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Molecular mapping of genomic regions associated with wheat seedling growth under osmotic stress

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Abstract

A quantitative trait loci (QTL) approach was applied to dissect the genetic control of the common wheat seedling response to osmotic stress. A set of 114 recombinant inbred lines was subjected to osmotic stress from the onset of germination to the 8th day of seedling development, induced by the presence of 12 % polyethylene glycol. Root, coleoptile and shoot length, and root/shoot length ratio were compared under stress and control conditions. In all, 35 QTL mapping to ten chromosomes, were identified. Sixteen QTL were detected in controls, 17 under stressed conditions, and two tolerance index QTL were determined. The majority of the QTL were not stress-specific. In regions on five chromosome arms (1AS, 1BL, 2DS, 5BL and 6BL) the QTL identified under stress co-mapped with QTL affecting the same trait in controls, and these were classified as seedling vigour QTL, in addition to those expressed in controls. Tolerance-related QTL were detected on four chromosome arms. A broad region on chromosome 1AL, including five QTL, with a major impact of the gene *Glu-A1* (LOD 3.93) and marker locus *Xksuh9d* (LOD 2.91), positively affected root length under stress and tolerance index for root length, respectively. A major QTL (LOD 3.60), associated with marker locus *Xcdo456a* (distal part of chromosome arm 2BS) determined a tolerance index for shoot length. Three minor QTL (LOD < 3.0) for root length and root/shoot length ratio under osmotic stress were identified in the distal parts of chromosome arms 6DL (marker locus *Xksud27a*) and 7DL (marker locus *Xksue3b*). Selecting for the favourable alleles at marker loci associated with the detected QTL for growth traits may represent an efficient approach to enhance the plants' ability to maintain the growth of roots, coleoptile and shoots in drought-prone soils at the critical early developmental stages.

Additional key words: drought, germination, ITMI, polyethylene glycol, quantitative trait loci, tolerance index, *Triticum aestivum*.

Introduction

Seed germination and early seedling growth are considered to be the most critical stages for wheat establishment, especially under stress (Blum 1996). In continental climate environments, autumn-sown wheat frequently experiences early season drought stress. Water deficiency interferes with cellular activity, induces numerous metabolic changes, and inhibits growth (Kerepesi and Galiba 2000, Nayyar 2003/4, Liu *et al.* 2006). Early setbacks can go on to inhibit subsequent growth and development, and may finally result in a significant reduction in yield. The basis of drought tolerance is particularly complex and is thought to involve many morphological and physiological components (*e.g.* Yordanov *et al.* 2003). Plant growth in normal conditions and growth response to stress are under polygenic control, with each gene having only a relatively small effect. The quantitative trait loci (QTL) mapping approach (Collard *et al.* 2005) allows the dissection of the genetic basis of quantitative traits. In wheat, it has been successfully applied as a tool for the genetic analysis of a growing number agronomically important traits (Sourdille *et al.* 1996, 2000, Perretant *et al.* 2000, Börner *et al.* 2002, Lohwasser *et al.* 2005), disease resistance (Nelson *et al.* 1997, Anderson *et al.* 2001, Simón *et al.* 2004, Faris and Friesen 2005, Schmolke *et al.* 2005) and abiotic stress tolerance (Galiba *et al.* 2005, Bálint *et al.* 2007).

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Abbreviations: IA - interval analysis; Cl, Rl, Sl - coleoptile, root and shoot length, respectively; ITMI - International *Triticeae* Mapping Initiative; LOD - logarithm of odds; PEG - polyethylene glycol; QTL - quantitative trait locus; RFLP - restriction fragment length polymorphism; RILs - recombinant inbred lines; RSR - root/shoot length ratio; SMA - single marker analysis; SSR - simple sequence repeats; TI - tolerance index
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The analysis of plant performance in a simulated environment can help identify tolerance-related traits, since this approach avoids much of the environmental noise associated with field experiments. High molecular mass polyethylene glycol (PEG) has been widely used to mimic osmotic stress in culture solutions (Almansouri *et al.* 2001). PEG treatment induces a plant response similar to that induced by natural drought, by, for example, causing a depression in seed germination, seedling vigour, and root and shoot growth (Blum *et al.* 1980, Dhanda *et al.* 2004, Mujtaba *et al.* 2005). Our objective was to perform a QTL analysis of the growth response of wheat seedlings under PEG-induced osmotic stress to identify which chromosome regions are associated with the ability of seedlings to maintain the growth of roots, coleoptiles and shoots under drought stress.

