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Location of a gene regulating drought-induced abscisic acid production on the long arm of chromosome 5A of wheat

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Abstract The accumulation of abscisic acid (ABA) by detached and partially dehydrated wheat leaves is known to be inherited in a quantitative manner. The location of genes having a major effect on drought-induced ABA accumulation in wheat was determined using a set of single chromosome substitution lines and populations derived from a cross between a high-ABA- and a low-ABA-producing genotype. Examination of a series of chromosome substitution lines of the high-ABA genotype 'Ciano 67' into the low-ABA recipient 'Chinese Spring' showed that chromosome 5A carries gene(s) that have a major influence on ABA accumulation in a drought test with detached and partially dehydrated leaves (DLT). A similar DLT was used to examine ABA accumulation in a population of F_2 plants and doubled haploid (DH) lines derived from the cross between 'Chinese Spring' (low-ABA) and 'SQ1' (high-ABA) in which the F_2 population (139 plants) and DH lines (96 lines) were also mapped partially with molecular markers. Analysis of variance of ABA accumulation between and within marker allele classes in the F_2 confirmed the location of a gene(s) regulating ABA accumulation on the long arm of chromosome 5A. MAPMAKER-QTL showed the most likely position for the ABA quantitative trait locus (QTL) to be between the loci *Xpsr575* and *Xpsr426*, about 8 cM from *Xpsr426*. A similar trend for high ABA accumulation was found in DH lines having the 'SQ1' allele at marker loci in the same region of chromosome 5AL, but the QTL effect was not significant. The function of the QTL is discussed.

Key words Abscisic acid · Drought stress · Quantitative trait locus (QTL) · Wheat

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Introduction

Physiological and biochemical responses to environmental stresses have been studied for many years to attempt to identify traits that confer an improved tolerance or adaptation to specific stresses, such as [^{13}C]-discrimination (e.g. Ehdaie et al. 1991), osmotic adjustment (Morgan 1984) and proline production (Singh et al. 1972). A major biochemical response to a wide spectrum of abiotic stresses is the increased production of the hormone abscisic acid (ABA). This has been best studied in relation to drought stress in cereals, where ABA has been shown to regulate many processes of growth and development (Hall and McWha 1981; Quarrie and Jones 1977; Quarrie 1982, 1984). In general, increased tissue ABA concentrations make the plant better adapted to withstand the effects of water shortage (Hall and McWha 1981; Mizrahi et al. 1974; Quarrie 1984; Watts et al. 1981). There is evidence from studies on wheat populations differing in ABA production that high-ABA-producing genotypes may outyield low-ABA-producing genotypes under some drought conditions (Innes et al. 1984). However, it is clear from the distributions of ABA content within segregating populations of wheat (Quarrie 1981, 1990) that the capacity for ABA accumulation is not simply inherited, but that several quantitative trait loci (QTL) are likely to regulate expression of the trait.

With the recent development of molecular markers for many crop species, including wheat (Devos and Gale 1993), it is now possible to construct closely-spaced genetic maps of a particular genome using an appropriate mapping population of plants. These maps allow the minimum number and location of QTL for any trait measured in the mapping population to be determined (e.g. Paterson et al. 1991). We have used this approach to locate a major QTL regulating ABA production in response to drought

stress in populations of wheat plants derived from crosses between two genotypes that differ markedly in drought-induced ABA production: 'Chinese Spring', low ABA (Quarrie 1981), and 'SQ1', high ABA (Quarrie et al. 1994). Preliminary information on the likely chromosomal location of genes affecting ABA accumulation was obtained by studying drought-induced ABA accumulation in a set of single chromosome substitution lines.

Materials and methods

ABA accumulation in chromosome substitution lines

Genetic stocks

The spring wheat genotypes (*Triticum aestivum* L.) 'Chinese Spring' (CS) and 'Ciano 67' were shown to differ in ABA accumulation in a detached-leaf drought test (Quarrie 1981). Genotypes tested in this experiment were the 21 lines derived by substituting each of the 'Ciano 67' chromosomes into a CS background and the donor, 'Ciano 67', and recipient, CS.

