Turkish Journal of Agriculture and Forestry

Volume 30 | Number 1 Article 6

1-1-2006

Genotypic Variation in Tolerance to Boron Toxicity in 70 Durum Wheat Genotypes

AYFER A. TORUN

ATİLLA YAZICI

HALİL ERDEM

İSMAİL ÇAKMAK

Turk J Agric For
30 (2006) 49-58

Genotypic Variation in Tolerance to Boron Toxicity in 70 Durum Wheat Genotypes

Ayfer A. TORUN[1], Atilla YAZICI[2], Halil ERDEM[3], İsmail ÇAKMAK[2]

[1]Çukurova University, Faculty of Agriculture, Department of Soil Science, Adana - TURKEY

[2]Sabancı University, Faculty of Engineering and Natural Sciences, 34956, İstanbul - TURKEY

[3]Çukurova University, Faculty of Agriculture, Department of Soil Science, Adana - TURKEY

Received: 26.12.2005

Abstract: By using 70 durum wheat (*Triticum durum*) genotypes, a greenhouse experiment has been carried out to study genotypic variation in tolerance to boron (B) toxicity in soil. Plants were grown in a soil containing 12 mg extractable B kg^{-1} soil and treated additionally with (+B: 25 mg kg^{-1} soil) and without B (-B: 0 mg B kg^{-1} soil). Following 30 days of growth, only shoots have been harvested and analyzed for dry matter production and shoot concentrations of B. There was a large genotypic variation in tolerance to B toxicity based on the severity of leaf symptoms and decreases in dry matter production caused by B toxicity. Among the genotypes tested, the growth of the genotypes Sabil-1, Stn "S", Aconhi-89 and Wadelmez-2 was not affected; even, there was a tendency for an increase in growth by B treatment. By contrast, the dry matter production of all other genotypes was markedly decreased by the applied B, particularly in the genotypes Lagost-3, Dicle-74, Brachoua/134xS-61 and Gerbrach. In case of the genotypes Brachoua/134xS-61 and Gerbrach, B application reduced dry weight of the plants by 2-fold. Interestingly, there was no relationship between shoot B concentrations and relative decreases in shoot dry weight by B toxicity. The most B-sensitive genotypes had generally much lower amount of B in shoot than the genotypes showing higher tolerance to B toxicity. This result indicates that the B-exclusion mechanism is not involved in differential expression of B tolerance within 70 durum wheat genotypes. It seems very likely that the internal mechanisms (e.g., adsorption to cell walls and compartementation of B in vacuoles) could be a more plausible explanation for B tolerance in the durum wheats tested in the present study.

Key Words: Boron toxicity, boron concentration, durum wheat, genotypic variation

Bor Toksisitesine Tolerans Bakımından 70 Makarnalık Buğdayda Genotipsel Farklılığın Araştırılması

Özet: Toprakta bor (B) toksisitesine karşı genotipsel farklılığın boyutunu araştırmak amacıyla 70 makarnalık buğday (*Triticum durum*) genotipi ile bir sera denemesi kuruldu. Bitkiler, extrakte edilebilir B'un 12 mg kg^{-1} olduğu bir toprakta iki ayrı B muamelesine tutularak (+B: 25 mg B kg^{-1} toprak; -B: 0 mg B kg^{-1} soil) yetiştirildi. Otuz günlük bir büyüme döneminden sonra bitkilerin yalnızca yeşil aksamı hasat edildi ve genotipler kuru madde ağırlığı ve yeşil aksam B konsantrasyonu bakımından analiz edildi. Genotipler arasında topraktaki B toksisitesine karşı, toksisite belirtilerinin şiddeti ve büyümedeki azalma bakımından büyük bir genotipsel varyasyonun olduğu bulundu. Test edilen genotiplerden Sabil-1, Stn "S", Aconhi-89 ve Wadelmez-2, B uygulamasından etkilenmedi ve hatta bu genotiplerde B'dan dolayı büyümede bir artma eğilimi ortaya çıktı. Buna karşılık, diğer genotiplerin tümünde B uygulaması sonucu kuru madde ağırlığında azalmalar ortaya çıktı; bu azalmalar özellikle Lagost-3, Dicle-74, Brachoua/134xS-61 ve Gerbrach genotiplerinde görüldü. Genotiplerden Brachoua/134xS-61 ve Gerbrach'da B'dan dolayı kuru madde oluşumundaki azalma 2 kattan daha fazlaydı. İlginçtir ki, yeşil aksam B konsantrasyonu ile B'dan dolayı kuru madde oluşumunda ortaya çıkan azalma yüzdesi arasında hiçbir ilişki bulunamadı. Genel olarak B toleransı yüksek genotipler yüksek miktarlarda B birikimi gösterirken, duyarlı genotiplerde düşük düzeylerde B birikimi görülmüştür. Bu sonuçlar, 70 genotip arasında görülen farklı B toleransının, B'un köklerce alınmayarak dışarıda tutulması mekanizması ile ilişkili olmadığını göstermiştir. Bu çalışmada test edilen genotipler arasındaki B'a karşı farklı duyarlılığı açıklamada B'un hücre duvarlarında tutulması gibi içsel tolerans mekanizmaları daha kabul edilebilir mekanizma olarak karşımıza çıkmaktadır.

