required to establish the effectiveness of the drought screening system in modelling water responses and in evaluating the stability of QTLs across environments. Our results indicate the existence of genes or gene clusters with major effects, which are involved in the control of significant proportions of the phenotypic variation in quantitatively inherited traits related to drought tolerance.

The QTLs and molecular markers for post-anthesis drought tolerance provide further evidence for the inheritance of the stem reserve mobilization. Compared with conventional methods, QTLs and molecular markers provide breeders new alternatives for selection. Marker-assisted selection can accelerate breeding by reducing the time to develop new cultivars (Tanksley and Hewitt, 1988; Paterson *et al.*, 1991). Further research is needed on molecular markers and QTL mapping to screen potential parents for drought tolerance in wheat.

5. SUMMARY

5.1. English summary

This work was carried out at the Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK), Gatersleben, Germany, during the wheat growing seasons, 2001, 2002 and 2003. Seventy-seven wheat accessions and two wheat mapping populations were used. The objectives of the present study were:

1. To define genotypes with high stem reserve mobilization ability.
2. To characterize the expression and inheritance of traits associated with post-anthesis drought tolerance and grain development.
3. To determine of the number, chromosome position and effects of the QTLs associated with drought tolerance.
4. To identify SSR and RFLP markers associated with the QTLs for drought tolerance.

The obtained results could be summarized as follows

5.1.1. Screening wheat genotypes for post-anthesis drought tolerance

1) Among the seventy-seven wheat genotypes tested in the wheat growing season 2001/2002, the 1000-grain weight stress tolerance index (mean damage values after desiccation) ranged from 22.26% to 87.78%.
2) The wheat genotypes ATRI 1896, ATRI 5283, ATRI 17620, Synthetic/N, ATRI 9882, ATRI 5951, W 7984 and ATRI 7099 exhibited the highest stress tolerance index values (87.78%, 82.41%, 80.23%, 78.46%, 77.71%, 74.33%, 70.80% and 70.06%, respectively).
3) The wheat genotypes ATRI 11457, ATRI 11445, ATRI 6931, ATRI 10213, Capelle-Desprez, ATRI 10197, ATRI 1634 and Bezostaya exhibited the lowest stress tolerance index values (22.26%, 25.72%, 26.60%, 26.88%, 30.29%, 30.37%, 30.55% and 31.13%, respectively).
4) There was genetic diversity in post-anthesis drought tolerance within the wheat germplasm.

5.1.2. Construction of the molecular linkage map

1) Of 442 Gatersleben Wheat Microsatellite (GWM) primer pairs tested, a total of 184 GWM (41.63%) assigned to the A and B genomes showed polymorphism between the parents ‘ATRI 5283’ (tolerant) and ‘ATRI 15010’ (sensitive) and were used for mapping in F_2 generation.
2) The map was constructed using the data of 184 *gwm*-SSR molecular markers on 81 F_2 plants using the F_2 model in the Mapmaker program. The base map spans 2,603.34 cM.

103 and 81 *gwm* markers were mapped on B and A genomes, respectively. The five chromosomes 6B, 4B, 2A, 3B and 7A included the highest number of loci mapped.

3) The average distance between marker pairs was 15.17 cM.
4) Chromosomes 2A, 4B, 6B and 7A showed marker clustering around the centromeric region.

5.1.3. Mapping QTLs for post-anthesis drought tolerance (PADT)

The PADT mapping population consisted of 81 F_3 families developed from the cross between 'ATRI 5283' and 'ATRI 15010'. Also, post-anthesis drought tolerance was recorded on the synthetic spring wheat genotype 'W 7984', the Mexican spring wheat variety 'Opata 85' and a set of 114 recombinant inbred lines (RILs) from the International Triticeae Mapping Initiative (ITMI) population.

5.1.3.1. Mapping QTLs for stem reserve mobilization (*Srm*)

1) Wide or continuous frequency distributions with transgressive segregants were observed in both populations as one would expect for QTLs. The continuous distributions of stem reserve mobilization indicated that the trait is polygenic in nature and quantitatively inherited. The transgressive segregation for high stem reserve indicated the potential for increasing the grain size under post-anthesis drought stress.
2) The individual QTLs for PADT were identified by the single marker analysis using the *QGENE* program. Six microsatellite markers (*Xgwm497a, Xgwm480, Xgwm247, Xgwm251, Xgwm1011a* and *Xgwm611*) showing an association with QTLs (designated as *QSrm.ipk-1A, QSrm.ipk-3A, QSrm.ipk-3B, QSrm.ipk-4B, QSrm.ipk-6A* and *QSrm.ipk-7B*) were located on chromosomes 1A, 3A, 3B, 4B, 6A and 7B, respectively, analysing the 'ATRI 5283' x 'ATRI 15010' cross. The percentage of the phenotypic variance (%PV) explained by a single QTL ranged from 13.41% to 24.74% in F_3 families. In the ITMI-population eight RFLP and microsatellite markers (*Xgwm357, Xmwg938b, Xgwm249a, Xgwm639c, Xfbb238b, Xgwm494, Xgwm302* and *Xfbb189b*) showed an association with QTLs (designated as *QSrm.ipk-1A, QSrm.ipk-1B, QSrm.ipk-2D, QSrm.ipk-5B, QSrm.ipk-5D, QSrm.ipk-6A, QSrm.ipk-7B* and *QSrm.ipk-7D*) for stem reserve mobilization that mapped to chromosomes 1A, 1B, 2D, 5B, 5D, 6A, 7B and 7D, respectively. The percentage of the phenotypic variance (%PV) explained by a single QTL ranged from 10.17% to 42.22%.
3) In the 'ATRI 5283' x 'ATRI 15010' cross, the 'stable' QTLs were located on chromosomes 3A, 4B and 7B. Other three 'stable' QTLs were located on chromosomes 2D, 5D and 7D in the ITMI population.

5.1.3.2. Mapping QTLs for vegetative traits

1) Wide or continuous frequency distributions with transgressive segregants were observed as one would expect for QTLs. The continuous distributions of plant height (*Ht*) and flowering time (*Flt*) indicated that plant height and flowering time are polygenic in nature and quantitatively inherited.
2) In F_3 families of the 'ATRI 5283' x 'ATRI 15010' cross, eight QTLs were detected for plant height on chromosomes 1A, 2A, 2B, 3A, 3B, 4A, 5A and 7A. For flowering time, four QTLs were identified on chromosomes 1A, 2A, 3B and 7A. The phenotypic variance (%PV) ranged from 12.08% to 22.96% and from 12.37% to 23.33% for plant height and flowering time, respectively. Analysing the ITMI population for plant height, four QTLs were detected on chromosomes 3B, 4D, 5A and 6D. Whereas for flowering time, seven QTLs were identified on chromosomes 1A, 2B, 3D, 5B, 5D, 7B and 7D. The phenotypic variance (%PV) ranged from 15.91% to 30.01% and from 12.91% to 22.61% for plant height and flowering time, respectively.
3) In the 'ATRI 5283' x 'ATRI 15010' cross, four 'stable' QTLs were located on chromosomes 2A, 3A, 5A and 7A for plant height. For flowering time, three stable QTLs were identified on chromosomes 2A, 3B and 7A analysing the 'ATRI 5283' x 'ATRI 15010' cross, whereas one 'stable' QTL for flowering time was located on chromosome 2B in the ITMI population.

5.1.3.3. Mapping QTLs for grain character

1) Wide or continuous frequency distributions with transgressive segregants were observed in F_3 families and RILs. The presence of transgressive segregants for all the grain trait STIs suggested that the parents selected for this analysis had alleles associated with low and high values of these traits. The continuous distributions indicated that the characters are polygenic in nature and quantitatively inherited.
2) In the present, the main QTLs for grain morphology STIs were located on chromosomes 1A, 1B, 1D, 2A, 2B, 2D, 3B, 3D, 4A, 4B, 4D, 5A, 5B, 5D, 6A, 6B, 6D, 7A, 7B and 7D.

5.2. Zusammenfassung

Die Arbeit wurde in den Jahren 2001, 2002 und 2003 am Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK), Gatersleben, durchgeführt. Siebenundsiebzig Weizen-akzessionen und zwei Kartierungspopulationen wurden analysiert. Die Ziele der Arbeit waren:

1. Das Auffinden von Genotypen mit der Fähigkeit in hohem Maße Halmreserven zu mobilisieren.
2. Die Charakterisierung der Expression und Vererbung von Merkmalen, welche für die Trockentoleranz nach der Blüte und die Kornentwicklung verantwortlich sind.
3. Das Feststellen der Anzahl, der Position auf dem Chromosom und der Effekte von QTL, welche die Trockentoleranz steuern.
4. Die Identifizierung von SSR und RFLP Markern, die zu QTLs für Trockentoleranz gekoppelt sind.