Plant growth, treatment and ABA analysis

Plants were grown in pots in a controlled environment cabinet exactly as described in Henson and Quarrie (1981). Within 1 day of the appearance of the ligule of leaf 4 of the main stem, leaf 4 was cut off, dehydrated to 90% fresh weight with the aid of laboratory air blowers and incubated in the dark in humidified tubes at 20°C for 6 h as described in Henson and Quarrie (1981). Leaves were frozen and subsequently assayed for ABA as described by Quarrie (1978). Six replicate leaves of each genotype were given the drought treatment and assayed.

QTL analysis of ABA accumulation

Genetic stocks

The genotypes tested for ABA accumulation were the low-ABA genotype CS and high-ABA genotype 'SQ1' (a sibling line at F_7 of line 25/3/2 from the cross 'Highbury'×'TW269', Quarrie 1981, 1990, 1991), 139 F_2 plants and 48 doubled haploid (DH) lines derived from the cross 'Chinese Spring' (CS)×'SQ1'. The DH lines are part of a mapping population of 96 lines developed by pollinating emasculated ears of F_1 plants of CS×'SQ1' with pollen from maize or pearl millet (Laurie and Reymondie 1991).

Plant growth and treatments

In the F_2 experiment, the parents and F_2 plants were grown in a controlled environment cabinet operating at 16°C continuously with a 16-h photoperiod of approximately 350 μmol m^{-2} s^{-1} (440–700 nm) provided by 400 W metal halide and tungsten lamps at a relative humidity of 65–70%. Plants were grown in 9-cm-diameter pots containing a John Innes No. 2 compost made with Osmocote slow release fertiliser and with the pH adjusted to approximately 7.2 with added lime. Leaf 4 of the main stem of the parents and F_2 plants was sampled at ligule emergence and given the detached-leaf test (DLT) for drought-induced ABA accumulation as described above, except that leaf incubation took place at 16°–20°C.

In the experiment with the DH lines, plants were grown in the same compost in 5-cm-deep seed trays with the cabinet conditions modified to 18°C continuously with a 12-h photoperiod of approximately 250 μmol m^{-2} s^{-1} (440–700 nm) and relative humidity of 60%. Leaf 1 of the parents and DH lines was cut off at or shortly before ligule emergence (9 days after sowing the dry seeds) and dehydrated to 10% weight loss. Partially-dehydrated leaves were then wrapped closely in aluminium foil and incubated as above. Five replicate leaves of each of the parents and DH lines were treated, with the sowing date of each replicate staggered so that one replicate of each genotype was sampled each day.

Ten DH lines and the parents were grown on a second occasion to compare ABA accumulation in leaf 1 and leaf 4 of the same plants. Plants were grown in pots in cabinet conditions as described above for the DH experiment. Leaf 1 and leaf 4 were given stress treatments as described for the DH and F_2 plants, respectively. Six replicate plants of each genotype were treated.

ABA analysis

About 20 discs of 4.5 mm in diameter were collected along each leaf 4 at the end of the stress treatment for ABA analysis. Discs were first frozen and then thawed, and the ABA extracted by shaking with water. Leaf 1 of the DH plants and the parents was frozen and freeze-dried after the stress treatment, ground to a powder and extracted with water for ABA. After extraction of all samples at 4°C overnight, ABA was measured in the crude aqueous extracts by radioimmunoassay with a monoclonal antibody (MAC62) specific for (S)-ABA free acid (Quarrie and Galfre 1985; Quarrie et al. 1988). The assay was validated for crude aqueous extracts of wheat leaves in Quarrie et al. (1988). Further technical details of the assay are given in Pekić and Quarrie (1987).

RFLP and isozyme analysis

Several leaves were collected from each parent and F_2 plant and 96 DH lines. They were frozen and freeze-dried and genomic DNA extracted as detailed in Sharp et al. (1988). DNA was cut with the restriction enzymes *Eco*RI, *Eco*RV, *Hin*dIII, and the parents and DH lines also with *Dra*I. Restriction digests, gel electrophoresis, Southern transfer, probe labelling and filter hybridisation were also carried out essentially as described by Sharp et al. (1988).

The 5A isozyme marker Ibf-1 (iodine binding factor) was scored in the parents, F_2 plants and DH lines. The endosperm half of mature grains was removed, crushed with pliers and incubated in 70 μl of 0.01 M dithiothreitol for 1 h at room temperature. Isoelectric focusing of endosperm extracts on polyacrylamide gels and gel staining were carried out as in Liu and Gale (1989).