Materials and methods

Experimental material: A set of 114 recombinant inbred lines (RILs) derived from the cross between the spring common wheat (*Triticum aestivum* L.) cv. Opata 85 and the synthetic hexaploid wheat W7984 (the so-called "ITMI mapping population") was analysed. W7984 was the product of an interspecific cross between *Aegilops tauschii* (the D genome donor of hexaploid wheat) and the durum wheat cv. Altar 84. The genetic map deduced from this population is one of the densest available in the public domain, with a total length of 3551cM, including over 1000 restriction fragment length polymorphism (RFLP) (Nelson *et al*. 1995a,b,c, Van Deynze *et al.* 1995, Marino *et al.* 1996) and 800 single sequence repeats (SSR; Röder *et al.* 1998, Röder *et al.* unpublished results) loci.

Osmotic stress tests: Eight seeds per recombinant inbred line (RIL) were placed in covered transparent plastic boxes on two layers of filter paper moistened with 12 % PEG 6000, and held in a growth chamber at 21 ± 1 °C in the dark for 3 d, followed by 5 d at a 12-h photoperiod (irradiance of 200 μmol m^{-2} s^{-1}). A control treatment was carried out using distilled water instead of PEG. The root length (Rl), coleoptile length (Cl), shoot length (Sl) and root/shoot length ratio (RSR) of five seedlings per RIL were measured on the eighth day. A tolerance index (TI) was defined for Rl, Cl, Sl and RSR as the ratio between the mean trait value obtained under stress and the corresponding trait value under control. Three independent replicates of the experiment were conducted. Statistical analysis of the data (analysis of variance and correlation analysis) was performed for each replicate and for the mean values over the three replicates.

QTL analysis: The presence of a QTL was determined with the *QGene* software package (Nelson 1997) using single marker analysis (SMA) to identify markers significantly associated with phenotypic variation, or interval mapping analysis (IA) to define the chromosome regions having a major impact on the trait assessed. For each trait, analyses were carried out separately on each replicate, as well as on the mean values across the replicates. The QTL obtained were classified into major (LOD > 3.0) and minor (LOD 2.0 - 3.0) ones. The existence of a QTL was declared when a significant ($P < 0.01$) marker/trait association was recorded in at least two of the three replicates. The relatively low LOD threshold was used to differentiate between a QTL for a given trait identified either in control, or in stressed conditions but co-mapping with the same trait QTL in the control (referred to hereinafter as a seedling vigour QTL) and QTL expressed only under stress (tolerance-related QTL).

Results

Analysis of phenotypic data: The PEG treatment induced a reduction in growth parameters Rl, Sl and RSR, but an increase in Cl (Table 1). Although the parental differences were non-significant under both control and stressed conditions, the analysis of variance identified significant differences among the RILs. The

Table 1. Growth characteristics of wheat seedlings in the parents and the set of RILs of the ITMI mapping population determined in control and after 8-d treatment with 12 % PEG.