Die erzielten Ergebnisse können wie folgt zusammengefasst werden

5.2.1. Screening von Weizengenotypen auf Trockentoleranz nach der Blüte

1) Innerhalb der 77 analysierten Weizengenotypen schwankte der 1000-Korngewicht-Stresstoleranz Index (mittlere Schädigung nach Dessikation) zwischen 22,26% und 87,78%.
2) Die Weizengenotypen ATRI 1896, ATRI 5283, ATRI 17620, Synthetic/N, ATRI 9882, ATRI 5951, W 7984 und ATRI 7099 hatten die höchsten Stresstoleranz Indices. Diese betrugen 87,78%, 82,41%, 80,23%, 78,46%, 77,71%, 74,33%, 70,80% bzw. 70,06%.
3) Die Weizengenotypen ATRI 11457, ATRI 11445, ATRI 6931, ATRI 10213, Capelle-Desprez, ATRI 10197, ATRI 1634 und Bezostaya hatten die geringsten Stresstoleranz Indices. Diese betrugen 22,26%, 25,72%, 26,60%, 26,88%, 30,29%, 30,37%, 30,55% bzw. 31,13%.
4) Innerhalb der Weizenkollektion war eine Variabilität für Trockentoleranz nach der Blüte nachweisbar.

5.2.2. Konstruktion der molekularen Kopplungskarte

1) Von den getesteten 442 Gatersleben Weizen Mikrosatelliten (GWM) Primerpaaren zeigten 184 (41,63%) der auf dem A oder B Genom lokalisierten GWM einen Polymorphismus zwischen den Eltern ‘ATRI 5283’ (tolerant) und ‘ATRI 15010’ (sensitive). Diese wurden für die Kartierung der F_2 Population genutzt.
2) Unter Verwendung der 184 *gwm*-SSR Maker und 81 F_2 Pflanzen wurde eine Karte mittels Mapmaker Programm (F_2 Modell) konstruiert. Die Karte überspannt 2603,34 cM. Auf

dem A bzw. B Genom wurden 103 bzw. 81 *gwm* Marker kartiert. Auf den Chromosomen 6B, 4B, 2A, 3B und 7A konnten die meisten Marker Loci kartiert werden.

3) Der mittlere Abstand zwischen den Markern beträgt 15,17 cM.
4) Auf den Chromosomen 2A, 4B, 6B und 7A waren die Marker in Zentromerbereich geklustert.

5.2.3. Kartierung von QTLs für Trockentoleranz nach der Blüte

Die Kartierungspopulation bestand aus 81 F_3 Familien, hervorgegangen aus der Kreuzung zwischen 'ATRI 5283' und 'ATRI 15010'. Außerdem wurde die Trockentoleranz nach der Blüte bei dem sythetischen Sommerweizen 'W 7984', der mexikanischen Sommerweizensorte 'Opata 85' und insgesamt 114 rekombinanten Inzuchtlinien (RILs) einer Population der Internationalen Triticeae Mapping Initiative (ITMI) bestimmt.

5.2.3.1. Kartierung von QTLs für Halmreserve Mobilisierung

1) In beiden Kartierungspopulationen wurden kontinuierliche Verteilungen mit Transgressionen gefunden, wie man es für QTLs erwarten kann. Die kontinuierliche Verteilung des Merkmals Halmreserve Mobilisierung bestätigt den polygenen Charakter und die quantitative Vererbung. Die aufgefundenen Transgressionen weisen darauf hin, dass Genotypen mit erhöhter Halmreserve Mobilisierung und demzufolge erhöhtem Korngewicht unter Trockenstress nach der Blüte selektiert werden können.
2) Die QTLs für Trockenstress nach der Blüte wurden unter Verwendung des Programms *QGENE* identifiziert. In der 'ATRI 5283' x 'ATRI 15010' Population waren insgesamt sechs Mikrosatelliten Marker (*Xgwm497a, Xgwm480, Xgwm247, Xgwm251, Xgwm1011a* und *Xgwm611*) zu QTLs (bezeichnet mit *QSrm.ipk-1A, QSrm.ipk-3A, QSrm.ipk-3B, QSrm.ipk-4B, QSrm.ipk-6A* und *QSrm.ipk-7B*) gekoppelt. Diese waren auf den Chromosomen 1A, 3A, 3B, 4B, 6A bzw. 7B lokalisiert. Die phänotypische Varianz (%PV), errechnet für die einzelnen QTLs, betrug zwischen 13,41% und 24,74%. In der ITMI-Population waren acht RFLP und Mikrosatelliten Marker (*Xgwm357, Xmwg938b, Xgwm249a, Xgwm639c, Xfbb238b, Xgwm494, Xgwm302* und *Xfbb189b)* zu QTLs (bezeichnet mit *QSrm.ipk-1A, QSrm.ipk-1B, QSrm.ipk-2D, QSrm.ipk-5B, QSrm.ipk-5D, QSrm.ipk-6A, QSrm.ipk-7B* und *QSrm.ipk-7D*) gekoppelt. Die QTLs waren auf den Chromosomen 1A, 1B, 2D, 5B, 5D, 6A, 7B und 7D lokalisiert. Die phänotypische Varianz (%PV), errechnet für die einzelnen QTLs, betrug zwischen 10,17% und 42,22%.

3) In der ‘ATRI 5283’ x ‘ATRI 15010’ Population wurden ‘stabile’ QTLs auf den Chromosomen 3A, 4B und 7B lokalisiert. Drei weitere ‘stabile’ QTLs befanden sich auf den Chromosomen 2D, 5D und 7D in der ITMI-Population.

5.2.3.2. Kartierung von QTLs für vegetative Merkmale

1) Kontinuierliche Verteilungen mit Transgressionen wurden in beiden Kartierungspopulationen gefunden. Die kontinuierlichen Verteilungen der Merkmale Pflanzenlänge und Tage bis zur Blüte bestätigen den polygenen Charakter und die quantitative Vererbung beider Merkmale.
2) In den F_3 Familien der ‘ATRI 5283’ x ‘ATRI 15010’ Population wurden acht QTLs für Pflanzenlänge auf den Chromosomen 1A, 2A, 2B, 3A, 3B, 4A, 5A und 7A detektiert. Für das Merkmal Tage bis zur Blüte wurden vier QTLs auf den Chromosomen 1A, 2A, 3B und 7A identifiziert. Die phänotypische Varianz (%PV), errechnet für die einzelnen QTLs, betrug zwischen 12,08% und 22,96% für das Merkmal Pflanzenlänge und zwischen 12,37% und 23,33% für das Merkmal Tage bis zur Blüte. Die Analyse der ITMI Population führte zur Identifizierung von vier QTLs für Pflanzenlänge auf den Chromosomen 3B, 4D, 5A und 6D, während für das Merkmal Tage bis zur Blüte sieben QTLs auf den Chromosomen 1A, 2B, 3D, 5B, 5D, 7B und 7D gefunden wurden. Die phänotypische Varianz (%PV), errechnet für die einzelnen QTLs, betrug zwischen 15,91% und 30,01% für die Pflanzenlänge und zwischen 12,91% und 22,61% für die Tage bis zur Blüte.
3) Stabile QTLs konnten auf den Chromosomen 2A, 3A, 5A und 7A (Pflanzenlänge) und 2A, 3B und 7A (Tage bis zur Blüte) in der ‘ATRI 5283’ x ‘ATRI 15010’ Population gefunden werden. In der ITMI Population gab es nur einen stabilen QTL für Tage bis zur Blüte auf dem Chromosom 2B.

5.2.3.3. Kartierung von QTLs für Kornmerkmale

1) In beiden Kartierungspopulationen wurden kontinuierliche Verteilungen mit Transgressionen gefunden. Die kontinuierlichen Verteilungen der Kornmerkmale bestätigen den polygenen Charakter und die quantitative Vererbung.
2) Haupt-QTLs für Kornmerkmale wurden auf den Chromosomen 1A, 1B, 1D, 2A, 2B, 2D, 3B, 3D, 4A, 4B, 4D, 5A, 5B, 5D, 6A, 6B, 6D, 7A, 7B und 7D gefunden.