Anahtar Sözcükler: Bor toksisitesi, bor konsantrasyonu, makarnalık buğday, genotipsel farklılık

*Correspondence to: atorun@cu.edu.tr

Introduction

Boron toxicity is a common mineral nutritional problem in arid and semiarid regions, causing significant decreases in growth and yield as reported for many countries (Nable et al., 1997). Also in Turkey, B toxicity has been reported as an important constraint to crop production, particularly in Central Anatolia (Sillanpaa, 1982). According to a soil survey study conducted by Gezgin et al. (2002) the concentration of extractable B with 0.01 M mannitol in 898 soil samples ranged from 0.01 to 63.9 mg kg^{-1} soil with a mean value of 2.48 mg kg^{-1}. Nearly 10 % of the soils sampled in Central Anatolia contained more than 5 mg extractable B per kg soil which is widely accepted critical concentration for occurrence of B toxicity in crop plants (Nable et al., 1997). A similar observation has been recently made by Avcı and Akar (2005) in a survey study on the barley grown fields in Central Anatolia and Transitional zones. According to this survey study, 15% and 6% of the samples collected at 189 sites showed light and severe B toxicity symptoms, respectively.

There are several approaches to B toxicity-related decreases in crop production, such as leaching B from soil profile and application of several organic compounds to inactivate (immobilize) B in soil (Keren and Bingham, 1985; Nable et al., 1997). However, such approaches to ameliorate B toxic soils are not practical and economically feasible to apply on large scale of areas with B toxicity. Alternatively, new plant genotypes could be developed with higher genetical ability to tolerate B toxicity in soils. Several screening studies have been conducted to determine the extent of genotypic variation in tolerance to B toxicity in different crop species such as wheat (Paull et al., 1988; Yau et al., 1995; Jamjod, 1996) and barley (Nable, 1988; Mahalakshmi et al., 1995). These studies showed existence of a large genotypic variation in susceptibility to B toxicity. Genotypes with higher tolerance to B toxicity in soil can be used in breeding programs to develop new and more B-tolerant cultivars for B-toxic soils.

Despite large number studies on B toxicity, physiological mechanisms affecting differential expression of B toxicity stress between genotypes are not well understood. Differences in root uptake, root-to-shoot transport and shoot accumulation of B should play a decisive role in differential expression of B tolerance between genotypes. As reviewed by Nable et al. (1997), the level of B accumulated in shoot does not always correlate with the severity of B toxicity symptoms. In some genotypes, reduced uptake of B by roots plays a critical role in development of high tolerance to B toxicity while in some genotypes internal mechanisms (e.g., detoxification of B at cellular level) are involved in B tolerance.

As reported by Yau et al. (1995), durum wheats are highly sensitive to B toxicity. In durum wheat, genotypic variation to B is much lower than barley and bread wheat. Due to higher tolerance to B toxicity it is important to test new durum wheat germplasms to identify new genotypes with much higher tolerance to B toxicity. For a successful breeding program for development of B-tolerant genotypes, existence of a substantial genotypic variation is essential. In order to achieve a large genetic variation in B tolerance large number of genotypes should be used in the screening studies. However, in most cases, the screening studies related to the B toxicity tolerance included only a few genotypes (see Nable et al., 1997 for references). Therefore, in the present work, 70 durum wheat genotypes have been used to study the extent of genotypic variation in tolerance to B toxicity in soil. In addition, we have also studied the relationship between shoot B concentration and susceptibility of genotypes to B toxicity.

Materials and Methods

Using 70 durum wheat genotypes (*Triticum durum*) a greenhouse experiment has been carried out to study genotypic variation for tolerance to B toxicity in soils. Seeds of 70 durum wheat genotypes were obtained from the Department of Field Crops of the University of Çukurova, Adana. Plants were grown on a B-toxic soil which was transported from a B-toxic field close to Eskişehir in Central Anatolia (Torun et al., 2003). The soil, used in the pot experiment had the following chemical and physical properties: texture loamy, $CaCO_3$ 33.4%, pH 7.69, organic matter 1.97%, and the DTPA-extractable concentration of Zn, Fe, Mn and Cu were 0.23, 1.11, 5.63 and 0.59, respectively. All analysis of the mentioned chemical and physical properties of soils was carried out by using standard methods described by Page et al. (1982), Klute et al. (1986) and Lindsay and Norvell (1978). The concentration of B extracted by $CaCl_2$/ Mannitol method was 12 mg kg^{-1} soil and

measured by using the method described in Cartwright et al. (1983).