Length [cm]	Control					PEG-treatment					Tolerance Index				
	Opata 85	W7984	RILs			Opata 85	W7984	RILs			Opata 85	W7984	RILs		
			Max	Min	Average			Max	Min	Average			Max	Min	Average
Root	15.88	15.77	19.46	10.34	16.26±1.65	11.71	10.36	16.39	7.13	11.82±1.62	0.74	0.66	0.90	0.42	0.73±0.07
Coleoptile	3.19	3.17	4.00	2.45	3.05±0.24	3.18	3.58	4.21	2.67	3.34±0.26	1.00	1.13	1.23	0.97	1.10±0.05
Shoot	10.84	11.45	14.67	8.79	11.88±1.08	8.55	8.04	12.89	6.94	9.71±1.03	0.79	0.70	0.98	0.70	0.82±0.06
Root/shoot	1.46	1.38	1.67	0.96	1.37±0.11	1.37	1.30	1.59	0.71	1.22±0.15	0.93	0.95	1.21	0.54	0.90±0.10

Table 2. Summary of QTL detected by single marker analysis affecting growth characteristics of wheat seedlings of the ITMI mapping population in control (distilled water) and under osmotic stress (12 % PEG).* - $P < 0.01$, ** - $P < 0.001$; [a]QTLs, for which LOD > 2.0 was obtained by interval analysis.

Trait	QTL symbol	Chromosome	Max LOD	*F*-value	R^2	Nearest flanking marker	Additive effect	Source
Root length in control (*Rlc*)	*QRlc.ipk-5B*	5BL	1.91[a]	8.97*	0.08	*Xam72c*	0.49	W7984
Root length in PEG (*Rlp*)	*QRlp.ipk-1A*	1AL	3.93	19.42**	0.16	*Glu1A*	-0.77	Opata 85
		1AL	2.59	12.39**	0.11	*Xmwg55*	-0.68	Opata 85
		1AL	2.50	11.93**	0.10	*Xbcd265a*	-0.62	Opata 85
		1AL	2.23	10.57*	0.09	*Xcdo312b*	-0.59	Opata 85
	QRlp.ipk-6D	6DL	1.92[a]	9.03*	0.07	*Xksud27a*	-0.49	Opata 85
	QRlp.ipk-7D	7DL	2.39	11.40**	0.10	*Xksue3b*	-0.59	Opata 85
Root length TI under PEG (*Rltip*)	*QRltip.ipk-1A*	1AL	2.05	9.69*	0.08	*Xksuh9d*	-0.02	Opata 85
Coleoptile length in control (*Clc*)	*QClc.ipk-1A*	1AS	1.63[a]	7.62*	0.07	*Xabc156c*	0.07	W7984
	QClc.ipk-1B.1	1BL	2.01	9.49*	0.08	*Xdo1173*	-0.08	Opata 85
	QClc.ipk-1B.2	1BL	2.39	11.37**	0.10	*Xbcd1150a*	-0.07	Opata 85
	QClc.ipk-6B	6BL	3.09	14.91**	0.12	*Xksug30*	-0.09	Opata 85
	QClc.ipk-7D	7DL	1.82[a]	8.74*	0.14	*Xfbb079*	-0.10	Opata 85
Coleoptile length in PEG (*Clp*)	*QClp.ipk-1A*	1AS	2.13	10.08*	0.09	*Xabc156c*	0.09	W7984
		1AS	2.03	9.59*	0.08	*Xksue18D*	0.07	W7984
	QClp.ipk-1B	1BL	3.28	15.91**	0.13	*Xdo1173*	-0.11	Opata 85
	QClp.ipk-6B	6BL	3.34	16.29**	0.14	*Xwg341*	-0.10	Opata 85
		6BL	2.57	12.28**	0.10	*Xksug30*	-0.10	Opata 85
Shoot length in control (*Slc*)	*QSlc.ipk-2D*	2DS	3.85	18.87**	0.14	*Xcdo1379*	0.47	W7984
		2DS	3.60	17.53**	0.14	*Xcdo1479*	0.46	W7984
		2DS	3.50	17.01**	0.14	*Xbcd262*	0.46	W7984
		2DS	2.41	11.48**	0.10	*Xcdo405a*	0.37	W7984
	QSlc.ipk-5B	5BL	2.10	9.90*	0.08	*Xwg889*	0.32	W7984
Shoot length in PEG (*Slp*)	*QSlp.ipk-2D*	2DS	3.29	15.93**	0.12	*Xcdo1479*	0.39	W7984
		2DS	3.16	15.24**	0.12	*Xbcd262*	0.39	W7984
		2DS	2.74	13.11**	0.10	*Xcdo1379*	0.36	W7984
	QSlp.ipk-5B	5BL	2.04	9.64*	0.08	*Xwg889*	0.33	W7984
Shoot length TI under PEG (*Sltip*)	*QSltip.ipk-2B*	2BS	2.80	13.43**	0.11	*Xcdo456a*	-0.02	Opata 85
Root/shoot in control (*RSRc*)	*QRSRc.ipk-2A*	2AL	2.01	9.49*	0.08	*Xksue16*	0.03	W7984
	QRSRc.ipk-2D	2DS	2.66	12.70**	0.10	*Xcdo1379*	-0.04	Opata 85
		2DS	2.26	10.72*	0.09	*Xcdo1479*	-0.04	Opata 85
	QRSRc.ipk-3D.1	3DL	2.23	10.58*	0.09	*Xmwg688*	0.03	W7984
	QRSRc.ipk-3D.2	3DL	2.27	11.08**	0.17	*Xfbb269*	0.05	W7984
Root/shoot in PEG (*RSRp*)	*QRSRp.ipk-2D*	2DS	2.08	9.81*	0.08	*Xcdo1379*	-0.04	Opata 85
	QRSRp.ipk-6D	6DL	2.89	13.89**	0.11	*Xksud27a*	-0.05	Opata 85

