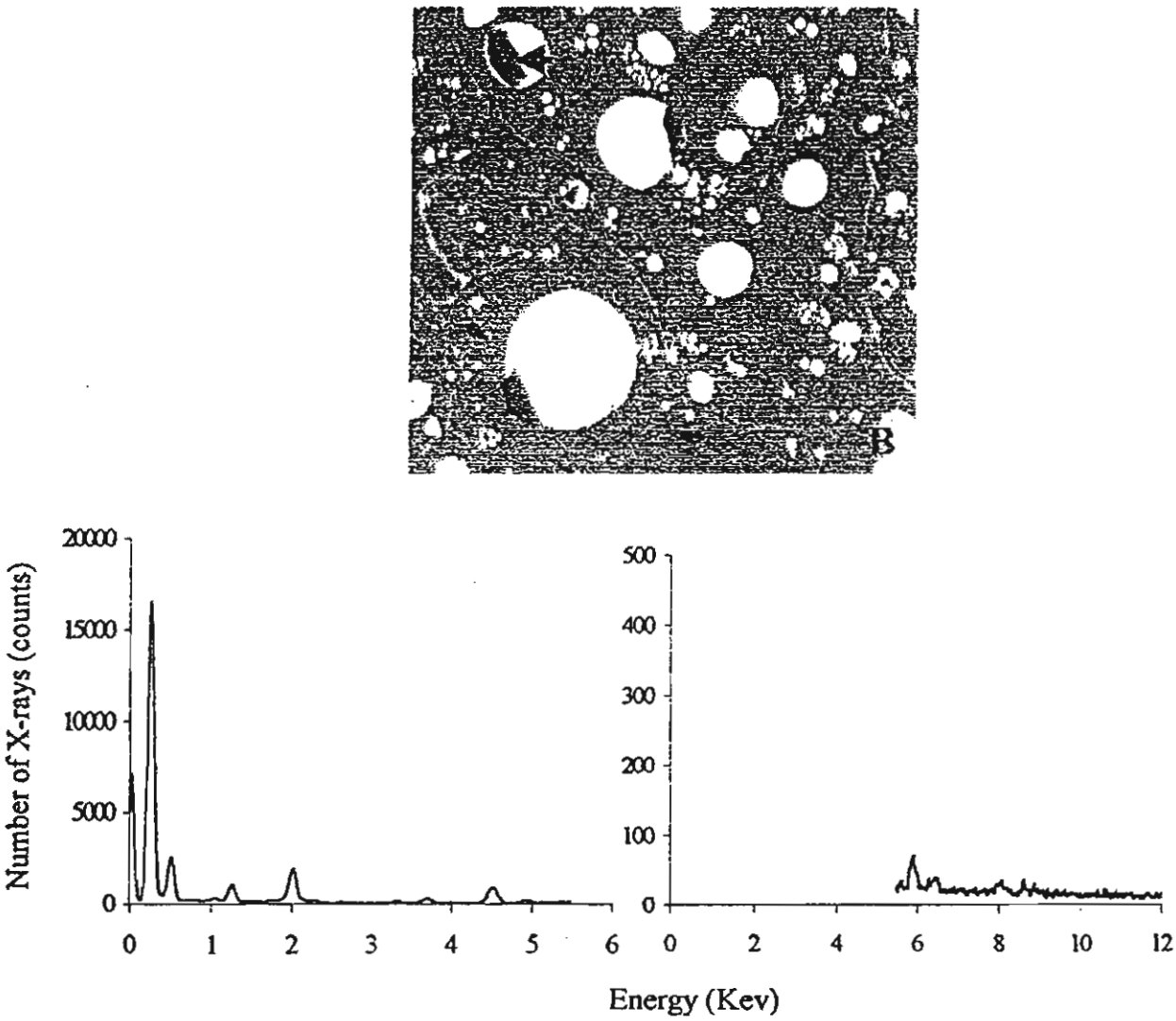

Fig. 5 Electron micrographs of protein bodies (A, B; arrow) in embryonic cell with phytin inclusion of IR68144 (A) and EDX-analysis spectrum from A (macronutrient; A1 and micronutrient; A2). Protein bodies without phytin inclusion of KDML105 (B) and EDX-analysis spectrum from B have no minerals showing in the spectrum (macronutrient; B1 a micronutrient; B2).