Statistical analyses

Deviations from the expected segregation ratios for each marker locus (1:2:1 for the F_2 population and 1:1 for DH lines) was analysed using the Chi-square test. Genetic linkage maps were then constructed using MAPMAKER (Lander et al. 1987), with the order of loci on chromosome 5A based on the map presented by Xie et al. (1993). Map distances in centiMorgans (cM) were calculated using the Kosambi (1944) mapping function.

Initially, a simple one-way ANOVA of differences in ABA content among the marker genotype classes at each locus was carried out to test for the presence of QTL regulating ABA accumulation. The interval mapping programme MAPMAKER-QTL (Lander and Botstein 1989) was then used to construct a QTL location likelihood map for the ABA QTL in the mapped region of chromosome 5A. A LOD score threshold of 2.0 (equivalent to significance at the 1% level) was used to indicate a significant likelihood.

Results

ABA accumulation in the chromosome substitution lines

The difference in ABA accumulation in the DLT between

'Ciano 67' and CS (Fig. 1) was not as large as had been expected on the basis of previous work (Quarrie 1981), which showed that 'Ciano 67' accumulated almost twice as much ABA as CS. Nevertheless, ANOVA showed that the substitution lines varied significantly in ABA accumulation ($P< 0.001$, least significant difference 51 ng gFW^{-1}), with 5A having the most ABA and 2D and 6D the least. ABA accumulation in the 5A substitution line was significantly higher (30%, $P=0.01$) than that of CS. The overall mean ABA accumulation of the remaining 20 substitution lines (242 ng gFW^{-1}) was very close to that of CS (247 ng gFW^{-1}). Chromosome 3B had the second largest ABA accumulation, but this was not significantly different from that of CS.

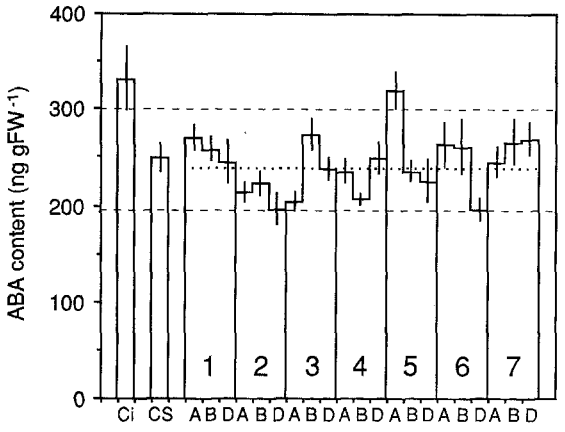

Fig. 1 ABA accumulation in the DLT in leaf four of single chromosome substitution lines of the donor genotype Ciano 67 (Ci) into the recipient Chinese Spring (CS). ABA data for the parents are also shown. *Dotted line* indicates the mean ABA accumulation over all substitution lines, excluding line 5A. *Dashed lines* indicate least significant differences (5% level) from CS. *Vertical bars* indicate ±SE of the mean of data for six replicate leaves. Chromosomes are numbered and the genome letter of each is indicated below the histogram

Distributions of ABA accumulation in F_2 and DH populations

In the F_2 population, ABA accumulation in the DLT varied amongst the 139 plants from about 50 to 560 ng gFW^{-1} (Fig. 2a) with a population mean of 218.2 ng gFW^{-1}. The distribution was slightly skewed towards low ABA contents, showing that ABA accumulation in the DLT was a partially recessive trait, though the population mean was not significantly different from the mid-parent value (258.3 ng gFW^{-1}). Mean ABA accumulation in the two parents was 113.5 and 403.0 ng gFW^{-1} for CS and 'SQ1', respectively.

ABA accumulation in leaf 1 was greater than it was in leaf 4, with CS and 'SQ1' accumulating 306.0 and 550.6 ng gFW^{-1}, respectively, in leaf 1. The distribution amongst the DH lines of mean ABA accumulation for each line was normal (Fig. 2b), varying from 360 to 575 ng gFW^{-1} with a population mean of 453.3 ng gFW^{-1}. There was no evidence of epistatic effects.