traits measured in the control treatment were significantly correlated with one another, with a coefficient of correlation ranging from 0.25 for Rl-Cl ($P < 0.01$) to 0.64 for Rl-Sl ($P < 0.001$). Under the PEG-induced drought condition, the correlations between the traits were still significant, but lower in value – from 0.18 for Cl-Sl ($P < 0.05$) to 0.51 for Rl-Sl ($P < 0.01$), while the correlations relating to each trait when measured in control and stressed conditions were highly significant – from 0.73 for Rl ($P < 0.001$) to 0.85 for Cl ($P < 0.001$).

QTL mapping: A summary of all the significant QTL detected using SMA is given in Table 2. The chromosome regions containing individual QTL or a cluster of QTL associated with adjacent markers are illustrated in Fig. 1, which displays the highest LOD value for each trait/marker association, whether obtained by SMA or by IA. In particular, the LOD score obtained by IA was higher in cases where a wide chromosome region affects the trait, accompanied with a large gap in the genetic map (*e.g.* on 1AL and 2DS). The IA detected four minor QTL on chromosome arms 1AS, 5BL, 6DL and 7DL in addition to those identified by SMA.

In all, 35 QTL for seedling growth traits were identified by SMA, of which nine were major ones. Almost half of the QTL (16) were detected in controls, 17 under stress and two QTL were determined for tolerance index. The QTL were distributed across ten chromosomes, ranging from a single QTL mapping to chromosome 2B, to ten located on chromosome 2D.

More QTL were located on D-genome chromosomes (16) than on either the B (ten) or the A (nine) genomes. The contribution of individual QTL to the overall phenotypic variation was low, ranging from 7 to 17 %. For each of the genomic regions identified, the flanking marker alleles allowed the parent contributing the positive QTL allele to be identified. Thus the majority of the QTL enhancing root and coleoptile growth were derived from Opata 85, while most of those with positive effects on shoot growth came from W7984. Almost all the tolerance-related QTL were derived from Opata 85. Seedling vigour QTL were present on chromosome arms 1AS, 1BL, 2AL, 2DS, 3DL, 5BL, 6BL and 7DL, of which those on 1AS, 1BL, 2DS, 5BL and 6BL were expressed in both stressed and controlled non-stressed conditions. The tolerance-related QTL were detected on 1AL, 2BS, 6DL and 7DL. The QTL identified are described below.

