

THE POSSIBILITIES OF APPLYING MARKER ASSISTED SELECTION IN BREEDING BORON TOLERANT WHEAT

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The aim of this study was to investigate the possibilities of applying molecular markers-microsatellites in breeding boron tolerant wheat. The study comprised the investigation of allelic variability of sixty bread wheat accessions in two microsatellite loci (*Xgwm46-7B* and *Xgwm577-7B*) for which was assumed that are placed near the *7B* chromosome locus involved in the expression of boron tolerance in wheat. Phenotypic variability concerning boron tolerance was assessed via root length reduction of wheat seedlings grown in the presence of high external boron, applied as boric acid solution (concentrations 50, 100 and 150 mg/l, boron treatments B50, B100 and B150). The indication of marker-trait associations was determined by comparing the allelic variability in the two microsatellite loci with the phenotypic variability in boron tolerance. Nonparametric Kruskal-Wallis test was used for the comparisons. The indication of marker-trait association was found for both *Xgwm46-7B* and *Xgwm577-7B*; on B150 and B50 treatments, respectively. Allelic forms identified in *Xgwm577-7B* locus may be related to tolerance, medium tolerance and sensitivity to high boron. This was not the case for *Xgwm46-7B*, where the identified alleles were related only to boron tolerance and sensitivity. Therefore, *Xgwm577-7B* may be preferred over *Xgwm46-7B* when studying boron tolerance in wheat. However, a considerable portion of boron tolerant accessions carried different alleles in the investigated loci, implying boron tolerance as a quantitative trait with more than one chromosomal region involved in its expression. Therefore, the allelic variability of more than the analyzed two loci should be investigated.

Key words: wheat, boron tolerance, marker-assisted selection, microsatellites

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INTRODUCTION

One of the preconditions for healthy growth and development of higher plants is an adequate supply of micronutrient boron. Thus, both boron deficiency and toxicity may adversely affect agricultural plants leading to decreased yields. Since boron deficiency can be successfully managed by the application of appropriate fertilizers, boron toxicity seems to be a more difficult problem.

As a monocot plant, wheat has comparatively low boron requirements. Consequently, toxicity symptoms are likely to develop on the plants growing on soils containing the element in concentrations even moderately higher than the optimal ones. Hence ameliorating boron laden soils is difficult and expensive, breeding tolerant cultivars would be the most acceptable solution to the problem (NABLE *et al.*, 1997; YAU and RYAN, 2008; REID, 2010).

The first research on the mode of inheritance and chromosomal location of the genes involved in the expression of boron tolerance in wheat has been performed by PAULL *et al.* (1988; 1991), and CHANTACHUME (1995). The results showed that at least three (*Bo1*, *Bo2*, *Bo3*) major loci acting in additive manner and located on *4A*, *4B*, *7B* and/or *7D* chromosomes are included in controlling boron tolerance. The work of JEFFERIES *et al.* (2000) confirmed the role of regions on *7B* and *7D* chromosomes. The *7B* region (*Bo1*) was studied in more details by SCHNURBUSCH *et al.* (2007), who identified microsatellite markers that could be used in marker-assisted selection for boron tolerance.

This study was undertaken in order to investigate the possibility of applying molecular markers-microsatellites in selection of boron tolerant wheat genotypes. If successfully applied, the technique may significantly shorten the period required for breeding tolerant cultivars.

MATERIALS AND METHODS

Sixty bread wheat accessions (high yielding local and foreign cultivars and lines, boron tolerance/sensitivity checks) have been included in the study and two assays have been performed.

Phenotypic variability concerning boron tolerance was assessed by filter paper technique involving root length reduction in presence of excess external boron as selection criterion for distinguishing boron tolerant, medium tolerant, medium sensitive and sensitive accessions. This assay was performed at seedling stage and included control (0.015 mM H₃BO₃) and treatments of 50, 100 and 150 mg/l H₃BO₃ solution (B50, B100 and B150). It is described in details in CHANTACHUME *et al.* (1995).