Twenty seeds were sown in plastic pots containing 1.6 kg soil with (25 mg B per kg soil) and without B supply. Boron was supplied in form of boric acid (H_3BO_3). Before potting the soil was homogeneously treated with a basal application of 200 mg N kg^{-1} soil as $Ca(NO_3)_2$. $4H_2O$, 100 mg P kg^{-1} soil and 125 mg K kg^{-1} soil as KH_2PO_4. After emergence, the plants were thinned to 10 seedlings per pot. After 30 days of growth under greenhouse conditions (when the symptoms of B toxicity were severe for most of genotypes), only shoots were harvested and dried at 70 °C and ashed in microwave by using 2 ml of 35% H_2O_2 and 4 ml of 65% HNO_3. Following digestions, plant samples have been analyzed for B concentration by using the Azomethin-H method as described by Bingham (1982). Boron measurements were checked by using the certified B values in standard leaf samples obtained from the National Institute of Standards and Technology (Gaithersburg, MD, USA).

The total amount (content) of B per shoot was calculated by multiplying shoot B concentration with the shoot dry weights. The relative decrease in yield by B supply was calculated as given below:

Decrease % = [1-(Shoot dry weight at +B) / (Shoot dry weight at-B)] x 100

All measurements were taken in independent 3 replications. The data given in all tables represent means ± SD of three independent replications.

Results

There was an important variation in severity and development time of B toxicity symptoms on leaves of 70 durum wheat genotypes when treated with B after 30 days. Among the genotypes tested, the genotypes with the number 5, 33 and 34 developed most rapidly B toxicity symptoms while the genotypes 3 and 4 developed very slight symptoms. Boron toxicity symptoms first appeared on the tips of older leaves by causing development of necrosis and drying of leaf tissue. With time, the symptoms became more severe and developed on the most part of older leaves. In most of genotypes, severity of B toxicity symptoms was associated with corresponding decreases in shoot dry matter production (Table 1).

There was a substantial genotypic difference in decreases of shoot dry matter production caused by B toxicity. While in some genotypes dry matter production was not affected from B toxicity, most of genotypes were, however, particularly sensitive ones and showed marked decreases in dry matter production. Interestingly, application of B at 25 mg per kg soil did not decrease the growth of the genotypes 1, 2, 3 and 4, but, even tended to improve the dry matter production. In contrast to these 4 genotypes, all other genotypes were severely affected from B-toxicity especially 67, 68, 69 and 70. In these 4 B-susceptible genotypes given at the bottom of Table 1, the shoot dry matter production was decreased nearly by factor 2 as a consequence of B application (Table 1).

Shoot B concentration of the genotypes ranged from 324 mg kg^{-1} (Lahn / Haucan-1) to 648 mg kg^{-1} (Mrb 16/3/Ente/Mario//) with an average value of 475 mg kg^{-1} (Table 2). Most of the genotypes had B concentrations between 400 to 500 mg kg^{-1}. Boron application increased shoot concentration of all genotypes from 475 to 1525 mg kg^{-1} dry weight. All genotypes contained more than 1000 mg B per kg shoot dry weight, indicating very high B accumulation in tissue after B application (Table 2). Among the genotypes tested, Andorrio-1, Omruf-3, Brachoua/134xS-61 and 85-ÇZT-14 had the highest B concentrations with around 1700 mg kg^{-1} dry weight, while the genotypes 86-ÇZT-0198, Wadelmez-6 and Wadelmez-2 were the genotypes possessing the lowest B concentration in shoot (e.g., around 1100 mg kg^{-1}) under B supply (Table 2). Also in the case of the total amount of B (content) genotypes showed large variation under both B treatments (Table 2). When B was not supplied, the shoot content of B varied from 63 µg $plant^{-1}$ (Zeina-2) to 163 µg $plant^{-1}$ (Dicle-74) with an average value of 100 µg $plant^{-1}$. Interestingly, the most B sensitive genotype Gerbrach-1 had the lowest amount of B in shoot, while the second most tolerant genotype Stn "S" contained the highest level of shoot B content (Table 2).

The relative decreases in shoot dry matter production were compared with the concentration and content of B in plants at B treatment (Figure 1). There was no significant relationship between the B concentration of plants and the decreases in shoot dry weight by B application (R^2 = 0.0018). Most interestingly, the total amount of B in shoot showed a very significant (R^2 = 0.49***) negative correlation with decreases in shoot dry

Table 1. Effect of varied supply of B (+B = 25 mg B kg^{-1}) on the dry matter production of 70 durum wheat genotypes grown for 30 days under greenhouse conditions on a soil containing 12 mg extractable B kg^{-1}. Data represent means ± SD of 3 independent replications.