Boron efficient germplasm identified in *Vigna mungo* (L.) Hepper and *Vigna radiata* (L.) Wilczek

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Abstract

Boron (B) deficiency affect to seedling vigor of mungbean, black gram (*Vigna mungo* (L.) Hepper) and green gram (*Vigna radiata* (L.) Wilczek) and it affect to seed yield of black gram. Using B efficient genotypes can alleviate boron deficiency in mungbean. The aims of this study were to evaluate responses to B in black gram (*Vigna mungo* (L.) Hepper) and green gram (*Vigna radiata* (L.) Wilczek) genotypes, to determine the range of B efficiency in the two species and to identify germplasm for a breeding program to improve B efficiency. Sixteen genotypes of black gram (BG) and 26 genotypes of green gram (GG) were screened for B efficiency in sand culture without added B by scoring symptoms in 3 weeks old seedlings. In black gram, 81.3% of the genotypes were rated as inefficient, 12.5% as moderately inefficient and one genotype (M1) was identified as efficient. In green gram, no genotypes were rated as inefficient, 58% were rated as moderately inefficient and 42% as moderately efficient. Six mungbean genotypes: M1 (BG: efficient), Regur (BG: inefficient), CPI79563 (BG: inefficient), KPS1 (GG: moderately efficient), VC2755 (GG: moderately efficient), VC1163 (GG: moderately inefficient) were

selected from the first screening and evaluated in sand culture with 4 levels of applied B: 0, 0.5, 3 and 5 μM (designated as B0, B0.5, B3, and B5, respectively). In B0, seed yield of Regur, CPI79563 and VC1163 were depressed by B deficiency but M1, KPS1 and VC2755 were unaffected. Seed yield of M1, KPS1 and VC275, however, were limited when grown in high B (≥3 μM B for M1; 5 μM B for KPS1 and VC2755). The results suggest that B-efficient mungbean genotypes can be readily identified by screening growth of three weeks old seedlings in sand culture without added B. The M1 (black gram), KPS1 and VC2755 (green gram) genotypes were apparently B-efficient genotypes and could be used on low B soil and in breeding for increasing the B efficiency of mungbean.

Key words: Boron deficiency, Boron efficiency, Black gram, Genotypic variation, Green gram, Mung bean

Introduction

Soils with low available-B are widespread (Sillanpaa, 1982) and extensive areas of low B soil have been identified in northern Thailand (Rerkasem et al., 1989). Boron deficiency enhanced abnormal seedlings (Rerkasem et al.,1990) and depressed seed yield of black gram and green gram in northern Thailand (Predisripipat, 1988). Boron deficiency could be alleviated by applying B fertilizer but the availability of B fertilizer depends on many factors such as soil pH, soil texture (Goldberg, 1997), soil and air temperature (Forno et al., 1979). Alternatively, B-efficient genotypes could be used on these problem soils.

Some genetic variation in B efficiency was found in green gram and black gram genotypes, although most green gram lines were not as sensitive to B deficiency as black gram (Rerkasem, 1990). However, some genotypes of green gram were moderately sensitive to B deficiency and some genotypes of black gram were moderately tolerant to low soil B. A suitable and rapid screening method is needed to identify B-efficient germplasm for a breeding program for mungbean in northern Thailand. If the prevalence of abnormal seedling growth in low B is related to seed yield in low B, than seedlings could be used to screen for B efficiency. The objectives of this study were to evaluate responses to B deficiency in green gram and black gram germplasm and determine the range of B efficiency in the two species at both the seedling stage and at maturity. The aim was to evaluate the effectiveness of a potential screening method that could identify B-efficient genotypes early in seedling growth.

Materials and methods

Experiment 1: Sand culture screening of seedlings

Sixteen genotypes of black gram and twenty-six genotypes of green gram were multiplied at Agronomy Department Faculty of Agriculture Chiang Mai University then all genotypes were screened for B efficiency in sand culture. The screening was conducted in trays (0.45 m wide, 0.7 m long and 0.35 m deep) containing washed river quartz sand. Before sowing, the B concentration of each genotype was determined using the Azomethine – H procedure (Lohse, 1982) after

dry ashing . Twenty-four seeds of each genotype were sown separately in 0.4 m rows. There are were 12 rows per tray. Check varieties with known B efficiency, Regur (black gram: inefficient Predisripipat, 1988) and KPS1 (green gram: moderately efficient Rerkasem ,1990) were sown in every tray. Two replication trays were tested. Trays were supplied twice daily with complete nutrient solution without added B. The nutrient solution, adapted from Broughton and Dilworth (1971), consisted of (μM): KNO_3, 5000; $CaCl_2$ 1000; $MgSO_4$ 250; KH_2PO_4 500; $C_6H_5O_7Fe$ 10; K_2SO_4 250; $MnSO_4$ 2; $ZnSO_4$ 0.5; $CuSO_4$ 0.1; Na_2MoO_2 0.1. At three weeks after sowing, seedlings were classified into 8 classes (Table 1) according to symptoms of abnormal apical and leaf growth (after Rekasem at al., 1990).