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7. APPENDIX

Appendix Table (1): Quantitative trait loci (QTLs) for abiotic stress tolerance

Trait	Species	Population	Type *	QTL	Reference
Specific root and shoot responses under drought					
Root traits	Rice	CT9993 x IR62266	DHL*	8	Kamoshita *et al.* (2002)
Tiller and root number, thickness, dry weight	Rice	CO39 x Moroberekan	RIL*	18	Champoux *et al.* (1995)
Root morphology and root distribution	Rice	IR64 x Azucena	DHL	39	Yadav *et al.* (1997)
Various root growth traits	Rice	Azucena x Bala	RIL	<24	Price *et al.*, (2002a)
Root length, number, thickness, penetration index	Rice	IR58821 x IR52561	RIL	28	Ali *et al.* (2000)
Root architecture and water acquisition	Lettuce	Salians x UC92G489	F_2	13	Johnson *et al.* (2000)
Root thickness, root penetration index	Rice	CT9993 x IR62266	DHL	5	Zhang *et al.* (2001)
Tiller and root number, penetration ability	Rice	CO39 x Moroberekan	RIL	39	Ray *et al.* (1996)
Root thickness, root penetration index	Rice	IR64 x Azucena	DHL	12	Zheng *et al.* (2000)
Roots traits and yield	Maize	Lo964 x Lo1016	F_3	<11	Tuberosa *et al.* (2002)
Yield and root traits under limited water	Rice	IR64 x Azucena	DHL		Venuprasad *et al.* (2002)
Osmotic adjustment					
Osmotic adjustment and dehydration tolerance	Rice	CO39 x Moroberekan	RIL	7	Lilley *et al.* (1996)
Osmoregulation under drought	Wheat	Songlen x Cobdor*4/3Ag14	RIL	1	Morgan and Tan (1996)
Osmotic adjustment under drought	Barley	Tadmor x Er/Amp	RIL	12	Teulat *et al.* (1998)
Osmotic adjustment under drought	Rice	CT9993 x IR62266	DHL	5	Zhang *et al.* (2001)
Whole plant drought tolerance					
Flowering parameters under drought, ASI	Maize	Ac7643S5 x Ac7729/TZSRWS5	F_2	7	Ribaut *et al.* (1996)

Plant height, ear number, days to silking, yield	Maize	SD34 x SD35	F_3	5	Agrama and Moussa (1996)
Morphological and physiological traits	Rice	IR64 x Azucena	DHL	15	Hemamalini *et al.* (2000)
Leaf rolling, leaf drying, RWC, growth rate	Rice	IR64 x Azucena	DHL	42	Courtois *et al.* (2000)
Dehydration avoidance traits	Rice	Bala x Azucena	RIL	17	Price *et al.* (2002b)
Grain yield and components under stress	Pearl millet	H77 x PRLT 2/89-33s	various		Yadav *et al.* (2002)
Yield, biomass, Osmotic adjustment, roots	Rice	CT9993 x IR62266	DHL	47	Chandra *et al.* (2003)
Hormonal responses under drought					
Abscisic acid concentration	Wheat	Chinese Spring x Ciano 67	DHL F_2	1	Quarrie *et al.* (1994)
Leaf size and ABA accumulation	Rice	IR20 x 63-83	F_2	17	Quarrie *et al.* (1997)
Leaf ABA concentration	Maize	Os420 x IABO78	F_3	16	Tuberosa *et al.* (1998)
Water-use and photosynthetic activity under drought					
WUE, RWC, Dry matter, carbon discrimination	*S. scabra*	CPI93116 x Fitzroy	F_2	36	Thumma *et al.* (2001)
Yield, maturity, water use efficiency	Soybean	Minsoy x Noir 1	RIL	3	Specht *et al.* (2001)
Photosynthesis and water status traits	Sunflower	PAC2 x RHA266	RIL	19	Hervé *et al.* (2001)
Vacuolar invertase activity	Maize	F_2 x I0	RIL	18	Pelleschi *et al.* (1999)
Cellular membrane stability (CMS)					
CMS under drought	Rice	CT9993 x IR62266	DHL	9	Tripathy *et al.* (2000)
Submergence/flooding tolerance					
Leaf and internode elongation under submergence	Rice	IR74 x Jalamagna	RIL	25	Sripongpangkul *et al.* (2000)
Submergence tolerance	Rice	IR74 x FR13A	RIL	4	Nandi *et al.* (1997)
Submergence tolerance	Rice	IR49830 x CR6241; FR13A x CT6241; JaoHom Nin x KDML105	DHL; RIL;F_2		Toojinda *et al.* (2003)

Submergence tolerance	Rice (Jasmine)	KDML105 x FR13A; IR67819; IR49830	BC	1	Siangliw *et al.* (2003)
Flooding survival	Wheat	Forno x Oberkulmer	RIL	5	St. Burgos *et al.* (2001)
Salinity tolerance					
Na^+, K^+ uptake and concentration	Rice	Nona Bokra x Pokkali //IR4630 x IR10167	RIL	16	Flowers *et al.* (2000)
Dry mass, Na^+, K^+ uptake, concentration and ratio	Rice	IR4630 x IR15324	RIL	25	Koyama *et al.* (2001)
Na+ K+ absorption	Rice		RIL	2	Bonilla *et al.* (2002)
Growth and germination	Arabidopsis	Columbia-4 x Landsberg erecta	RIL	Up to 11	Quesada *et al.* (2002)
Cold and chilling tolerance					
Winter hardiness, fall growth, freezing injury	Alfalfa	Blazer XL 17 x Peruvian 13	BC	14	Brouwer *et al.* (2000)
Shoot wilting and ammonium uptake	Tomato	TS5 x LA1778	BC	15	Truco *et al.* (2000)
Cold tolerance at the booting stage	Rice	Akihikari x Koshihikari	DHL	3	Takeuchi *et al.* (2001)
Cold Tolerance	Rice	Norin-PL8 x Silewah	NIL	2	Saito *et al.* (2001)
Chilling tolerance for spikelet sterility	Rice	M202 x IR50	RIL	2+	Andaya and Mackill (2003)
Freezing tolerance	Citrus	*C. grandis* x *P. trifoliata*	F_1	1+	Weber *et al.* (2003)
Photosynthesis under chilling stress	Maize	Ac7643 x Ac7729/TZSRW	RIL	8	Fracheboud *et al.* (2002)
Heat tolerance					
Heat tolerance in grain filling	Wheat	Ventor x Karl92	F_1, F_2, F_3	2	Yang *et al.* (2002)
Stay-green (non-senescence)					
Stay green, chlorophyll content	Sorghum	B35 x TX7000	RIL	13	Xu *et al.* (2000b)
Stay green under drought	Sorghum	QL39 x QL41	RIL	5	Tao *et al.* (2000)
Stay green, chlorophyll content	Sorghum	B35 x TX430	RIL	7	Crasta *et al.* (1999)

Stay green, pre-flowering drought stress	Sorghum	SC56 x TX7000	RIL	9	Kebede *et al.* (2001)
Stay green	Sorghum	B35 x Tx7000	RIL	4	Sanchez *et al.* (2002)
Stay green	Sorghum	IS9830 x E36-1 N13 x E36-1	RIL	5-8	Haussmann *et al.* (2002)
Stay green; chlorophyll content	Rice	Mutagenesis of Hwacheong-wr	Mutant	1	Cha *et al.* (2002)
Mineral Deficiency tolerance					
Manganese deficiency	Barley	Aagi Nijo x WI2585	F_2	1	Pallotta *et al.* (2000)
Manganese deficiency	Wheat	Stojocri 2 x Hazar	F_2	1	Khabaz-Saberi, *et al.* (2002)
Iron deficiency chlorosis (in the field)	Soybean	Pride B216 x A15, Anoka x A7	F_2	7, 4	Lin *et al.* (2000a)
Boron deficiency	Brassica napus	Qingyou10 x 'Bakow'	F_2	4	Xu *et al.* (2001)
Activity of acid phosphatase	Rice	IR20 x IR55178-3B-9-3	RIL	6	Hu *et al.* (2001)
Phosphorus uptake (PUP1)	Rice	Nipponbare x Kasalath	F_2/F_3 NIL	1	Wissuwa *et al.* (2002)
Mineral toxicity resistance					
Aluminum tolerance	Wheat	Bh1146 x Anahuac	RIL	1	Riede and Anderson (1996)
Aluminum tolerance	Rice	Azucena x IR1552	RIL	8	Wu *et al.* (2000)
Aluminum tolerance (relative root length)	Rice	IR64 x Oryza rufipogon	RIL	5	Nguyen *et al.* (2003)
Aluminum tolerance	Soybean	Young x PI416937	F_4	11	Bianchi-Hall *et al.* (2000)
Aluminum tolerance	Barley	Yambla x WB229	F_2	1	Raman *et al.* (2002)
Aluminum tolerance	Maize	Cat-100-6 x S1587-17	F_2	2	Sibov *et al.* (2000)
Aluminum tolerance	Rye	M39A-1-6 x M77A-1	RIL	3	Miftahudin *et al.* (2002)
Aluminum tolerance	Alfalfa	M. sativa subsp. coerulea	F_2	2	Sledge *et al.*, (2002)
Aluminum tolerance	Arabidopsis	Lansberg erecta	RIL	2	Kobayashi and

		x Columbia			Koyama (2002)
Boron tolerance (uptake, root length, shoot dry weight)	Barley	Sahara3771 x Clipper	DHL	4	Jefferies *et al*. (1999)
Iron Toxicity tolerance	Rice	Nipponbare x Kasalath	BC lines	4	Wan *et al*. (2003)
Manganese tolerance	Rice	Azucena x IR1552	RIL	8	Wang *et al*. (2002)

(*) DHL = doubled haploids; RILs = Recombinant inbred lines; BC = Back cross; BIL = Backcross recombinant inbred lines; NIL = Near-isogenic line

Appendix Table (2): Description of 184 wheat microsatellites, their annealing temperature, fragment size (bp), motif, repeats and chromosomal location