To test whether the same genes were likely to be regulating ABA accumulation in both leaf 1 and leaf 4, ABA accumulation in both leaves of 10 DH lines covering the range of ABA accumulation amongst the DH population and the parents was examined. On a genotype mean basis, the linear correlation between ABA accumulation in leaves 1 and 4 was highly significant ($r_{10\ df}=0.85$). As the relative genetic differences in ABA accumulation in leaf 1 amongst the DH lines were maintained in leaf 4, it seems likely that ABA accumulation in leaf 1 and leaf 4 would be regulated by the same QTL.

Linkage analysis

Using selective genotyping (Lander and Botstein 1989) to simplify the analysis, only 48 F_2 individuals from the tails of the ABA distribution were initially selected for testing (Fig. 2a). These 48 plants were genotyped for 26 restriction fragment length polymorphism (RFLP) and isozyme markers that covered 12 of the 21 wheat chromosomes. Following the results of ABA accumulation in the chromosome substitution experiment, several markers to loci

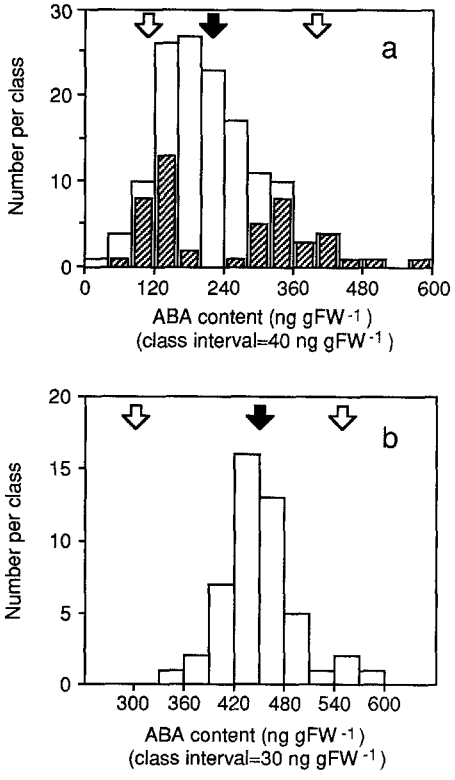

Fig. 2 Frequency distribution of ABA accumulation in **a** leaf four of 139 F_2 plants and **b** leaf one of 48 DH lines from the cross CS × SQ1. *Shaded regions* of the F_2 histogram indicate those plants that were tested with all molecular probes. *Open arrowheads* indicate the mean ABA contents of CS (low-ABA) and SQ1 (high-ABA) and *filled arrowheads* indicate the population mean ABA contents

Table 1 Mean ABA contents (ng gFW^{-1}) of leaves of 24 high-ABA and 24 low-ABA F_2 plants classified according to CS, SQ1 and heterozygote genotypes with probes (and their chromosomal locations) that gave significant ANOVA *F*-ratios

Probe/enzyme[a]	Chromosome	ABA content (no.of plants)			Significance level
		CS genotype	Heterozygote	SQ1 genotype	
psr903/1	3BS	163 (11)	267 (22)	282 (15)	0.05
psr911/4	5AL	195 (14)	244 (22)	315 (12)	0.07
ABA2/2	5AL	150 (12)	246 (23)	358 (12)	< 0.001
psr575/4	5AL	163 (8)	234 (25)	387 (10)	< 0.001
psr426/4	5AL	166 (6)	211 (28)	357 (13)	< 0.001
psr145/4	5AL	211 (12)	226 (26)	373 (8)	0.01
Embp/2[b]	6AL	138 (8)	270 (28)	264 (11)	0.04

[a] 1=*Eco*RI, 2=*Eco*RV, 4=*Hin*dIII
[b] The probe Embp was a gift from Dr. R.S. Quatrano