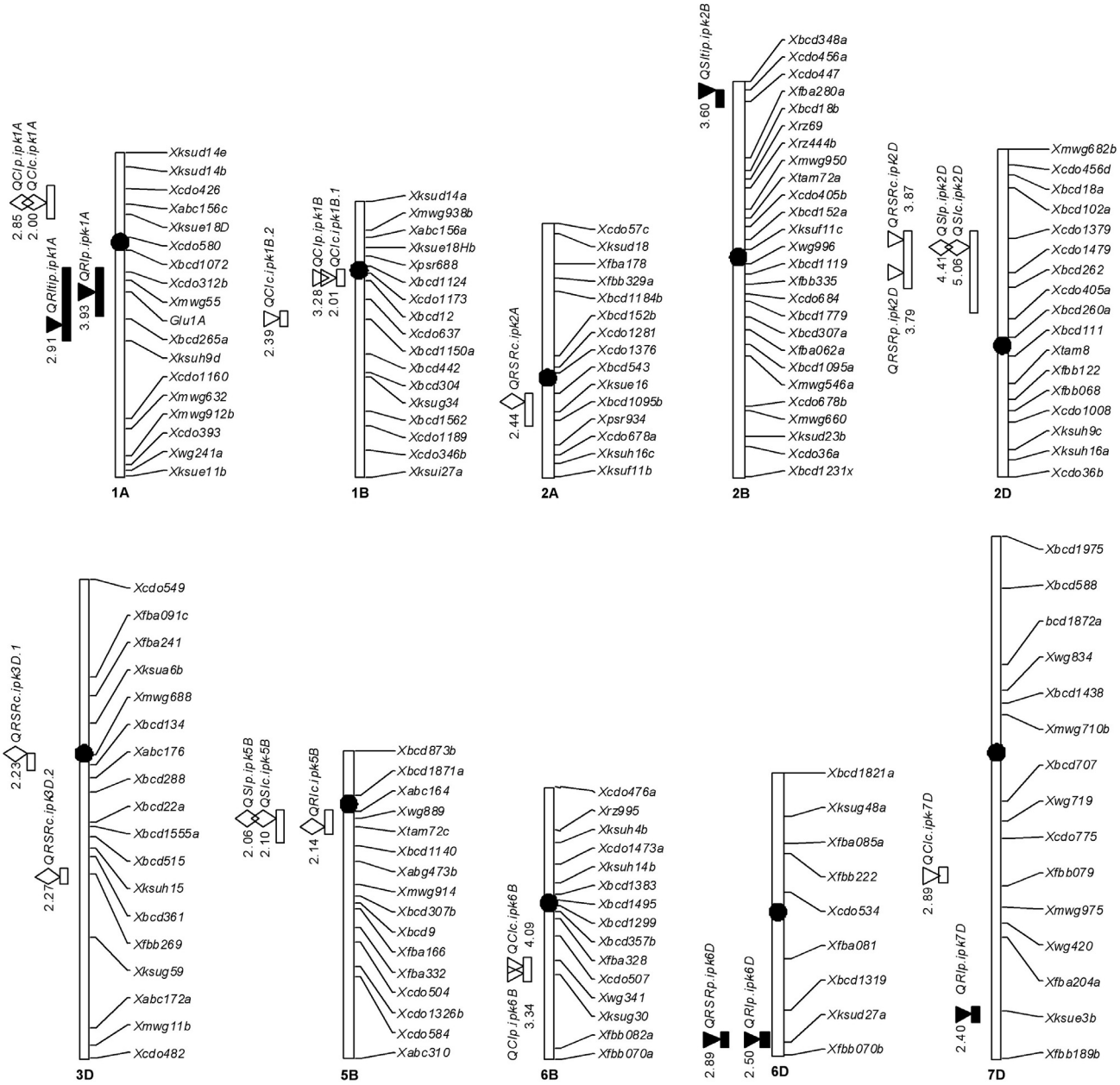

Fig. 1. Chromosomal regions affecting the growth characteristics of wheat seedlings of the ITMI mapping population in control (distilled water) and under osmotic stress (12 % PEG). *Vertical bars* represent QTL clusters, or depict influential chromosome regions as determined by interval analysis. The most significant marker/trait association is presented by the max LOD score, obtained either by single marker analysis, or by interval analysis. Tolerance related QTL regions and seedling vigour QTL regions are depicted, respectively, in black and white. The contribution of the mapping parents Opata 85 and W7984 is indicated by a *triangle* and a *diamond*, respectively. The QTL abbreviations are detailed in Table 2.

Root length: One QTL in the non-stressed treatment was detected on chromosome 5BL with relatively low LOD score (denoted as *Rlc*, Table 2, Fig. 1). For the same trait measured under osmotic stress conditions, six *Rlp* QTL were detected on chromosomes 1A, 6D and 7D, which together explain 63 % of the phenotypic variation. The *Rlp* region on chromosome arm 1AL was large enough to include four distinct QTL between the marker loci *Xcdo312b* and *Xbcd265a*. The QTL with the highest LOD score (3.93) in this region was associated with the gene *Glu-A1,* accounting for 16 % of the phenotypic variation.

Coleoptile length: QTL in the non-stressed treatment (*Clc*) were identified on chromosome arms 1AS, 1BL (two loci, one close to the centromere), 6BL and 7DL. These five QTL were responsible for 51 % of the phenotypic variation for coleoptile length. Five *Clp* QTL with a higher LOD score than that associated with the *Clc* were identified in three of these genomic regions (on 1AS, 1BL, the one close to the centromere, and 6BL).

Shoot length: Five *Slc* QTL mapped to the two chromosome arms 2DS and 5BL, explaining 60 % of the phenotypic variation. A cluster of three major and one minor QTL was present on chromosome arm 2DS defined by the interval between the marker loci *Xcdo1379* and *Xcdo405a*. The four *Slp* QTL mapped to chromosome arms 2DS and 5BL, and accounted for 42 % of the phenotypic variation. The *Slp* QTL cluster on 2DS overlap with the *Slc* region with highest LOD score QTL linked to the marker loci *Xcdo1479* and *Xbcd262* as detected by the SMA. According to the IA the most potent *Slc* and *Slp* QTL were both closer to the marker locus *Xcdo1379.*