Microsatellite	Annealing Temperature	Fragment size in 'Chinese Spring' (bp)	Motif	Repeats	Chromosomal location
Xgwm0006	55 °C	205	GA	40	4B
Xgwm0018	50 °C	186	CA, TA	17, 4	1B
Xgwm0030	60 °C	206	AT, GT	19, 15	3A
Xgwm0033a	60 °C	123	GA	19	1A
Xgwm0071	60 °C	128	GT	20	2A
Xgwm0077	55 °C	153	CA,GAimp	10,38	3B
Xgwm0088	60 °C	121	GT	18	6B
Xgwm0095	60 °C	121	CA	16	2A
Xgwm0099	60 °C	119	CA	21	1A
Xgwm0107	60 °C	195	CT	21	4B
Xgwm0108	60 °C	132	GTimp	29	3B
Xgwm0112	55 °C	101	CTimp	29	7B
Xgwm0113	60 °C	148	GT	12	4B
Xgwm0114	60 °C	206(177)	GA	49	3B
Xgwm0126	60 °C	196	CA	15	5A
Xgwm0131	60 °C	131	CT	22	1B
Xgwm0133	60 °C	118	CT	36	6B
Xgwm0148	60 °C	163	CA	22	2B
Xgwm0162	60 °C	208	CA	18	3A
Xgwm0164	55 °C	120	CT	16	1A
Xgwm0179	55 °C	181	GT	15	5A
Xgwm0186	60 °C	140	GA	26	5A
Xgwm0191	60 °C	128	CT	19	2B, 6B
Xgwm0192	60 °C	191	CT	44	4B
Xgwm0193	60 °C	171	CT,CA	22, 9	6B
Xgwm0219	60 °C	181	GAimp	34	6B
Xgwm0247	60 °C	158	GA	24	3B
Xgwm0251	55 °C	103	CA	28	4B
Xgwm0274	50 °C	179	GT	27	1B
Xgwm0275	50 °C	107	CT	21	2A
Xgwm0294	55 °C	100	GAimp	9, 15	2A
Xgwm0297	55 °C	150	GT, GA	12, 18	7B
Xgwm0304	55 °C	217	CT	22	5A
Xgwm0333	55 °C	150	GA	19	7B
Xgwm0334	50 °C	123	GA	19	6A
Xgwm0339	50 °C	159	CT	22	2A
Xgwm0340	60 °C	132	GA	26	3B
Xgwm0350	55 °C	146	GT	14	7A
Xgwm0357	55 °C	123	GA	18	1A
Xgwm0359	55 °C	217	CT,CTTi	20, 13	2A
Xgwm0361	60 °C	126	GAi	35	6B

Xgwm0369	60 °C	188	CTi	32	3A
Xgwm0371	60 °C	170	CA, GA	10, 32	5B
Xgwm0374	60 °C	213	GT	17	2B
Xgwm0376	60 °C	147	CA, GAimp	16, 22	3B
Xgwm0382	60 °C	115	GA	26	2A, 2B
Xgwm0388	60 °C	162	CT,CA,CA	4,11,12	2B
Xgwm0389	60 °C	130	CT,GT	14, 16	3B
Xgwm0397	55 °C	179	CT	21	4A
Xgwm0400	60 °C	139	CA	21	7B
Xgwm0413	60 °C	94	GA	18	1B
Xgwm0415	55 °C	131	GAimp	25	5A
Xgwm0427	50 °C	215	CA	7, 22	6A
Xgwm0429	50 °C	221 (290)	CT	25	2B
Xgwm0459	55 °C	>138	GA	>28	6A
Xgwm0480	60 °C	188	CT, CA	16, 13	3A
Xgwm0493	60 °C	208	CAi	43	3B
Xgwm0495	60 °C	168	GA	20	4B
Xgwm0497	55 °C	>106	GTimp	24	1A
Xgwm0508	50 °C	165	GTimp	19	6B
Xgwm0512	60 °C	185	GT	16	2A
Xgwm0513	60 °C	144	CA	12	4B
Xgwm0515	60 °C	134	GTimp	17, 7	2A, 2D
Xgwm0518	55 °C	166	CA	34	6B
Xgwm0537	60 °C	209	CA, TA	18, 13	7B
Xgwm0540	55 °C	129	CTimp	19	5B
Xgwm0554	60 °C	160	CT,GTimp	13, 16	5B
Xgwm0558	55 °C	125	CA	15	2A
Xgwm0573	50 °C	212	CA	30	7A, 7B
Xgwm0577	55 °C	133	CA,TA	14, 6	7B
Xgwm0601	60 °C	148	CT	17	4A
Xgwm0604	50 °C	119	GA	29	5B
Xgwm0610	60 °C	168	GAi	17	4A
Xgwm0611	55 °C	168	GAi	32	7B
Xgwm0614	60 °C	152	Gai	23	2A
Xgwm0617	60 °C	131	GA	43	6A
Xgwm0626	50 °C	102	CT, GT	5, 13	6B
Xgwm0630	60 °C	120	GT	16	2B
Xgwm0631	60 °C	197	GT	23	7A
Xgwm0633	60 °C	136	CA	22	1A
Xgwm0635	60 °C	107	CA, GA	10, 14	7A
Xgwm0636	50 °C	110	GAi	28	2A
Xgwm0644	60 °C	166	GA	20	6B
Xgwm0666	60 °C	100	CA	13	7A
Xgwm0680	55 °C	123	GT, GAimp	8, 24	6B
Xgwm0685	47 °C	119	GT	29	3B
Xgwm0691	60 °C	154	CT	20	1A

Xgwm0698	60 °C	213	GA	44	7A
Xgwm0705	50 °C	97	GA	?	3B
Xgwm0726	50 °C	136	GT	35	2A
Xgwm0736	60 °C	187	TA,GA	5,4	4B
Xgwm0739	50 °C	158	CAimp	>49	2A
Xgwm0748	60 °C	131	CA	16	7A
Xgwm0750	60 °C	217	GA	21	1A
Xgwm0751	50 °C	126	CA, GA	13, 24	3A
Xgwm0752	55 °C	125	GT	26?	1A
Xgwm0757	60 °C	102	CA	22+8	3A
Xgwm0761	55 °C	100	CTimp	15+8	2A
Xgwm0768	60 °C	182	CT,CA	18,8	6B
Xgwm0771	50 °C	100	GT,Gimp	8, 18	6B
Xgwm0777	60 °C	113	CAimp	24	5B
Xgwm0778	60 °C	207	CAimp	24	1A
Xgwm0785	60 °C	134	GAimp	17	6B
Xgwm0786	60 °C	139	CT	32	6A
Xgwm0790	55 °C	215	CT	53	5B
Xgwm0802	60 °C	132	CA	25	3B
Xgwm0806	50 °C	136	CA	24	1B
Xgwm0810	60 °C	131	CT	16	5B
Xgwm0816	60 °C	194	GT	21	6B
Xgwm0817	47 °C	165	CA	24	2A
Xgwm0818	50 °C	149	CA	16	1B
Xgwm0825	55 °C	110	GA	28	6B
Xgwm0834	55 °C	225	CTimp, GT	42,6	7A
Xgwm0846	60 °C	121	GA	30	2B
Xgwm0853	60 °C	112	GT	20	3B
Xgwm0855	50 °C	155	GT	34	4A
Xgwm0856	50 °C	112	CTimp	28	4B
Xgwm0857	60 °C	186	GT	16,5	4B
Xgwm0870	50 °C	122	GT,CT	3,14	7A
Xgwm0871	60 °C	148	GT	16	7B
Xgwm0877	55 °C	101	CA	14	2B
Xgwm0888	60 °C	197	GTimp	20	4B
Xgwm0889	60 °C	142	CT	21	6B
Xgwm0890	50 °C	131	GT	39	7A
Xgwm0898	55 °C	104	GT	16	4B
Xgwm0910	55 °C	148	AT,GTimp	2,25	4B
Xgwm0921	60°C	213	GA	42	6B
Xgwm0925	60 °C	186	GAi	20, 9	4B
Xgwm0926	60 °C	193	GAimp, GT,CG	5,8,3	1B
Xgwm0929	55 °C	138	CA	19	4A
Xgwm0930	50°C	186	GT	12	4B
Xgwm0937	60 °C	162	CAimpGA	17,17	4A
Xgwm0938	55 °C	156	GA	29	3B