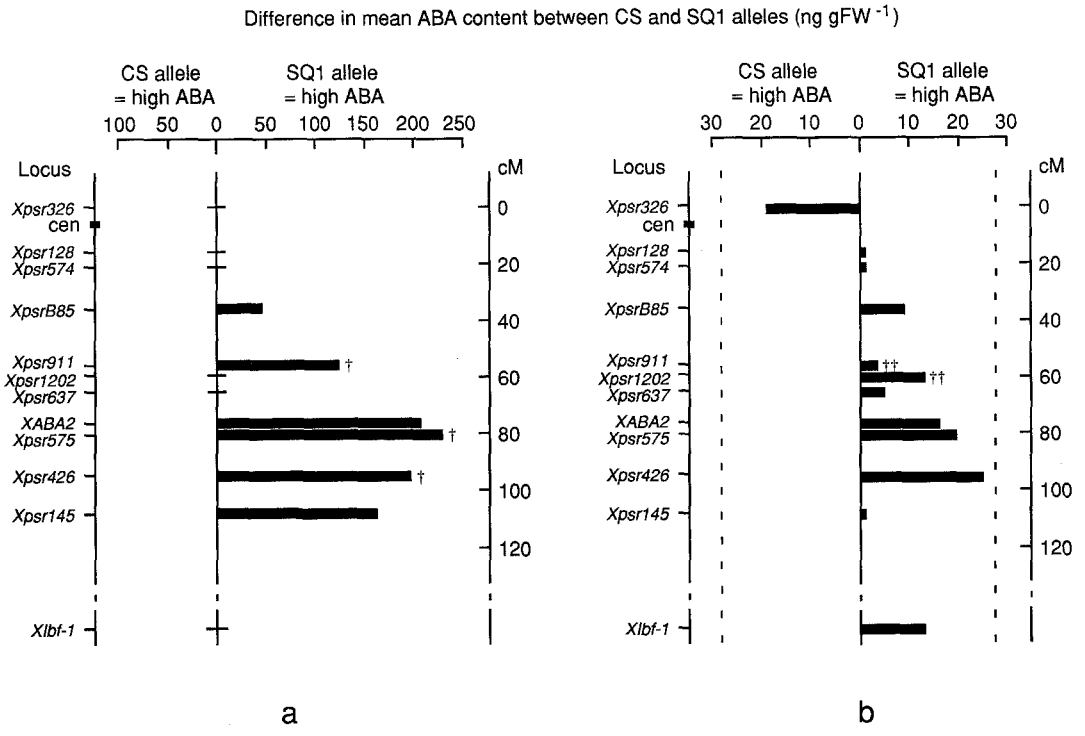

Fig. 3 Genetic map of chromosome 5A from F_2 plants (**a**) and DH lines (**b**) from the cross CS × SQ1 and differences (SQ1 allele minus CS allele) between mean ABA contents of CS and SQ1 alleles at each locus tested. In **a** either 48 or 139 (†) F_2 plants were tested with 6 probes. In **b** either 96 or 72 (††) DH lines were tested with 12 probes. *Dashed lines* in **b** indicate significance at $P< 0.05$ for 48 DH lines. *cen* approximate location of centromere. ABA2 is a barley cDNA responsive to ABA treatment (Gulli et al. 1992). Other markers are from the Cambridge Laboratory collection (Xie et al. 1993). The Ibf marker segregated on a 3:1 basis in the F_2 population and was omitted from the ANOVA

on chromosome 5A were tested and a partial linkage map for this chromosome was constructed (Fig. 3a). The most likely order of these markers was consistent with the linkage map constructed by Xie et al. (1993), though the map distances between pairs of markers were sometimes different. ANOVA of these 48 F_2 plants showed a significant association between differences in ABA accumulation and the genotype of markers on the long arm of chromosome 5A, 1 marker locus (*Xprs903*) on the short arm of chromosome 3B and 1 marker locus (*XEmbp*) on the long arm of chromosome 6A (Table 1). The association between ABA accumulation and genotype was confirmed for marker loci on chromosome 5AL by ANOVA of ABA data for all 139 F_2 plants (P=0.06, $P< 0.001$, $P< 0.001$ for *Xpsr911*, *Xpsr575* and *Xpsr426*, respectively). ABA means for the heterozygotes of markers with significant QTL effects (Table 1) were less than the mid-parent value, showing that low ABA accumulation was partially dominant. ANOVA of all F_2 plants showed that the associations between ABA concentration and genotype at the marker loci on chromosomes 3BS (*Xpsr903*) and 6AL (*XEmbp*) were no longer significant, though a trend for higher ABA accumulation in plants with the 'SQ1' allele was still present at both those loci.