Root/shoot length ratio: Five *RSRc* QTL were identified, mapping to chromosome arms 2AL, 2DS (two loci) and 3DL (two loci), explaining 53 % of the phenotypic variation. The most potent QTL (17 % of the variation), albeit associated with a relatively low LOD score (2.27), co-segregated with the marker locus *Xfbb269* on chromosome arm 3DL. A single *RSRp* QTL was located on both chromosome arms 2DS and 6DL, explaining only 19 % of the phenotypic variation.

Tolerance index: Only two tolerance index QTL were identified: one was a minor *Rltip* QTL for root length mapping to chromosome arm 1AL in the region of marker locus *Xksuh9d*, and overlapping with the *Rlp* region as identified by the IA; the other was a major *Sltip* QTL for shoot length located in the distal region of 2BS, associated with marker locus *Xcdo456a.*

Discussion

Drought has a large influence on plant growth during germination, and the vegetative and the reproductive stages. At each stage, it acts as a constraint to crop productivity. However, drought occurring at the early developmental stages has been largely neglected in studies of drought tolerance. The effects of abiotic stress on plant growth at germination and the early seedling stage have been described for wheat (Mujtaba *et al.* 2005), pea (Okçu *et al.* 2005), rice (Pirdashti *et al.* 2003), and oat (Willenborg *et al.* 2005), although much of these analyses was confined to an assessment of the physiological effects of osmotic stress. The inhibitory effect of PEG treatment on the growth of roots and shoots that we have observed agrees well with the documented negative effects of osmotic stress, which are brought about by a disturbance of cell metabolism. Unexpectedly, we have noted an enhancement of coleoptile growth under drought stress. The process of seed germination is under the control of numerous genes (McCarty 1995, Bewley 1997), whose expression may be differentially modulated by osmotic stress, thereby affecting the rate of early seedling growth. At the same time, the plant's response to the imposition of abiotic stress results from the activation of complex signal transduction networks (Shinozaki *et al.* 1999, Bartels and Souer 2003). Thus stress-induced coleoptile elongation is probably associated with tissue-specific hormone signalling and merits additional investigation.