Molecular marker assay included the analysis of allelic variability in two microsatellite loci (*Xgwm46-7B*, *Xgwm577-7B*, RÖDER *et al.*, 1998) for which was assumed that are located near the loci affecting the expression of boron tolerance in wheat (MARJANOVIĆ, 2005; SCHNURBUSCH *et al.*, 2007). The description of the markers is given in Table 1. Total genomic DNA was extracted following the CTAB procedure of DOYLE and DOYLE (1990). PCR amplifications were carried out in 20 µl volumes containing 30 ng of genomic DNA, 1 x B buffer, 2 mM MgCl₂, 0.2 mM of dNTPs, 10 pM of both forward and reverse primers and 2 units of Taq polymerase (Applied Biosystems). Initial denaturation (5 min, 94°C) was followed by 35 cycles with each including short denaturation (30 sec, 94°C), annealing (30 sec, 62°C for *Xgwm46-7B* or 55°C for *Xgwm577-7B*) and elongation (1 min, 72°C). Final extension (10 min) was performed at 72°C. The amplification products were separated by vertical electrophoresis on

6% polyacrylamide gels and visualized by silver staining as described in SANGUINETTI *et al.* (1994). The products have been marked by alphabetical order, starting with the shortest ones (A).

Table 1. Description of microsatellite markers

Primer	Sequence repeat	Sequences of primer pairs 5'-3'	Chromosome	Temperature (°C)
<i>Xgwm 46-7B</i>	(GA) ₂ GC(GA) ₃₃	(F): GCA CGT GAA TGG ATT GGA C (R): TGA CCC AAT AGT GGT GGT CA	7 B	62
<i>Xgwm 577-7B</i>	(CA) ₁₄ (TA) ₆	(F): ATG GCA TAA TTT GGT GAA ATT G (R): TGT TTC AAG CCC AAC TTC TAT T	7 B	55

Informativeness of the tested microsatellite loci in terms of determining variability of the analyzed accessions was expressed via *PIC* (Polymorphism Information Content) values. The values were calculated as: $PIC = 1 - \sum p_i^2$, where p_i represents the frequency of the i^{th} allele (ANDERSON *et al.*, 1993). In order to determine the indication of marker-trait associations, the variability of the tested loci was compared to the variability of seedling's root length reduction caused by boron toxicity. Since the results of the Shapiro-Wilk test showed that the frequencies of root length reduction are not normally distributed, Box-Cox transformation was performed (data not shown). Even then the hypothesis of normal frequency distribution was rejected; therefore the non-parametric Kruskal-Wallis test was used for comparing the arithmetic means of groups of accessions carrying the same allele in the tested microsatellite loci. All calculations have been performed using STATISTICA 8.0 software package (StatSoft, Tulsa, OK, USA; University license, Novi Sad, Serbia).

RESULTS AND DISCUSSION

Nineteen allelic forms (including null allele) have been found in microsatellite locus *Xgwm 46-7B* (Table 2). Fragment sizes were in the range between 75 and 200 bp with the majority of the fragments being closer to 200 bp, which is in accordance to the sizes reported by RÖDER *et al.* (2002) and MARJANOVIĆ (2005). The calculated *PIC* value was 0.909, implying the high diversity of the tested material (HAMZA *et al.*, 2004). Considering the size of 60 wheat accessions included in the analysis, as well as their diversity, the observed polymorphism of the *Xgwm 46-7B* locus corresponds to the polymorphism reported by other authors: AHMAD (2002), KOBILJSKI *et al.* (2002), RÖDER *et al.* (2002) and MARJANOVIĆ (2005) found 4, 25, 16 (including null) and 8 (including null) alleles in the samples of 13, 96, 502 and 106 wheat genotypes, respectively. Out of 19 allelic forms determined in our study, 10 were rare (found in one accession only), corresponding to the results of RÖDER *et al.* (2002), where 7 out of 16 alleles were rare.