A similar map of RFLP marker loci on chromosome 5A was constructed using the 96 DH lines (Fig. 3b). However, ANOVA of ABA data according to the genotype of 48 DH lines failed to show any significant association with any of

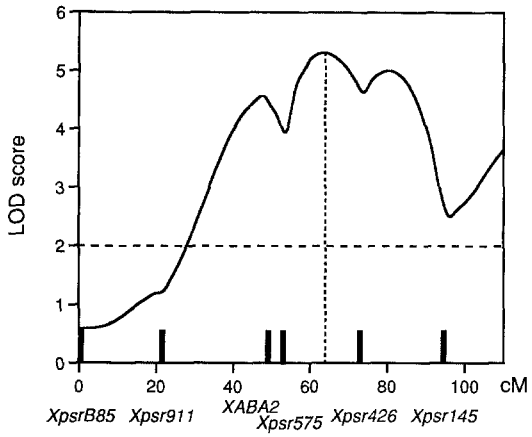

Fig. 4 Location likelihood profile for the ABA QTL on chromosome 5A from data for F_2 plants. *Dashed line* indicates the default setting for significance used by MAPMAKER-QTL. *Dotted line* indicates the maximun likelihood location for the ABA QTL. *Thick bars* indicate the location of mapped molecular markers

the marker loci on chromosome 5A, the marker locus having the biggest effect on ABA accumulation being *Xpsr426* (P=0.068). Nevertheless, a consistent trend for more ABA in lines with the SQ1 allele was present in the region of the chromosome showing the strong QTL effect with the F_2 plants (Fig. 3b). Of the 21 remaining markers so far mapped in the DH lines to other chromosomes, the only significant QTL effect on ABA accumulation in the DH lines was on chromosome 5BL (locus *XWG908*), though at this locus ABA accumulation was greater in CS than in 'SQ1'.

QTL-likelihood mapping

A QTL location-likelihood profile for the ABA QTL in the mapped region of chromosome 5AL was constructed with all the F_2 plants using MAPMAKER-QTL (Fig. 4). This gave a maximum likelihood position for the ABA QTL (LOD score 5.3) about 8 cM from *Xpsr426* towards *Xpsr575*. For the DH lines, the maximum likelihood location for the ABA QTL on chromosome 5A was at the marker locus *Xpsr426*, though the LOD score for this was only 0.8 (data not shown).

Discussion

The chromosome substitution series gave strong evidence for a gene(s) regulating ABA accumulation in the DLT on chromosome 5A, with another possible QTL for ABA accumulation on chromosome 3B. The presence of a major QTL for ABA accumulation on chromosome 5A was confirmed using an F_2 population by partial mapping of the chromosome with molecular markers, with a maximum likelihood location for the QTL occurring between the loci *Xpsr426* and *Xpsr575*. Although a LOD score of 4.6 at the adjacent locus *XABA2* was also highly significant, ABA2 is a gene belonging to the dehydrin family whose transcription is *induced* by ABA (Gulli et al. 1992). This gene is, therefore, unlikely to be involved in regulating the production of ABA itself. Other QTL for ABA accumulation may be present on chromosomes 3BS and 6AL, though further mapping of these chromosomes would be required to determine whether the small effects found in the F_2 population were due to major QTL located at some distance from the loci *Xpsr903*and *XEmbp* or to minor QTL close to these loci.

If the 5AL effect on ABA accumulation is real, a similar effect should have been seen using the DH lines. Although ANOVA of ABA data for leaf 1 failed to show any significant effect, the significant association between ABA accumulation in leaves 1 and 4 of the same plants suggests that the QTL for ABA accumulation on chromosome 5A should at least have been present in leaf 1. ABA accumulation in the DH lines was tested using leaf 1 for mainly technical reasons, so that a large number of plants could be handled simultaneously and each replicate could be treated under uniform environmental conditions. However, the smaller difference in ABA accumulation between CS and 'SQ1' using this leaf meant that the proportional variation in ABA accumulation amongst the DH lines was considerably smaller than that amongst the F_2 plants. This, together with the smaller population size examined, may explain why no significant QTL for ABA accumulation was found using ABA data for leaf 1 of the 48 DH lines.