Xgwm0946	60°C		CT		4B
Xgwm0951	60 °C	155	GA	34	7B
Xgwm0972	50 °C	148	GT	12	2B
Xgwm0982	55 °C	131	GT,GA	7,19	5A
Xgwm0984	50 °C	228	GT, GA	22, 15	7A, 7B
Xgwm0998	55°C	199	GT	18	4B
Xgwm1009	55°C	95	CT	18	6A
Xgwm1011	60°C	121	GA	20	2A, 6A
Xgwm1015	50°C	149	GT	20	3B
Xgwm1016	60°C	147	GA	18	5B
Xgwm1017	55°C	262	GT	26	6A
Xgwm1025	55°C	140	GA	18	7B
Xgwm1027	60°C	135	CA	15	2B
Xgwm1029	60°C	217	CT	15?	3B
Xgwm1034	55°C	115	GA	24	3B
Xgwm1037	55°C	140	GA	35	3B
Xgwm1040	60°C	141	GA	13	6A
Xgwm1042	50°C	99	GA	23	3A
Xgwm1043	60°C	146	GA	23	5B
Xgwm1045	55°C	189	GT, GC, GA	17, 3, 19	2A
Xgwm1063	60°C	120	CT	20	3A
Xgwm1065	60°C	119	CA	22	7A
Xgwm1066	60°C	139	CA	17	7A
Xgwm1067	55°C	179	CA	12	2B
Xgwm1070	60°C	120	CA	31	2B
Xgwm1076	55°C	131	GA	21	6B
Xgwm1078	55°C	144	GT	20	1B
Xgwm1083	50°C	108	CA	22	7A
Xgwm1084	60°C	179	CT	37	4B
Xgwm1089	60°C	150	CA	27	6A
Xgwm1100	50°C	227	CA (CGCA)	9 (7)	1B
Xgwm1104	50°C	167	GT	13	1A
Xgwm1110	55°C	194	TA,TG	6,15	3A
Xgwm1111	55°C	150	GT	12	1A
Xgwm1165	60°C	139	CA	15	5B
Xgwm1184	55°C	142	CA,TA	17,7	7B
Xgwm1185	55°C	224	GT,CT,GT	8,3,7	6A
Xgwm1187	60°C	108	GT	12	7A
Xgwm1233	60°C	142	CT	12	6B
Xgwm1236	60°C	147	GA	29	5A
Xgwm1246	55°C	232	GA	40	5B
Xgwm1258	60°C	196	GA	28	7A
Xgwm1266	60°C	157	CT		3B
Xgwm1303	50°C	244	CA	15	7A
Xtaglgap	60°C	282	CAA	31	1B

Appendix Table (3): Stress tolerance index for 1000-grain weight in tetraploid and hexaploid wheats

Species	Accession/ Variety	Seasonality	Ploidy level	Origin	STI
T. turgidum	HTRI 4446	Winter	4x	Hungary	52,78
T. turgidum	HTRI 4270	Winter	4x	Italy	53,57
T. turgidum	HTRI 4461	Winter	4x	Europe	54,57
T. turgidum	HTRI 1781	Winter	4x	Germany	33,96
T. turgidum	HTRI 17446	Winter	4x	Germany	50,32
T. turgidum	HTRI 7099	Winter	4x	Europe	70,06
T. turgidum	HTRI 1782	Winter	4x	Germany	44,62
T. turgidum	ATRI 5283	Spring	4x	China	82,41
T. turgidum	ATRI 4341	Spring	4x	Europe	68,71
T. turgidum	ATRI 9548	Spring	4x	Armenia	68,71
T. turgidum	ATRI 9652	Spring	4x	Unknown	65,00
T. turgidum	ATRI 4082	Spring	4x	Portugal	37,83
T. turgidum	ATRI 3241	Spring	4x	Canada	68,76
T. turgidum	ATRI 3261	Spring	4x	Spain	65,67
T. turgidum	ATRI 3411	Spring	4x	USSR	65,91
T. turgidum	ATRI 4354	Spring	4x	Canada	62,20
T. turgidum	ATRI 5911	Spring	4x	Iran	58,33
T. turgidum	ATRI 5948	Spring	4x	Iran	61,71
T. turgidum	ATRI 5951	Spring	4x	Iran	74,33
T. turgidum	ATRI 17620	Spring	4x	Kazakhstan	80,23
T. turgidum	ATRI 4045	Spring	4x	Europe	63,54
T. durum	ATRI 9882	Spring	4x	Tunisia	77,70
T. durum	ATRI 17608	Spring	4x	Unknown	55,50
T. durum	ATRI 2719	Spring	4x	Iran	48,35
T. polonicum	ATRI 1896	Spring	4x	Unknown	87,78
T. polonicum	ATRI 1951	Spring	4x	Germany	59,48
T. turanicum	ATRI 6075	Spring	4x	Iran	42,25
T. petropavlovskyi	ATRI 12908	Spring	4x	Portugal	58,09
T. aestivum	Synthetic/N	Winter	6x	USA	78,46
T. aestivum	HTRI 4745	Winter	6x	UK	32,36
T. aestivum	HTRI 1634	Winter	6x	Albania	30,54
T. aestivum	HTRI 10204	Winter	6x	USA	36,56
T. aestivum	HTRI 11081	Winter	6x	USA	47,04
T. aestivum	HTRI 10197	Winter	6x	USA	30,37
T. aestivum	HTRI 10203	Winter	6x	USA	38,18
T. aestivum	HTRI 11445	Winter	6x	Unknown	25,72
T. aestivum	HTRI 10213	Winter	6x	USA	26,88
T. aestivum	HTRI 11449	Winter	6x	Unknown	33,11
T. aestivum	HTRI 11448	Winter	6x	Unknown	35,23
T. aestivum	HTRI 10216	Winter	6x	USA	33,53
T. aestivum	HTRI 11074	Winter	6x	USA	31,46

T. aestivum	HTRI 11437	Winter	6x	Unknown	22,26
T. aestivum	HTRI 6931	Winter	6x	USA	26,60
T. aestivum	HTRI 7965	Winter	6x	USA	31,79
T. aestivum	HTRI 11444	Winter	6x	Unknown	38,59
T. aestivum	HTRI 10210	Winter	6x	USA	34,33
T. aestivum	ATRI 637	Spring	6x	Greece	46,33
T. aestivum	ATRI 2094	Spring	6x	Greece	41,59
T. aestivum	ATRI 15010	Spring	6x	Ethiopia	46,81
T. aestivum	ATRI 16973	Spring	6x	Poland	33,53
T. aestivum	ATRI 16821	Spring	6x	Unknown	56,98
T. aestivum	ATRI 2732	Spring	6x	China	40,46
T. aestivum	ATRI 10427	Spring	6x	Mexico	39,67
T. aestivum	ATRI 11944	Spring	6x	Unknown	34,27
T. aestivum	ATRI 397	Spring	6x	USA	53,04
T. aestivum	ATRI 9723	Spring	6x	Canada	40,39
T. aestivum	ATRI 11085	Spring	6x	Australia	48,09
T. aestivum	ATRI 9890	Spring	6x	Germany	42,71
T. aestivum	ATRI 11944	Spring	6x	Iran	49,74
T. aestivum	ATRI 9715	Spring	6x	Pakistan	35,28
T. aestivum	Chinese Spring/N	Spring	6x	Unknown	42,62
T. aestivum	Miriam	Spring	6x	Unknown	33,57
T. aestivum	Weaver	Spring	6x	Unknown	41,99
T. aestivum	Giza 144	Spring	6x	Egypt	31,47
T. aestivum	Yecora Rojo	Spring	6x	Unknown	44,00
T. aestivum	Opata 85	Spring	6x	Mexico	33,37
T. aestivum	W 7984	Spring	6x	Mexico	70,80
T. aestivum	Saratoskaya 29	Spring	6x	USSR	44,04
T. aestivum	Yanetzki Probat	Spring	6x	Germany	41,77
T. aestivum	Capelle-Desprez	Winter	6x	France	30,29
T. aestivum	Bezostaya	Winter	6x	Russia	31,13
T. aestivum	Apollo	Winter	6x	Germany	45,72
T. aestivum	Spark	Winter	6x	UK	33,34
T. aestivum	Soissons	Winter	6x	UK	44,07
T. aestivum	Rialto	Winter	6x	UK	48,65
T. aestivum	DwarfA	Winter	6x	UK	35,99
T. aestivum	Fiorello	Winter	6x	Argentina	32,40

Appendix Table (4): Phenotypic variation of grain characters of ‘ATRI 5283’ and ‘ATRI 15010’ from two environments

Character	**Environment**	**Parents**	
		‘ATRI 5283’	**‘ATRI 15010’**
Grain area (STI %)	2002	81.18	76.57
	2003	96.67	88.87
Grain length (STI %)	2002	91.96	88.46
	2003	98.24	95.49
Grain width (STI %)	2002	85.85	85.53
	2003	99.82	91.46
Grain circumference (STI %)	2002	91.52	88.13
	2003	98.82	95.19
Grain roundness (STI %)	2002	99.51	98.54
	2003	99.03	97.85
Grain form density factor (STI %)	2002	99.06	60.27
	2003	80.27	64.95

Appendix Table (5): Putative QTLs detected for stem reserve mobilization in wheat F_3 families of the cross 'ATRI 5283' x 'ATRI 15010'.