The indication of the marker-trait boron tolerance association was determined by comparing the variability of the tested locus to the variability of wheat seedling's root length reduction caused by boron toxicity. The comparisons have been made by nonparametric Kruskal-Wallis test. Accessions carrying the rare alleles have been excluded from further analyses, since no conclusion can be made based on root length reduction of a single case. The data concerning phenotypic variation of the tested accessions in root length and other traits affected by the

imposed boron treatments have been discussed in details in BRDAR-JOKANOVIĆ *et al.* (2010) and BRDAR-JOKANOVIĆ *et al.* (2013).

Table 2. Allelic variability in *Xgwm 46-7B* and *Xgwm 577-7B* loci and root length reduction (RLR) on B treatments with respect to control in wheat

Accession	<i>Xgwm 46-7B</i> allele and its frequency (%)	<i>Xgwm 577-7B</i> allele and its frequency (%)	RLR on B50 (%)	RLR on B15 (%)	Accession	<i>Xgwm 46-7B</i> allele and its frequency (%)	<i>Xgwm 577-7B</i> allele and its frequency (%)	RLR on B50 (%)	RLR on B150 (%)
Arija	M (6.67)	F (1.67)	17.7	45.9	Teodora	G	C	+81.2	+46.8
Astra	I (6.67)	L (21.67)	7.4	33.0	Vila	M	D	+5.2	22.9
Balerina	J (10.00)	B (10.00)	34.6	32.0	NS 100/01	C	B	2.6	35.0
Cipovka	J	G (10.00)	18.0	34.5	NS 73/02	NULL	C	17.6	15.6
Diva	J	B	3.2	17.2	NS 103/02	D	L	12.3	37.4
Donna	J	E (5.00)	+6.7	30.7	NS 53/03	NULL	C	2.8	30.1
Dragana	D (13.33)	N (1.67)	+29.3	7.7	Apache	D	C	+2.8	31.3
Etida	D	L	6.8	20.2	Bezostaja 1	D	B	1.3	33.8
Evropa 90	F (1.67)	J (5.00)	1.6	27.6	Bolal 2973	G	A (5.00)	15.4	60.2
Helena	E (8.33)	C (21.67)	2.0	39.9	Condor	Q (1.67)	NULL(1.67)	24.2	77.2
Janja	C (5.00)	L	17.7	33.3	Dagdas	NULL	H (1.67)	4.9	71.9
Kantata	G (10.00)	J	+0.2	45.8	Donjecka 48	D	B	24.8	45.6
Košuta	J	L	13.7	36.5	Fundulea 4	NULL	A	23.5	41.4
Lana	E	G	+6.6	28.2	ITMI 22/00	K (1.67)	E	+6.9	21.7
Ljiljana	D	L	5.4	9.4	ITMI 43/00	G	L	24.7	28.7
Milijana	I	P (1.67)	4.4	38.2	Kalyan Sona	B (1.67)	J	+15.6	38.9
Mina	L (1.67)	K (3.33)	+11.2	1.6	Kenya Farmer	H	L	43.8	67.2
Nevesinjka	A (1.67)	G	+5.2	39.6	Kirac 66	P (1.67)	A	+7.3	10.2
NS 40S	NULL(16.67)	K	12.3	50.1	Magdalena	D	C	22.7	50.0
Oda	G	C	1.7	39.6	Mironovska 808	M	I (1.67)	8.1	40.3
Partizanka	I	L	17.9	45.3	Norin10/Brevor14	E	G	4.0	53.9
Pesma	H (6.67)	L	19.4	59.9	Peking 11	NULL	L	+1.1	16.2
Pobeda	H	D (3.33)	7.2	43.1	Pergamino Gab.	NULL	B	33.8	39.4
Rapsodija	G	C	1.3	28.2	Radika	C	G	24.0	22.9
Renesansa	M	M (3.33)	19.4	59.9	Renan	E	G	27.0	54.3
Rusija	O (1.67)	C	8.1	57.3	Stephens	NULL	O (1.67)	+28.2	8.4
Simfonija	H	L	1.7	24.6	Synth. Norwich	R (1.67)	M	1.1	12.7
Simonida	I	L	+0.2	47.2	Trakija	E	C	3.2	28.5
Sofija	NULL	C	12.0	45.9	Yanetzky Probat	J	C	+3.1	17.6
Sonata	N (1.67)	E	2.3	45.4	Žitarka	NULL	C	+15.8	64.6