The presence in the DH lines of the ABA QTL on chromosome 5AL is supported by results for the 10 DH lines used to test ABA accumulation in leaf 1 and leaf 4. These indicated that a stronger 5A effect on ABA accumulation would probably have been present if leaf 4 had been tested instead of leaf 1. Of the 10 DH lines used for this comparison, 6 had the CS allele in the region of the ABA QTL, 3 had the 'SQ1' allele and 1 was indeterminate. ANOVA of ABA accumulation in leaf 4 of the 10 DH lines grouped according to genotype at the presumed ABA QTL showed significantly ($P< 0.01$) more ABA in lines with the 'SQ1' allele (374 and 528 ng gFW^{-1} for means of CS and SQ1 alleles, respectively). In contrast, ANOVA of the corresponding ABA data for leaf 1 of the same plants showed no significant difference between the genotypes (361 and 397 ng gFW^{-1} for means of CS and 'SQ1' alleles, respectively). In addition, using the same 48 DH lines in an experiment to test their responses to salt stress, we have also found a significant QTL determining ABA concentrations in upper leaves on chromosome 5AL within 2 cM of the drought-induced ABA QTL detected in the F_2 population reported here (Semikhodsky and Quarrie, unpublished data).

There was no evidence for a QTL for ABA accumulation on either of the homoeologous chromosomes 5B or 5D, though only 5B was mapped in the region corresponding to the ABA QTL. An advantage of the DH lines is that they give a better estimate of the purely additive effects than the F_2 plants that also exhibit dominance (Moreno-Gonzales 1993).

This is the first report of a QTL affecting the accumulation of ABA in detached and dehydrated leaves, though other QTL for leaf ABA content in intact plants subjected to drought stress have recently been reported (Sanguineti et al. 1994; Quarrie et al. 1994). In a study of ABA accumulation in a population of DH lines of barley (Sanguineti et al. 1994), a weak QTL for leaf ABA content under droughted conditions was located in a region of barley chromosome 7 (R. Tuberosa, personal communication) that is homoeologous to the region of chromosome 5 containing the ABA QTL in wheat. Several significant QTL for leaf ABA content have been located on maize chromosomes 1, 3 (Quarrie et al. 1994) and 2 (Steed and Quarrie, unpublished data). Although no comparative maps of wheat and maize are yet available, it is possible to estimate chromosomal locations for some of those maize QTL in wheat by comparison of RFLP maps for maize and rice (Ahn and Tanksley 1993) and rice and wheat (Kurata et al. 1994). These show that the maize ABA QTL are likely to be on chromosomes 4, 3 and 2 of wheat, respectively.

Without detailed examination of biochemical, molecular and biophysical factors known to affect the accumulation of ABA in droughted leaves, it is not possible to deduce the function of the gene(s) determining the QTL for ABA on wheat chromosome 5A. These factors would include ABA precursor pool sizes, ABA-specific enzyme activities, factors inducing the transcription of genes necessary for ABA accumulation and membrane sensitivities to the loss of cell water. However, evidence is beginning to show that genetic variation in ABA accumulation in the DLT may be reflecting variation in the capacity of membranes to respond to the loss of water from the cells. ABA accumulation in the DLT was significantly correlated both with ion leakage from leaf discs in response to low temperature treatment and with the uptake of sodium into leaves when plants were subjected to salinity stress (Quarrie 1993). In addition, using single chromosome recombinant lines of wheat, Galiba, Quarrie, Sutka and Snape (manuscript submitted) have recently shown that the region of chromosome 5A carrying the ABA QTL contains a major gene determining frost tolerance; the differences in frost tolerance amongst the recombinant lines have also been associated with consistent differences in ABA concentration when plants were subjected to drought stress (Galiba and Quarrie, unpublished data). If the QTL on chromosome 5A affects ABA accumulation through a modification of membrane structure or function, then this QTL may have an important effect on plant responses to other stresses where membrane integrity is challenged. The parents of the F_2 population and DH lines used here (CS and 'SQ1') are already known to differ widely in responses to salt stress, heat stress (ion leakage) and nutrient stress (Mahmood, Clarkson and Quarrie, unpublished results). These DH lines should, therefore, be suitable genetic stocks for QTL analysis of responses to several abiotic stresses.

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