	Genotypes	Dry Weight (mg $plant^{-1}$) -B	Dry Weight (mg $plant^{-1}$) +B	Decrease (%) in Dry Weight by B
1	Sabil-1	191 ± 3	213 ± 33	-11.5
2	Stn "S"	205 ± 21	228 ± 11	-11.2
3	Aconchi-89	171 ± 15	177 ± 47	-3.5
4	Wadelmez-2	217 ± 21	225 ± 27	-3.6
5	Yav "S"//H. Red	199 ± 10	193 ± 24	3.0
6	Dipper-6	197 ± 44	191 ± 41	3.0
7	Omruf-1	170 ± 12	161 ± 4	5.3
8	Mrb 16/3/Ente/Mario//	212 ± 6	200 ± 42	5.7
9	Mque/Oyca "S"//Cta "S"/Guil "S"	198 ± 4	186 ± 11	6.1
10	Chanst	225 ± 5	208 ± 20	7.6
11	Genil-3	202 ± 12	186 ± 17	7.9
12	Stn "S"//Hui "S"/Somo "J"	205 ± 1	188 ± 40	8.3
13	Bicre/Guerou 1	191 ± 37	175 ± 38	8.4
14	Diyarbakır-81	218 ± 30	199 ± 4	8.7
15	Chacan	197 ± 17	180 ± 23	8.6
16	86 ÇZT 0918	238 ± 36	216 ± 20	9.2
17	Yavaros-79	228 ± 31	206 ± 11	9.6
18	Stn//Hui/Somo	221 ± 25	197 ± 21	10.9
19	Bartramia-1	273 ± 10	239 ± 18	12.5
20	Nehama-22	179 ± 11	156 ± 3	12.8
21	Gediz-75	214 ± 20	183 ± 18	14.5
22	Fardes	176 ± 34	149 ± 16	15.3
23	Balcalı-85	225 ± 15	182 ± 14	19.1
24	Ausn/5/Cando/4/By*2	177 ± 23	143 ± 27	19.2
25	Heican-1	194 ± 18	157 ± 35	19.1
26	Korifla	223 ± 14	180 ± 3	19.3
27	D-5456	224 ± 24	181 ± 13	19.2
28	Awalbit-6	186 ± 7	150 ± 6	19.4
29	Memo/Yav//Auk	213 ± 7	171 ± 4	19.7
30	Platalea-10	228 ± 18	179 ± 1	21.5
31	DUKEM-15	216 ± 7	166 ± 11	23.1
32	Gersabil-1	196 ± 23	150 ± 6	23.5
33	Stn//Hui/Somo	211 ± 35	161 ± 13	23.7
34	Waha (Sham-I)	213 ± 25	162 ± 31	23.9
35	Lahn	237 ± 5	179 ± 24	24.5

Table 1. Continued.

		Dry Weight (mg plant^{-1})		% Decrease in Dry Weight by B
	Genotypes	-B	+B	
36	AJAIA-11	225 ± 29	169 ± 35	24.9
37	AAZ	183 ± 7	137 ± 16	25.1
38	Om Rabi-3	191 ± 28	142 ± 48	25.7
39	Altar/Somo//Auk	151 ± 15	111 ± 52	26.5
40	Bagan-5	227 ± 51	167 ± 16	26.4
41	Moulsabil-1	216 ± 13	158 ± 23	26.9
42	Genil-5	204 ± 5	149 ± 44	27.0
43	Korifla (Sham-III)	214 ± 28	156 ± 20	27.1
44	Zeina-2	184 ± 26	131 ± 7	28.8
45	Omruf-2	221 ± 22	157 ± 27	29.0
46	Haucan/omRabi 12	246 ± 35	174 ± 14	29.3
47	85 ÇZT 14	192 ± 2	133 ± 33	30.7
48	Om Rabi-6	199 ± 14	137 ± 10	31.2
49	Guil/Apo//Ru/3/Chahbz	242 ± 48	166 ± 0	31.4
50	Wadelmez-6	212 ± 8	145 ± 49	31.6
51	Zeina-4	197 ± 11	134 ± 8	32.0
52	Lahn/Haucan-1	207 ± 18	140 ± 0	32.4
53	Gutruos-5	252 ± 6	170 ± 8	32.5
54	Omruf-3	189 ± 32	126 ± 28	33.3
55	Lahn/Haucan-2	209 ± 15	135 ± 18	35.4
56	Gdo V2 512/Cit//Ruff	229 ± 21	148 ± 0	35.4
57	Yazı-40	209 ± 41	131 ± 55	37.3
58	Nehama-15	193 ± 16	121 ± 61	37.3
59	Aw12/Bit	176 ± 17	108 ± 25	38.6
60	Stojocri-7	217 ± 13	132 ± 14	39.2
61	Waha-1	188 ± 2	114 ± 8	39.4
62	Om Rabi5/Omguer-3	205 ± 44	124 ± 25	39.5
63	Waha-2	197 ± 24	119 ± 7	39.6
64	Andorrio-1	180 ± 8	106 ± 34	41.1
65	TE 8606 (Portugal)//Ch67//	255 ± 17	148 ± 37	42.0
66	Lagost-3	294 ± 28	165 ± 52	43.9
67	Dicle-74	321 ± 21	176 ± 23	45.2
68	Brachoua/134xS-61	242 ± 10	131 ± 78	45.9
69	Jabiru-4	227 ± 11	109 ± 18	52.0
70	Gerbrach-1	198 ± 12	87 ± 41	56.1
	Mean	217	165	23.6