The indication of marker-trait association was determined on the strongest (B150) treatment. On average, the accessions carrying the H, M and I alleles were more susceptible to excess boron than the accessions with J allele in *Xgwm 46-7B* locus. Also, the accessions with H allele were more susceptible than those with D allele (Table 3). Therefore, the alleles J and D may be related to boron tolerance and the alleles H, M and I with boron susceptibility in wheat.

In case of *Xgwm 577-7B* locus 17 alleles have been found, including null allele. Seven alleles were rare (Table 2). The fragment sizes were in the range between 100 and 250 bp and *PIC* value was 0.873. The observed polymorphism was in accordance to those reported by AHMAD (2002) and RÖDER *et al.* (2002), who detected 5 and 22 allelic forms in samples of 13 and 502 wheat accessions, respectively. In addition, RÖDER *et al.* (2002) reported fragment sizes from 126 to 214 bp, 10 rare alleles and null allele, which is also in accordance to our results.

For locus *Xgwm 577-7B*, the indication of marker-trait association was determined on the weakest boron treatment (Table 4). The results of the performed Kruskal-Wallis test revealed significant differences between the accessions with C, J and E alleles and those with L and B alleles; with J and E alleles and those with G allele, as well as between those with E and A allele. On average, the accessions carrying C, J and E alleles were more boron tolerant when compared to those with L and B alleles. G and A allelic forms may be related to medium tolerance to excess boron.

Table 3. Kruskal-Wallis test for significance of differences of root length reduction mean values (B150 treatment) in groups of wheat accessions carrying the same allele in *Xgwm 46-7B* locus

allele	G	M	NULL	I	D	E	J	C
H	0.354	1.000	1.000	1.000	0.008**	1.000	0.001**	0.051
G	-	1.000	1.000	1.000	1.000	1.000	1.000	1.000
M	-	-	1.000	1.000	0.227	1.000	0.026*	0.539
NULL	-	-	-	1.000	1.000	1.000	0.102	1.000
I	-	-	-	-	0.191	1.000	0.021*	0.476
D	-	-	-	-	-	0.500	1.000	1.000
E	-	-	-	-	-	-	0.057	1.000
J	-	-	-	-	-	-	-	1.000

*, ** - significant at the 0.05 and 0.01 levels of probability, respectively

Table 4. Kruskal-Wallis test for significance of differences of root length reduction mean values (B50 treatment) in groups of wheat accessions carrying the same allele in *Xgwm 577-7B* locus

allele	C	J	E	D	M	A	K	G	B
L	0.001**	0.000**	0.000**	0.351	1.000	1.000	0.411	1.000	1.000
C	-	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.003**
J	-	-	1.000	1.000	0.243	0.091	1.000	0.035*	0.000**
E	-	-	-	1.000	0.133	0.044*	1.000	0.014*	0.000**
D	-	-	-	-	1.000	1.000	1.000	1.000	0.209
M	-	-	-	-	-	1.000	1.000	1.000	1.000
A	-	-	-	-	-	-	1.000	1.000	1.000
K	-	-	-	-	-	-	-	1.000	0.244
G	-	-	-	-	-	-	-	-	1.000

*, ** - significant at the 0.05 and 0.01 levels of probability, respectively

The obtained results are the indication for further research on possibilities for including accessions carrying J or D allele in *Xgwm 46-7B* and C, J or E allele in *Xgwm 577-7B* loci in breeding boron tolerant wheat cultivars, or recommending those accessions for growing on boron laden soils. However; in addition to boron tolerance and sensitivity, allelic forms identified in *Xgwm 577-7B* locus may be related to medium tolerance to high boron, which was not possible in the *Xgwm 46-7B* case. The fact justifies preferring *Xgwm 577-7B* over *Xgwm 46-7B* when studying boron tolerance in wheat.