Drought tolerance is recognized to be a complex quantitative trait involving a wide range of morphological, physiological and biochemical responses, which can be expressed at various stages of plant development. Since the root is responsible for the uptake of water, a selection for longer roots should bolster the efficiency with which limited soil water can be exploited by the plant. The ability to form a long coleoptile under drought stress has been suggested to be a significant component of drought tolerance, since it favours rapid seedling emergence and also allows the option of deeper sowing. In addition, plants able to maintain shoot growth under stress accelerate the process of ground cover, thereby minimizing soil water evaporation (Reinolds *et al.* 2000). The expression of numerous genes is affected by dehydration (Bartels and Souer 2003), and this hinders the identification of genes and/or chromosome regions of priority which genuinely confer stress tolerance. The present study has revealed that a substantial number of QTL, spread over ten chromosomes, is involved in governing the seedling growth response to osmotic stress. Thus the tolerance to osmotic stress, as defined by the plant capacity to maintain the growth of roots, coleoptiles and shoots under stress, is a very complex trait. In rice, the majority of the chromosomal regions identified as containing drought tolerance-related QTL also carried

QTL conditioning root morphology (Champoux *et al.* 1995). In maize, the genetic control of root characteristics under non-stressed conditions involves QTL for seminal root traits, and these were generally found to overlap with QTL for grain yield under field drought conditions (Tuberosa *et al.* 2002). Thus the selection for favourable alleles affecting root characteristics may be an effective strategy to achieve a drought tolerant plant. Of interest in this context is the cluster of root growth QTL expressed in conditions of osmotic stress on chromosome arm 1AL, and the QTL affecting root growth or the root/shoot length ratio on chromosome arms 6DL and 7DL. In the *Triticeae*, QTL for drought tolerance component traits have been localized at rather similar positions on group 1 (long arm) and group 7 chromosomes, and at various positions on the group 6 chromosomes (Cattivelli *et al.* 2002). These latter QTL were identified from materials at a later developmental stage, and may therefore operate via a different set of tolerance mechanisms.

A complex set of factors, both genetic and environmental, acts to determine coleoptile length (Botwright *et al.* 2001). Among the major genetic contributors is the semi-dwarfing *Rht-B1* locus. Rebetzke *et al.* (2001) have identified a major QTL coinciding with *Rht-B1* on chromosome arm 4BS, which accounts for up to 45 % of the genotypic variation in coleoptile length across a range of temperatures; and a further major coleoptile length QTL, located close to the marker locus *XksuC2* on chromosome arm 4BL, which accounted for up to 27 % of the variation. Earlier genetic analyses have shown that final coleoptile length is controlled by genes on chromosomes 1A, 4A, 4D, 5A and 5B, with a major influence of group 5 chromosomes (Matsui *et al.* 1998). The seedling vigour QTL for coleoptile length we have detected were located on chromosomes 1A, 1B, 6B and 7D, while no QTL were mapped to the *Rht-B1* region. Both Opata 85 and Altar 84 carry the dwarfing allele *Rht-B1b* (Worland *et al.* 1998, Börner unpublished), so no genetic variation is expected at this locus. However, our analyses suggest that both a coleoptile length QTL under PEG stress (LOD < 2.0) and a tolerance index QTL (LOD > 2.0) may be present on chromosome arm 4BL in the region between the marker loci *Xbcd1265* and *Xfbb178,* where the second coleoptile length QTL on 4B has been identified (Rebetzke *et al.* 2001) (data not shown since the detected QTL did not fully conform with the here accepted definition of a QTL.)