Trait	QTL symbol	Marker	Chromosome	Gatersleben Field		LOD[a]	%PV[b]	Additive[d]	Source
				2002	2003				
1000-grain weight STI% (*Srm*)	*QSrm.ipk-1A*	*Xgwm497a*	1A	ns	**-[c]	2.67	22.60	-15.69	ATRI 15010
	QSrm.ipk-3A	*Xgwm480*	3A	**-	*-	2.18	13.93	-5.45	ATRI 15010
	QSrm.ipk-3B	*Xgwm247*	3B	***+	ns	3.27	24.74	15.94	ATRI 5283
	QSrm.ipk-4B	*Xgwm251*	4B	***+	*+	3.47	20.39	6.28	ATRI 5283
	QSrm.ipk-6A	*Xgwm1011a*	6A	**+	ns	2.16	13.41	9.85	ATRI 5283
	QSrm.ipk-7B	*Xgwm611*	7B	*+	**+	2.31	20.23	9.19	ATRI 5283

Significance levels: * P<0.1; ** P<0.01; *** P<0.001; **** P<0.0001

[a]LOD score from the year with underlined P-value

[b] % PV is the proportion of the phenotypic variance explained by the QTL after accounting for co-factors

[c] Underlined P-value indicates year for which LOD, % PV and additive were calculated

[d] +/- Additive effects indicate an additive main effect of the parent contributing the higher value allele: positive values indicate that higher value alleles are from 'ATRI 5283' and the negative values indicate that higher value alleles are from 'ATRI 15010'

Appendix Table (6): Putative QTLs detected for vegetative traits in wheat F_3 families of the cross 'ATRI 5283' x 'ATRI 15010'.

Trait	QTL symbol	Marker	Chromosome	Gatersleben Field		LOD[a]	%PV[b]	Additive[d]	Source
				2002	2003				
Plant height (*Ht*)	*QHt.ipk-1A*	*Xgwm357*	1A	**+[c]	ns	2.80	16.61	9.77	ATRI 5283
	QHt.ipk-2A	*Xgwm761*	2A	**-	***-	3.64	22.12	-13.62	ATRI 15010
	QHt.ipk-2B	*Xgwm877a*	2B	**-	ns	2.15	13.54	-18.59	ATRI 15010
	QHt.ipk-3A	*Xgwm1042*	3A	**-	*-	2.41	14.29	-20.70	ATRI 15010
	QHt.ipk-3B	*Xgwm802*	3B	ns	**-	2.34	15.28	-9.97	ATRI 15010
	QHt.ipk-4A	*Xgwm601*	4A	**+	ns	2.27	13.53	9.12	ATRI 5283
	QHt.ipk-5A	*Xgwm179*	5A	*-	*-	2.01	12.08	-17.04	ATRI 15010
	QHt.ipk-7A	*Xgwm1258c*	7A	***-	***-	4.08	22.96	-17.92	ATRI 15010
Flowering time (*Flt*)	*QFlt.ipk-1A*	*Xgwm357*	1A	*-	ns	2.04	12.37	-1.36	ATRI 15010
	QFlt.ipk-2A	*Xgwm515a*	2A	*-	**-	2.39	16.04	-1.45	ATRI 15010
	QFlt.ipk-3B	*Xgwm802*	3B	*+	***+	3.69	23.33	2.48	ATRI 5283
	QFlt.ipk-7A	*Xgwm890*	7A	**+	**+	3.04	17.89	1.60	ATRI 5283

Significance levels: * $P<0.1$; ** $P<0.01$; *** $P<0.001$; **** $P<0.0001$

[a]LOD score from the year with underlined *P*-value

[b] % PV is the proportion of the phenotypic variance explained by the QTL after accounting for co-factors

[c] Underlined *P*-value indicates year for which LOD, % PV and additive were calculated

[d] +/- Additive effects indicate an additive main effect of the parent contributing the higher value allele: positive values indicate that higher value alleles are from 'ATRI 5283' and the negative values indicate that higher value alleles are from 'ATRI 15010'

Appendix Table (7): Putative QTLs detected for grain area, grain width and grain length in wheat F_3 families of the cross 'ATRI 5283' x 'ATRI 15010'.

Trait	QTL symbol	Marker	Chromosome	Gatersleben Field		LOD[a]	%PV[b]	Additive[d]	Source
				2002	2003				
Grain area STI% (*Gae*)	*QGae.ipk-1A*	*Xgwm752*	1A	ns	***+ [c]	3.80	23.92	4.61	ATRI 5283
	QGae.ipk-2B	*Xgwm191b*	2B	**-	ns	2.91	20.01	-6.22	ATRI 15010
	QGae.ipk-4A	*Xgwm610*	4A	**-	ns	3.07	18.77	-6.16	ATRI 15010
	QGae.ipk-5B	*Xgwm1165*	5B	ns	***+	4.11	24.93	3.77	ATRI 5283
	QGae.ipk-6A	*Xgwm786*	6A	**-	ns	2.12	13.40	-3.50	ATRI 15010
	QGae.ipk-6B	*Xgwm816*	6B	ns	***-	3.67	22.60	-4.29	ATRI 15010
Grain width STI% (*Gwd*)	*QGwd.ipk-1A*	*Xgwm752*	1A	ns	**+	2.31	15.32	2.67	ATRI 5283
	QGwd.ipk-2B	*Xgwm846d*	2B	**-	ns	2.68	16.80	-3.87	ATRI 15010
	QGwd.ipk-4A	*Xgwm610*	4A	**-	ns	2.12	13.91	-3.52	ATRI 15010
	QGwd.ipk-5B	*Xgwm1165*	5B	ns	***+	4.15	25.16	2.83	ATRI 5283
Grain length STI% (*Glt*)	*QGlt.ipk-1A*	*Xgwm633*	1A	ns	**+	2.35	15.12	2.09	ATRI 5283
	QGlt.ipk-1B	*Xgwm1078*	1B	ns	**-	2.20	15.28	-3.69	ATRI 15010
	QGlt.ipk-2A	*Xgwm512*	2A	ns	**+	2.60	17.57	4.33	ATRI 5283
	QGlt.ipk-4A	*Xgwm610*	4A	**-	ns	2.74	16.92	-3.64	ATRI 15010
	QGlt.ipk-6A	*Xgwm427*	6A	**+	ns	2.81	17.80	2.22	ATRI 5283
	QGlt.ipk-6B	*Xgwm816*	6B	ns	***-	4.20	25.39	-2.89	ATRI 15010
	QGlt.ipk-7A	*Xgwm1066*	7A	**-	ns	2.47	15.39	-1.79	ATRI 15010
	QGlt.ipk-7B	*Xgwm611*	7B	**-	ns	2.36	15.16	-2.16	ATRI 15010

Significance levels: * P<0.1; ** P<0.01; *** P<0.001; **** P<0.0001

[a]LOD score from the year with underlined P-value

[b] % PV is the proportion of the phenotypic variance explained by the QTL after accounting for co-factors

[c] Underlined P-value indicates year for which LOD, % PV and additive were calculated

[d] +/- Additive effects indicate an additive main effect of the parent contributing the higher value allele: positive values indicate that higher value alleles are from 'ATRI 5283' and the negative values indicate that higher value alleles are from 'ATRI 15010'

Appendix Table (8): Putative QTLs detected for grain circumference, grain roundness and grain form density factor in wheat F_3 families of the cross 'ATRI 5283' x 'ATRI 15010'.

Trait	QTL symbol	Marker	Chromosome	Gatersleben Field		LOD[a]	%PV[b]	Additive[d]	Source
				2002	2003				
Grain circumference STI % (*Gcc*)	*QGcc.ipk-1A*	*Xgwm752*	1A	ns	**+ [c]	2.94	19.06	2.18	ATRI 5283
	QGcc.ipk-1B	*Xgwm274a*	1B	**-	ns	2.27	14.46	-1.85	ATRI 15010
	QGcc.ipk-2A	*Xgwm359*	2A	*-	ns	2.03	13.04	-4.45	ATRI 15010
	QGcc.ipk-4A	*Xgwm610*	4A	**-	**-	2.78	17.40	-3.21	ATRI 15010
	QGcc.ipk-5B	*Xgwm1165*	5B	ns	*+	2.08	13.51	1.43	ATRI 5283
	QGcc.ipk-6A	*Xgwm786*	6A	**-	ns	2.34	14.85	-2.00	ATRI 15010
	QGcc.ipk-6B	*Xgwm816*	6B	ns	****-	5.10	29.92	-2.69	ATRI 15010
	QGcc.ipk-7A	*Xgwm1303*	7A	ns	**-	2.22	14.38	-1.85	ATRI 15010
	QGcc.ipk-7B	*Xgwm611*	7B	**-	ns	2.28	14.91	-1.89	ATRI 15010
Grain roundness STI % (*Grs*)	*QGrs.ipk-4B*	*Xgwm736a*	4B	ns	**+	2.87	18.14	3.38	ATRI 5283
	QGrs.ipk-5B	*Xgwm540*	5B	**-	ns	2.37	15.05	-1.63	ATRI 15010
	QGrs.ipk-7A	*Xgwm573b*	7A	ns	*+	2.08	13.72	5.49	ATRI 5283
Grain form density factor STI % (*Gdf*)	*QGdf.ipk-2A*	*Xgwm726*	2A	**+	ns	2.40	15.01	6.01	ATRI 5283
	QGdf.ipk-3B	*Xgwm247*	3B	**+	*+	2.69	20.81	13.69	ATRI 5283
	QGdf.ipk-4B	*Xgwm251*	4B	***+	ns	3.77	22.55	6.60	ATRI 5283
	QGdf.ipk-6A	*Xgwm1011a*	6A	**+	ns	2.91	18.12	11.29	ATRI 5283
	QGdf.ipk-7B	*Xgwm611*	7B	ns	**+	2.50	23.02	12.91	ATRI 5283