However, there was a considerable portion of boron tolerant accessions carrying different alleles in the investigated microsatellite loci (Table 2). The result implies boron tolerance as a quantitative trait with more than two chromosomal regions involved in its expression. This corresponds to the results of ÖZ *et al.* (2009) and PADMANABHAN *et al.* (2012), who reported significantly altered expression of a great number of genes in response to high external boron. Similarly, ROESSNER *et al.* (2006) studied metabolic responses caused by boron toxicity in barley and concluded that none of the analyzed individual metabolites was sufficient to explain boron tolerance mechanism.

In addition, the region on 7B wheat chromosome (*Bo1*) was intensively studied inter alia because it has been considered as prevalent source of boron tolerance in Australian wheat germplasm (SCHNURBUSCH *et al.*, 2008). The problem of boron toxicity in cereals was firstly recognized 30 years ago (CHARTWRIGHT *et al.*, 1984) and intensively studied ever since exactly in Australia, often on material originating from the continent. On the contrary, the material analyzed in our study was highly divergent and originated from all over the world.

Therefore, the allelic variability of more than the analyzed two loci should be investigated in order to successfully incorporate the molecular marker approach in breeding boron tolerant wheat.

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MOGUĆNOSTI PRIMENE MARKER-ASISTIRANE SELEKCIJE U OPLEMENJIVANJU PŠENICE TOLERANTNE NA BOR

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Izvod

Cilj ovog rada je bilo ispitivanje mogućnosti primene molekularnih markera-mikrosatelita u oplemenjivanju pšenice tolerantne na bor. Ispitana je alelna varijabilnost kod šezdeset genotipova hlebne pšenice u dva mikrosatelitna lokusa (*Xgwm46-7B* i *Xgwm577-7B*) za koje se pretpostavlja da su pozicionirani u blizini lokusa na *7B* hromozomu koji utiče na ekspresiju ovog svojstva. Fenotipska varijabilnost u pogledu tolerantnosti na bor je utvrđena na osnovu redukcije dužine korenčića klijanaca pšenice gajenih u uslovima suviška bora (rastvor borne kiseline koncentracija 50, 100 i 150 mg/l, tretmani B50, B100, B150). Indikacija veze marker-svojstvo je utvrđivana na osnovu poređenja alelne varijabilnosti mikrosatelitnih lokusa i fenotipske varijabilnosti u pogledu tolerantnosti na bor. Za poređenja je korišćen neparametarski Kruskal-Wallis test. Indikacija veze marker-svojstvo je konstatovana za *Xgwm46-7B* na tretmanu B150, a za *Xgwm577-7B* na tretmanu B50. Alelne forme identifikovane u lokusu *Xgwm577-7B* se mogu dovesti u vezu sa tolerantnošću, srednjom tolerantnošću i osetljivošću na bor. Ovo nije bio slučaj kod *Xgwm46-7B*, gde su identifikovani aleli dovedeni u vezu samo sa tolerantnošću i osetljivošću na bor. Prema tome, za dalji rad se preporučuje *Xgwm577-7B*. Međutim, kod značajnog dela tolerantnih genotipova su identifikovani različiti aleli u proučavanim lokusima, što upućuje na zaključak da je u pitanju kvantitativno svojstvo u čiju ekspresiju je uključeno više od jednog hromozomskog regiona. Potrebno je ispitati alelnu varijabilnost više od dva mikrosatelitna lokusa.

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