Table 2. Effect of varied supply of B (+B = 25 mg B kg^{-1}) on the shoot B concentration and total amount of B (content) per shoot of 70 durum wheat genotypes grown for 30 days under greenhouse conditions on a soil containing 12 mg extractable B kg^{-1}. Data represent means ± SD of 3 independent replications.

		B Concentrations (mg kg^{-1})		B Content (µg $plant^{-1}$)	
	Genotypes	-B	+B	-B	+B
1	Sabil-1	501 ± 23	1443 ± 163	107 ± 2	305 ± 12
2	Stn "S"	508 ± 43	1654 ± 207	104 ± 5	378 ± 66
3	Aconchi-89	386 ± 16	1611 ± 195	66 ± 7	281 ± 41
4	Wadelmez-2	428 ± 18	1195 ± 279	93 ± 10	265 ± 31
5	Yav "S"//H. Red	574 ± 24	1663 ± 112	115 ± 10	322 ± 62
6	Dipper-6	405 ± 59	1528 ± 320	79 ± 14	285 ± 1
7	Omruf-1	555 ± 23	1606 ± 77	94 ± 5	258 ± 6
8	Mrb 16/3/Ente/Mario//	648 ± 21	1615 ± 109	137 ± 8	325 ± 90
9	Mque/Oyca "S"//Cta "S"/Guil "S"	496 ± 61	1709 ± 45	98 ± 12	318 ± 28
10	Chanst	558 ± 58	1405 ± 23	125 ± 10	292 ± 23
11	Genil-3	451 ± 47	1410 ± 29	91 ± 14	262 ± 19
12	Stn "S"//Hui "S"/Somo "J"	451 ± 11	1290 ± 70	93 ± 3	241 ± 38
13	Bicre/Guerou 1	501 ± 4	1615 ± 57	101 ± 22	281 ± 52
14	Diyarbakır-81	430 ± 18	1610 ± 145	93 ± 14	321 ± 36
15	Chacan	468 ± 41	1496 ± 52	93 ± 15	270 ± 43
16	86 ÇZT 0918	459 ± 19	1144 ± 28	109 ± 12	247 ± 17
17	Yavaros-79	521 ± 21	1584 ± 13	118 ± 12	326 ± 21
18	Stn//Hui/Somo	436 ± 31	1451 ± 21	97 ± 17	286 ± 27
19	Bartramia-1	389 ± 25	1508 ± 158	106 ± 6	359 ± 10
20	Nehama-22	467 ± 50	1506 ± 34	84 ± 11	235 ± 10
21	Gediz-75	548 ± 66	1391 ± 1	118 ± 26	254 ± 26
22	Fardes	495 ± 43	1479 ± 111	86 ± 9	221 ± 40
23	Balcalı-85	639 ± 16	1572 ± 36	144 ± 13	286 ± 16
24	Ausn/5/Cando/4/By*2	563 ± 52	1660 ± 42	99 ± 6	238 ± 51
25	Heican-1	424 ± 34	1268 ± 239	82 ± 7	195 ± 7
26	Korifla	366 ± 14	1672 ± 95	81 ± 5	301 ± 22
27	D-5456	452 ± 44	1472 ± 59	101 ± 13	267 ± 29
28	Awalbit-6	487 ± 24	1317 ± 95	91 ± 6	198 ± 22
29	Memo/Yav//Auk	593 ± 64	1566 ± 49	126 ± 17	268 ± 15
30	Platalea-10	383 ± 19	1439 ± 158	87 ± 3	257 ± 26
31	DUKEM-15	629 ± 8	1620 ± 17	136 ± 4	269 ± 16
32	Gersabil-1	509 ± 44	1412 ± 233	100 ± 19	212 ± 43
33	Stn//Hui/Somo	470 ± 11	1498 ± 2	100 ± 19	241 ± 19
34	Waha (Sham-I)	561 ± 72	1495 ± 15	120 ± 22	242 ± 49
35	Lahn	504 ± 67	1504 ± 83	119 ± 13	270 ± 51

Table 2. Continued.