Significance levels: * $P<0.1$; ** $P<0.01$; *** $P<0.001$; **** $P<0.0001$

[a] LOD score from the year with underlined *P*-value

[b] % PV is the proportion of the phenotypic variance explained by the QTL after accounting for co-factors

[c] Underlined *P*-value indicates year for which LOD, % PV and additive were calculated

[d] +/- Additive effects indicate an additive main effect of the parent contributing the higher value allele: positive values indicate that higher value alleles are from 'ATRI 5283' and the negative values indicate that higher value alleles are from 'ATRI 15010'

Appendix Table (9) Phenotypic variation of grain characters of ‘W 7984’ and ‘Opata 85’ from two environments

Traits	**Environment**	**Parents**	
		‘W 7984’	**‘Opata 85’**
Grain area (STI%)	2001	99.80	73.51
	2003	85.33	75.43
Grain length (STI%)	2001	99.71	96.49
	2003	94.07	93.77
Grain width (STI%)	2001	98.72	74.91
	2003	90.29	81.32
Grain circumference (STI%)	2001	98.46	92.39
	2003	92.91	91.01
Grain roundness (STI%)	2001	97.29	86.33
	2003	99.14	90.43
Grain density factor (STI%)	2001	97.76	47.70
	2003	88.19	66.71

Appendix Table (10): Putative QTLs detected for stem reserve mobilization in wheat RILs population of the cross 'W 7984' x 'Opata 85'

Trait	QTL symbol	Marker	Chromosome	Gatersleben Field		LOD[a]	%PV[b]	Additive[d]	Source
				2001	2003				
1000-grain weight STI% (*Srm*)	*QSrm.ipk-1A*	*Xgwm357*	1A	**- [c]	ns	1.52	11.21	-6.24	Opata 85
	QSrm.ipk-1B	*Xmwg938b*	1B	**-	ns	2.19	10.17	-5.89	Opata 85
	QSrm.ipk-2D	*Xgwm249a*	2D	*+	***+	3.10	42.22	6.94	W 7984
	QSrm.ipk-5B	*Xgwm639c*	5B	**+	ns	1.61	11.13	6.36	W 7984
	QSrm.ipk-5D	*Xfbb238b*	5D	*+	**+	2.45	37.54	6.17	W 7984
	QSrm.ipk-6A	*Xgwm494*	6A	ns	**-	1.79	15.51	-3.87	Opata 85
	QSrm.ipk-7B	*Xgwm302*	7B	ns	***-	3.15	24.75	-4.62	Opata 85
	QSrm.ipk-7D	*Xfbb189b*	7D	***+	*+	2.77	21.01	8.18	W 7984

Significance levels: * P<0.1; ** P<0.01; *** P<0.001; **** P<0.0001

[a]LOD score from the year with underlined P-value

[b] % PV is the proportion of the phenotypic variance explained by the QTL after accounting for co-factors

[c] Underlined P-value indicates year for which LOD, % PV and additive were calculated

[d] +/- Additive effects indicate an additive main effect of the parent contributing the higher value allele: positive values indicate that higher value alleles are from 'W 7984' and the negative values indicate that higher value alleles are from 'Opata 85'

Appendix Table (11): Putative QTLs detected for vegetative traits in wheat RILs population of the cross 'W 7984' x 'Opata 85'

Trait	QTL symbol	Marker	Chromosome	Gatersleben Field		LOD[a]	%PV[b]	Additive[d]	Source
				2001	2003				
Plant height (*Ht*)	*QHt.ipk-3B*	*Xcdo460c*	3B	No data	***+[c]	2.59	22.86	4.22	W 7984
	QHt.ipk-4D	*Xbcd15b*	4D	No data	**-	1.96	15.91	-4.08	Opata 85
	QHt.ipk-5A	*Xbcd1235b*	5A	No data	**+	1.78	14.62	3.93	W 7984
	QHt.ipk-6D	*Xfba085a*	6D	No data	**-	2.17	30.01	-5.26	Opata 85
Flowering time (*Flt*)	*QFlt.ipk-1A*	*Xgwm497a*	1A	ns	**+	1.70	17.78	0.91	W 7984
	QFlt.ipk-2B	*Xcdo405b*	2B	***-	*-	2.97	12.91	-1.47	Opata 85
	QFlt.ipk-3D	*Xcdo1435a*	3D	ns	***-	2.73	22.61	-0.82	Opata 85
	QFlt.ipk-5B	*Xbcd9*	5B	ns	**-	1.69	13.65	-0.63	Opata 85
	QFlt.ipk-5D	*Xbcd450a*	5D	****+	ns	4.93	18.19	1.87	W 7984
	QFlt.ipk-7B	*Xgwm569a*	7B	ns	**+	2.22	19.51	0.79	W 7984
	QFlt.ipk-7D	*Xgwm295*	7D	**-	ns	1.89	13.31	-1.46	Opata 85

Significance levels: * $P<0.1$; ** $P<0.01$; *** $P<0.001$; **** $P<0.0001$

[a]LOD score from the year with underlined *P*-value

[b] % PV is the proportion of the phenotypic variance explained by the QTL after accounting for co-factors

[c] Underlined *P*-value indicates year for which LOD, % PV and additive were calculated

[d] +/- Additive effects indicate an additive main effect of the parent contributing the higher value allele: positive values indicate that higher value alleles are from 'W 7984' and the negative values indicate that higher value alleles are from 'Opata 85'

Appendix Table (12): Putative QTLs detected for grain area, grain width and grain length in wheat RILs population of the cross 'W 7984' x 'Opata 85'.

Trait	QTL symbol	Marker	Chromosome	Gatersleben Field		LOD[a]	%PV[b]	Additive[d]	Source
				2001	2003				
Grain area STI% (*Gae*)	*QGae.ipk-1A*	*Xgwm357*	1A	**- [c]	ns	1.80	13.29	-3.13	Opata 85
	QGae.ipk-1B	*Xmwg938b*	1B	**-	ns	1.94	9.06	-2.59	Opata 85
	QGae.ipk-2D	*Xbcd260a*	2D	**+	*+	1.90	7.57	2.31	W 7984
	QGae.ipk-4D	*Xbcd15b*	4D	ns	**+	1.54	13.00	1.34	W 7984
	QGae.ipk-6B	*Xrz995*	6B	ns	**-	1.93	19.04	-1.62	Opata 85
	QGae.ipk-7D	*Xgwm1052b*	7D	**+	ns	1.72	11.00	3.06	W 7984
Grain width STI% (*Gwd*)	*QGwd.ipk-1B*	*Xmwg938b*	1B	**-	ns	2.07	9.64	-2.22	Opata 85
	QGwd.ipk-1D	*Xcdo89a*	1D	ns	**-	2.17	17.48	-2.19	Opata 85
	QGwd.ipk-3D	*Xgdm8*	3D	**+	ns	1.68	11.75	2.57	W 7984
	QGwd.ipk-5A	*Xgwm156*	5A	**-	ns	1.59	11.66	-2.86	Opata 85
	QGwd.ipk-5B	*Xgwm639c*	5B	**+	ns	1.73	12.08	2.63	W 7984
	QGwd.ipk-5D	*Xbcd450a*	5D	**+	ns	1.52	6.15	1.83	W 7984
	QGwd.ipk-6D	*Xksug48a*	6D	ns	**+	1.85	15.39	1.94	W 7984
	QGwd.ipk-7D	*Xgwm37*	7D	**+	ns	2.40	13.70	2.65	W 7984
Grain length STI% (*Glt*)	*QGlt.ipk-2D*	*Xbcd260a*	2D	***+	ns	2.61	10.27	1.04	W 7984
	QGlt.ipk-3D	*Xcdo549*	3D	**-	ns	1.60	6.46	-0.82	Opata 85
	QGlt.ipk-4D	*Xmwg634a*	4D	**+	ns	1.50	6.35	0.83	W 7984
	QGlt.ipk-5A	*Xbcd1871b*	5A	**-	ns	1.97	7.85	-0.91	Opata 85
	QGlt.ipk-7A	*Xfba127a*	7A	**+	ns	1.82	14.16	1.23	W 7984
	QGlt.ipk-7D	*Xgdm46*	7D	***+	ns	2.78	17.37	1.42	W 7984

Significance levels: * $P<0.1$; ** $P<0.01$; *** $P<0.001$; **** $P<0.0001$

[a]LOD score from the year with underlined *P*-value

[b] % PV is the proportion of the phenotypic variance explained by the QTL after accounting for co-factors

[c] Underlined *P*-value indicates year for which LOD, % PV and additive were calculated

[d] +/- Additive effects indicate an additive main effect of the parent contributing the higher value allele: positive values indicate that higher value alleles are from 'W 7984' and the negative values indicate that higher value alleles are from 'Opata 85'

Appendix Table (13): Putative QTLs detected for grain circumference, grain roundness and grain form density factor in wheat RILs population of the cross 'W 7984' x 'Opata 85'.