High seedling vigour is a pre-requisite for performance under stress. Clusters of seedling vigour QTL were identified on chromosome arms 2DS and 5BL in agreement with the determined trait correlations. The major cluster on 2DS coincides with the region which contains both the *Ppd-1* genes, controlling the response of wheat to day length (Worland *et al.* 1997) and QTL for heading and flowering time (Börner *et al.* 2002). Thus the genetic segment between marker loci *Xcdo1379* and *Xbc262* appears to be associated with a suite of genes governing plant development and adaptation at various phenological stages. Drought tolerance component traits have been mapped to various regions of the group 2 chromosomes (both the short arm and the distal part of the long arm) (Cattivelli *et al.* 2002). The second major cluster of seedling vigour QTL is on chromosome arm 5BL. A comparative analysis of chromosome regions involved in resistance to abiotic stress in the cereals has shown a key role for the group 5 chromosomes, where many of the QTL and major genes controlling adaptive traits such as heading time and frost resistance are located. The region linked to the marker locus *Xwg889* is also associated with tolerance to drought, salt and cold stress (Cattivelli *et al.* 2002).

We have presented an attempt to dissect the genetic control of early seedling traits that benefit the performance of wheat under osmotic stress. Selecting for favourable alleles at marker loci associated with growth trait QTL detected may represent an efficient approach to enhance the plant ability to maintain the growth of roots, coleoptile and shoots in drought-prone soils at the critical early developmental stages.

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Tracheary elements (S. Turner *et al*.) are important for transport of water and solutes in plants; these elements are specifically differentiated and finally form a network. Studies on model systems (Zinnia, trees, *Arabidopsis*) enabled to identify the respective genes, and analyse biosynthesis of components and development and functions of these elements. *Populus* (S. Jansson and C.J. Douglas) offers a model for studying wood formation, long term growth, flowering, biotic interactions and evolution, genotypic and phenotypic variability, *etc*.

Heterotrimeric G-protein complexes (mostly only two) in plants (B.R.S. Temple and A.M. Jones) couple extracellular signals *via* cell surface receptors to enzymes called effectors. Pre-messenger RNAs are alternatively spliced (A.S.N. Reddy) which is controlled by some regulators or stresses; this mechanism has its role in photosynthesis, defence against pathogens, induction of flowering, and grain formation of optimum quality. The review of P.A. Rea deals with ABC proteins of *Arabidopsis* and rice, the so-called ATP-binding cassette; these membrane proteins mediate transmembrane transport and function in polar auxin transport, lipid catabolism, xenobiotic detoxification, disease resistance, and stomatal functions. During biotic or abiotic stresses, ROS and reactive nitrogen species (I.M. Møller *et al*.) are produced in cells and may modify cells and damage their components (fatty acids, DNA, saccharides, proteins, *etc*.).

Genetic engineering has enabled the generation of seeds synthesizing non-native fatty acids (the so-called industrial fatty acids and very long chain polyunsaturated fatty acids). Transgenic plants thus offer production of demanded plant oils; the related mechanisms are explained in a review written by J.A. Napier. Auto-polyploidy and allopolyploidy (Z.J. Chen) are features that are very useful in plant breeding but often cause various instabilities, imbalances, and failures. The respective mechanisms and induced changes of gene expression and phenotype variation are evaluated.

All reviews are clearly arranged, important parts (abstract, summary points, future issues) have colour (yellow, grey) backgrounds, figures are often printed in colour, and in many reviews the most important references are printed in bold with supplemented explanation. Schemes on end-papers vividly show how to use electronic versions of Annual Reviews – by sending e-mail to authors, printing PDF article, downloading metadata to a citation manager, enlarging figures, linking references to source articles, *etc*. This valid source of information on modern topics of plant biology is a must for every library dealing with biochemistry, physiology, and genetics of plants.

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