	Genotypes	B Concentrations (mg kg^{-1}) -B	B Concentrations (mg kg^{-1}) +B	B Content (µg plant^{-1}) -B	B Content (µg plant^{-1}) +B
36	AJAIA-11	459 ± 97	1400 ± 45	99 ± 34	236 ± 42
37	AAZ	566 ± 78	1541 ± 54	103 ± 10	211 ± 17
38	Om Rabi-3	535 ± 33	1627 ± 79	101 ± 11	229 ± 67
39	Altar/Somo//Auk	511 ± 59	1220 ± 193	78 ± 17	130 ± 42
40	Bagan-5	465 ± 77	1589 ± 95	105 ± 30	265 ± 9
41	Moulsabil-1	589 ± 52	1654 ± 179	128 ± 18	259 ± 9
42	Genil-5	466 ± 47	1517 ± 119	95 ± 11	223 ± 49
43	Korifla (Sham-III)	430 ± 50	1588 ± 100	93 ± 22	247 ± 16
44	Zeina-2	339 ± 53	1629 ± 215	63 ± 15	213 ± 17
45	Omruf-2	448 ± 48	1674 ± 36	98 ± 4	262 ± 39
46	Haucan/omRabi 12	409 ± 13	1601 ± 45	100 ± 12	279 ± 30
47	85 ÇZT 14	626 ± 39	1781 ± 13	120 ± 7	237 ± 56
48	Om Rabi-6	427 ± 16	1639 ± 57	85 ± 3	224 ± 8
49	Guil/Apo//Ru/3/Chahbz	424 ± 74	1597 ± 13	103 ± 27	265 ± 2
50	Wadelmez-6	341 ± 29	1172 ± 219	72 ± 3	165 ± 26
51	Zeina-4	415 ± 39	1514 ± 111	81 ± 5	203 ± 28
52	Lahn/Haucan-1	376 ± 38	1441 ± 145	78 ± 7	202 ± 20
53	Gutruos-5	423 ± 25	1506 ± 6	106 ± 3	256 ± 14
54	Omruf-3	539 ± 9	1731 ± 138	102 ± 18	216 ± 32
55	Lahn/Haucan-2	324 ± 40	1495 ± 29	68 ± 12	201 ± 24
56	Gdo V2 512/Cit//Ruff	386 ± 75	1545 ± 11	87 ± 6	229 ± 2
57	Yazı-40	479 ± 53	1458 ± 76	99 ± 9	189 ± 70
58	Nehama-15	456 ± 46	1594 ± 22	89 ± 16	192 ± 94
59	Aw12/Bit	438 ± 42	1274 ± 139	77 ± 4	139 ± 47
60	Stojocri-7	550 ± 27	1568 ± 54	119 ± 1	207 ± 15
61	Waha-1	516 ± 1	1637 ± 1	97 ± 1	187 ± 14
62	Om Rabi5/Omguer-3	435 ± 54	1506 ± 3	88 ± 8	187 ± 39
63	Waha-2	499 ± 58	1589 ± 6	98 ± 9	189 ± 12
64	Andorrio-1	519 ± 60	1732 ± 127	93 ± 10	181 ± 45
65	TE 8606 (Portugal)//Ch67/	451 ± 75	1491 ± 40	114 ± 11	221 ± 61
66	Lagost-3	453 ± 70	1656 ± 13	134 ± 30	273 ± 84
67	Dicle-74	506 ± 18	1461 ± 18	163 ± 21	257 ± 36
68	Brachoua/134xS-61	345 ± 16	1770 ± 251	83 ± 9	222 ± 105
69	Jabiru-4	464 ± 96	1685 ± 205	105 ± 17	182 ± 9
70	Gerbrach-1	415 ± 61	1468 ± 223	83 ± 16	123 ± 41
Mean		475	1525	100	244

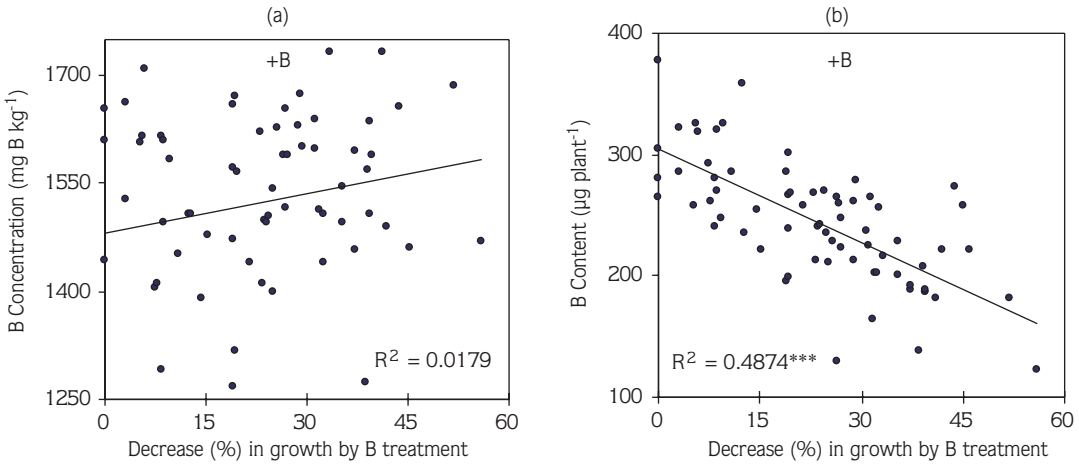

Figure 1. Relationships between the shoot concentration (a) and content (b) of B and the relative decreases in shoot growth caused by B treatment in seventy 30-day-old durum wheat genotypes grown on a soil treated with 25 mg B kg soil^{-1}.