Trait	QTL symbol	Marker	Chromosome	Gatersleben Field		LOD[a]	%PV[b]	Additive[d]	Source
				2001	2003				
Grain circumference STI% (*Gcc*)	*QGcc.ipk-1A*	*Xgwm357*	1A	**-[c]	ns	1.87	13.77	-1.31	Opata 85
	QGcc.ipk-2B	*Xmwg950*	2B	ns	**-	2.37	19.24	-0.81	Opata 85
	QGcc.ipk-2D	*Xbcd260a*	2D	***+	ns	2.57	10.10	1.10	W 7984
	QGcc.ipk-5B	*Xgwm68a*	5B	ns	**-	1.80	17.52	-0.76	Opata 85
	QGcc.ipk-5D	*Xgwm269*	5D	ns	**-	1.80	17.51	-0.79	Opata 85
	QGcc.ipk-6B	*Xgwm70*	6B	**-	ns	1.68	12.47	-1.25	Opata 85
	QGcc.ipk-7D	*Xgdm46*	7D	**+	ns	1.93	12.42	1.33	W 7984
Grain roundness STI % (*Grs*)	*QGrs.ipk-1B*	*Xgwm582b*	1B	**+	**+	2.14	16.12	1.83	W 7984
	QGrs.ipk-3D	*Xgwm645*	3D	**-	ns	1.74	17.79	-1.89	Opata 85
	QGrs.ipk-5A	*Xgwm156*	5A	**+	ns	2.02	14.56	1.94	W 7984
	QGrs.ipk-5D	*Xbcd450a*	5D	**-	ns	1.71	6.92	-1.29	Opata 85
	QGrs.ipk-7D	*Xgwm37*	7D	***-	ns	3.61	19.87	-1.95	Opata 85
Grain form density factor STI % (*Gdf*)	*QGdf.ipk-1B*	*Xmwg938b*	1B	**-	ns	1.95	9.12	-4.52	Opata 85
	QGdf.ipk-2D	*Xgwm249a*	2D	*+	***+	3.17	42.99	6.96	W 7984
	QGdf.ipk-5D	*Xfbb238b*	5D	**+	**+	2.46	37.59	6.38	W 7984
	QGdf.ipk-6A	*Xfba085b*	6A	*-	**-	1.76	25.95	-5.18	Opata 85
	QGdf.ipk-7B	*Xgwm302*	7B	ns	***-	3.13	24.65	-4.66	Opata 85
	QGdf.ipk-7D	*Xgwm37*	7D	**+	**+	2.34	13.39	5.49	W 7984

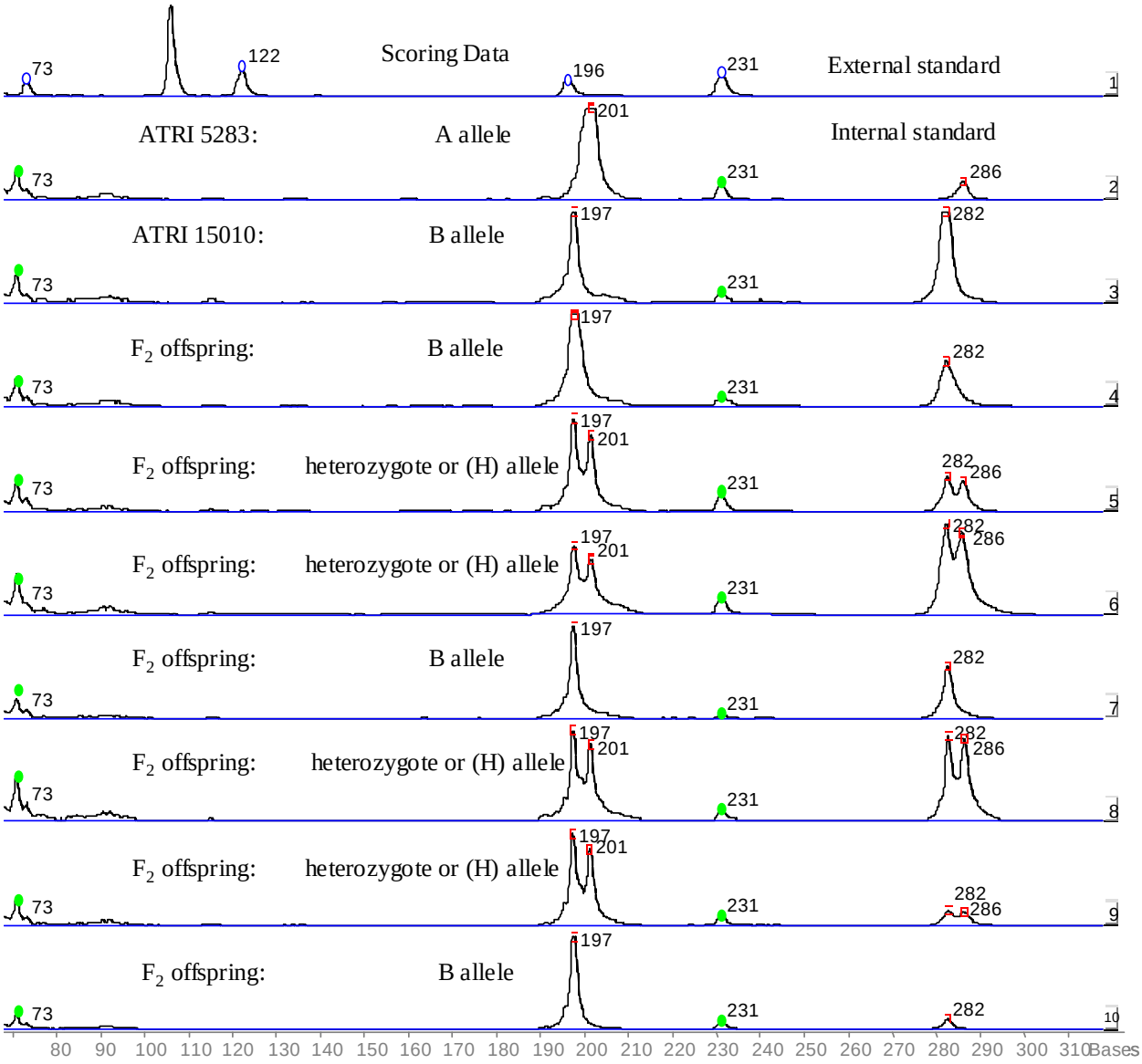
Significance levels: * $P<0.1$; ** $P<0.01$; *** $P<0.001$; **** $P<0.0001$

[a]LOD score from the year with underlined *P*-value

[b] % PV is the proportion of the phenotypic variance explained by the QTL after accounting for co-factors

[c] Underlined *P*-value indicates year for which LOD, % PV and additive were calculated

[d] +/- Additive effects indicate an additive main effect of the parent contributing the higher value allele: positive values indicate that higher value alleles are from 'W 7984' and the negative values indicate that higher value alleles are from 'Opata 85'



Appendix Figure (1): Electropherograms analysed using Fragment Analyser software version 1.02, of polymorphic microsatellite markers in two parental lines ('ATRI 5283' x 'ATRI 15010') and F_2 offspring, amplified with the SSR marker locus *gwm429*. The fragments were assigned to the short arm of chromosome 2BS. The peaks represent fragments of different alleles, whereas the horizontal scale indicates fragment sizes in base pairs calculated from internal standards (73 bp and 231 bp)

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ERKLÄRUNG

Hiermit erkläre ich, dass mit dieser wissenschaftlichen Arbeit noch keine vergeblichen Promotionsversuche unternommen wurden.

Die eingereichte Dissertation mit dem Thema: 'The Inheritance and Molecular Mapping of Genes for Post-anthesis Drought Tolerance (PADT) in Wheat' habe ich selbständig und nur unter Verwendung der angegeben Literatur und Hilfsmittel angefertigt.

Des weiteren erkläre ich, dass keine Strafverfahren gegen mich anhängig sind.

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3. **Salem K. F. M.** and A. Börner. (2003). Evaluation of wheat accessions from Gatersleben Genebank for post-anthesis drought tolerance in field. In: Gesellschaft für Pflanzenzüchtung, GPZ-Tagung, Vortragsveranstaltung zum Thema: "Abiotischer Streß – Herausforderung für die Pflanzenzüchtung'', 11-12 Juni 2003, Groß Lüsewitz, Germany.

4. **Salem K. F. M.**; Marion Röder and A. Börner. (2003). Mapping of quantitative trait loci (QTLs) for post-anthesis drought tolerance in bread wheat (*Triticum aestivum* L.). (2003). In: Gesellschaft für Pflanzenzüchtung, GPZ-Tagung, 11. Vortragsveranstaltung "Harnessing Genetic Diversity: Genomics and Allele Mining''., 16-17.09.2003, Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK), Gatersleben, Germany.

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