weight under B supply (Figure 1), indicating existence of a poor relationship between B concentration of plants and decreases in shoot growth under B toxicity.

Discussion

The results obtained indicate a substantial range of genotypic tolerance to B toxicity in soil between 70 durum wheat genotypes. This genotypic variation in tolerance to B toxicity was based on the decreases in dry matter production after growing genotypes under B supply (Table 1) and also the extent of the B-toxicity symptoms on the leaves. Among the genotypes tested the genotypes Sabil-1 and Stn "S" were the most tolerant, while the genotypes Jabiru-4 and Gerbrach-1 were classified as the most sensitive genotypes to B toxicity. When B added to soil at 25 mg kg^{-1} soil, the dry matter production capacity of Sabil-1 and Stn "S" was not affected, while there was around 50 % decrease in dry weight of the genotypes Jabiru-4 and Gerbrach-1 (Table 1). A similar genetic variation in tolerance to B toxicity was also shown in other durum wheat genotypes by Jamjod (1996) in 300 durum wheat and by Yau et al. (1995) in 19 durum wheat genotypes. Existence of such large genotypic variation is promising and can be exploited in breeding programs aiming at development of B-tolerant genotypes. In wheat, several chromosomal regions and DNA markers have been identified to use in molecular marker-assisted selection for B toxicity tolerant genotypes (Jefferies et al., 2000).

The reason for the large genotypic variation in tolerance to B toxicity could not be understood. Despite considerable differences in shoot B concentration of genotypes, there was a very poor relationship between shoot B concentration and decreases in growth caused by B toxicity (Figure 1; Table 2). For most of the genotypes, the shoot concentrations of B were not related to the B toxicity–induced decreases in shoot growth. Similar results were also reported for both greenhouse-grown (Mahalakshmi et al., 1995) and field-grown (Torun et al., 2003) barley genotypes. Differences in susceptibility to B toxicity in soil did not correlate with leaf or shoot concentration of B. Also in the case of durum wheat (Yau et al., 1995), the shoot B concentration was not related to the shoot growth under B toxicity conditions. By contrast, in several other studies conducted with cereal and legume species, it has been found that the genotypes having higher tolerance to B toxicity had accordingly lower concentration of B in shoot (Nable, 1988; Paull et al., 1992a, 1992b). The reason for the controversial results between different studies could not be understood, and might be related to the different experimental conditions and genotypes used in the corresponding studies. In good agreement with this suggestion, Figure 1 shows that some genotypes are available within the 70 durum wheat genotypes in which

a close relationship could be found between shoot B concentration and decreases in shoot growth due to B toxicity.

The concentration of B in shoot can be affected by the inherently different growth rates (dry matter production rates) of genotypes, which can cause a dilution or concentration effects on the B concentration in the tissue. Therefore, we calculated the total amount of B per shoot (e.g., B content). It was interesting to notice that there was a very clear inverse relationship between the total amount of B per shoot and the decreases in shoot dry matter production by B toxicity (Figure 1). This inverse relationship was statistically very significant (R^2 = 0.49***), and clearly indicates that for just all genotypes tested in the present study the B-exclusion mechanism does not operate as a tolerance mechanism, which could result in lower accumulation of B in the plant tissue. It seems very likely that the internal mechanisms are primarily involved in differential expression of B toxicity tolerance in the 70 durum wheat genotypes. As discussed by Nable et al. (1997) and Wimmer et al. (2003), there are several internal mechanisms affecting high B tolerance at cellular level, such as differential pattern in B distribution at cellular or organ level and adsorption (fixation) of B by cell walls. According to Wimmer et al. (2003), level of soluble B (not total B) concentration in cytoplasm could be an important physiological parameter for understanding the role of the tissue B in expression of B toxicity in plants.

Further work is, therefore, needed to test the most tolerant and sensitive genotypes presented in Table 1 for the amount of the cell wall-adsorbed B and the water soluble B. This work could contribute to a better understanding of the physiological mechanisms involved in differential expression of B toxicity within the 70 durum wheat genotypes. The results obtained from such physiological studies could be helpful in development of reliable screening parameters for selection of B-tolerant genotypes in breeding programs. In addition, the most promising genotypes should be tested under field conditions on B toxic soils to verify the results.

Acknowledgements

This research has been financially supported by the Çukurova University Research Fund.

References

Avcı, M. and T. Akar. 2005. Severity and spatial distribution of boron toxicity in barley cultivated areas of Central Anatolia and Transitional Zones. Turk. J. Agric. For. 29: 377-382.

Bingham, F.T. 1982. Methods of soil analysis. Part 2. Chemical and Microbiological Properties. Agronomy Monograph No: 9, 2nd Ed. Am Soc. of Agron. Soil Sci. Soc. of Am, USA.

Cartwright, B., K.G. Tiller, B.A. Zarcinas and L.R. Spouncer. 1983. The chemical assessment of the boron of soils. Aust. J. Soil Res. 21: 321-332.

Gezgin, S., N. Dursun, M. Hamurcu, M. Harmankaya, M. Önder, B. Sade, A. Topal, N. Çiftçi, B. Acar and M. Babaoğlu. 2002. Determination of Boron contents of soils in Central-Anatolia Cultivated Lands and its relationship, between soil and water characteristics. In: Boron in Plant and Animal Nutrition. 1st ed. (Ed: H. E. Goldbah). Kluwer Academic Pub. New York. pp: 391-400.

Jamjod, S. 1996. Genetics of boron tolerance in durum wheat. Ph. D. Thesis, The University of Adelaide, South Australia.

Jefferies, S.P., M.A. Palotta and J.G. Paull. 2000. Mapping and validation of chromosome regions conferring boron toxicity tolerance in wheat (*Triticum aestivum*) Theor. Appl. Gen. 101: 767-777.

Keren, R. and Bingham, F.T. 1985. Boron in water, soils and plants. Adv. Soil Sci. 1: 230-276.

Klute, A., G.S. Campbell, R.D. Jackson, M.M. Mortland and D.R. Nielsen. 1986. Methods of soil analysis. Part 1. Physical and Mineralogical Methods (Second edition). Madison, Wisconsin USA.

Lindsay, W.L. and W.A. Norvell. 1978. Development of DTPA soil test for zinc, iron, manganese, and copper. Soil Sci. Soc. Am. J. 42: 421-428.

Mahalakshmi, V., S.K. Yau, J. Ryan, and J.M. Peacock. 1995. Boron toxicity in barley (*Hordeum vulgare* L) seedlings in relation to soil temperature. Plant Soil 177: 151-156

Nable, R.O. 1988. Resistance to boron toxicity amongst several barley and wheat cultivars: a preliminary examination of the resistance mechanism. Plant Soil 112: 45-57.

Nable, R.O., G. S. Banuelos and J. G. Paull. 1997. Boron Toxicity. Plant Soil 198: 111-115.

Page , A.L., R.H. Miller, D.R. Keeney, D.E. Baker, R. Ellis and J.D. Rhoades. 1982. Methods of soil analysis. Part 2. Chemical and Microbiological Properties (Second edition). Madison, Wisconsin USA.

Paull, J.G., R.O. Nable and A.J. Rathjen. 1992a. Physiological and genetic control of the tolerance of wheat to high concentrations of boron and implications for plant breeding. Plant Soil 146: 251-260.

Paull, J.G., R.O. Nable, A.W.H. Lake, M.A. Materne and A.J. Rathjen. 1992b. Response of annual medics (*Medicago* spp) and field peas (*Pisum sativum*) to high concentrations of boron: genetic variation and the mechanism of tolerance. Aust. J. Agric. Res. 43: 203-213.

Paull, J.G., A.J. Rathjen and B. Cartwright. 1988. Genetic control of tolerance to high concentrations of soil boron in wheat. In Proc. 7th Int. Wheat Genetics Symposium, Cambridge. Eds. T.E. Miller and R.M.D. Koebner, pp 871-877.

Sillanpaa, M. 1982. Micronutrients and the nutrient status of soils: A global study. FAO Soils Bulletin 48. Rome: Food and Agriculture Organization of the United Nations.

Torun, B., M. Kalaycı, L. Öztürk, A. Torun, M. Aydın, and İ. Çakmak. 2003. Differences in shoot boron concentrations, leaf symptoms, and yield of Turkish barley cultivars grown on boron-toxic soil in field. J. Plant Nutr. 26: 1735-1747.

Wimmer, M.A., K.H. Muhling, A. Lauchli, P. H. Brown and H.W.E. Goldbach. 2003. The interaction between salinity and boron toxicity affects the subcellular distribution of ions and proteins in wheat leaves. Plant Cell Environ. 26: 1267-1274

Yau, S.K., M.M. Nachit, J. Ryan and J. Hamblin. 1995. Phenotypic variation in boron toxicity tolerance at seedling stage in durum wheat (*Triticum durum*). Euphytica 83: 185-191.