Experiment 2: The response of six mungbean genotypes to boron

Three black gram (M1, Regur and CPI79563) and three green gram genotypes (KPS1, VC2755 and VC1163) were chosen from experiment 1 to represent a range of B efficiency. The seeds of these genotypes were multiplied again at Agronomy Department. Than seven seeds of each genotype were sown in freely drained, earthenware pots (0.3 m diameter and 0.3 m deep) containing washed river quartz sand. Seeds were inoculated with Rhizobium. Pots were supplied twice daily with the nutrient solution described in experiment 1, but without KNO_3, amended with four levels of B: 0 (B0), 0.5 (B0.5), 3 (B3) and 5 (B5) μM. Boron treatments and genotypes were arranged in a factorial combination with 3 replications for each of two harvest times (H1 and H2). At 15 days after sowing seedlings were thinned to 3 plants per pot. At the R3 stage (H1), total dry matter, root dry matter, nodule dry matter and B concentration in the youngest fully expanded leaf (YFEL) of each pot were determined. At maturity (H2), total dry matter, root dry matter, nodule dry matter,

seed yield, pods per plant, seed per pod, 1000 seed weight and seed B concentration were determined. Boron concentration in plant tissue was determined as in experiment 1. Data were analysed statistically by analysis of variance. Mean of treatment was compared by Least Significant Difference (LSD). Correlation coefficient between characteristics was computed from the mean of two replications in experiment 1 and three replication in experiment 2.

Results

Experiment 1

At three weeks after germination, seedling scores of check varieties, Regur and KPS1, were 1-2 and 5-6, respectively. Genotypes were classified into 4 categories, namely, inefficient (I: seedling score 1-2), moderately inefficient (MI: seedling score 3-4), moderately efficient (ME: seedling score 5-6) and efficient (E: seedling score 7-8). In the black gram, 81.3% of the genotypes (13 genotypes) were rated as inefficient, 12.5% (2 genotypes) as moderately inefficient and only one genotype, M1, as efficient. For the green gram, no genotype was rated as inefficient, 57.7% of genotypes (15 genotypes) were rated as moderately in efficient and 42.3% (11 genotypes) as moderately efficient (Figure 1).

In the black gram population, there was no relationship between seedling score and seed B concentration but a significant correlation ($p<0.01$) between seed B concentration and seedling score was found when the M1 genotype was omitted ($r = 0.666$: Figure 2 a). In the green gram population, seed B concentration, which ranged

from 8.06 to 18.02 mg B kg^{-1}, did not correlate with seedling score (r=0.353: Figure 2 b).

Experiment 2

Boron concentrations in the YFEL of all genotypes increased with B supply. At the R3 stage, the B concentration in the YFEL of M1 was higher than in all other genotypes in B0, but at high B levels (B3 and B5), the B concentration in the YFEL of M1 was similar to most of the other genotypes (Table 2). Shoot dry matter of all genotypes, at the R3 stage, was not affected by B supply. However, at maturity, shoot dry matter of M1 and the three green gram genotypes was not affected by B deficiency but that of M1 and KPS1 was depressed in high B (B3 and B5 for M1; B5 for KPS1). Shoot dry matter at maturity of Regur and CPI79563 genotypes was depressed at B0 (Table 3).

Grain yield and pod number of Regur, CPI79563 and VC1163 genotypes were depressed by B deficiency at low B supply (B0 for Regur and VC1163: B0 and B0.5 for CPI79563) (Table 4). Grain yield and pod number of M1, KPS1 and VC2755 genotypes were not affected by B deficiency but grain yield of these genotypes was depressed in high B (Table 4). Most of the variation in seed yield in B0 could be explained by changes in pod number per plant (Figure 3).

Seed weight of Regur, CPI79563 and VC1163 genotypes was increased by B deficiency but seed weight of other genotypes was not affected by B levels (Table 5). In all genotypes except CPI79563 seed B concentration was increased by increasing B levels (Table 5). Seed B concentration of CPI79563 was very high in B0 although minimal seed was actually produced.

Discussion

As in previous studies (Rerkasem, 1990), we have found evidence in genetic variation of B efficiency in black gram and green gram genotypes. However, whereas previous reports emphasized the relative B efficiency of green gram and the inefficiency of black gram, the most efficient genotype in the two experiments was the black gram, M1. This suggest highly B efficient germplasm exists in both species and that selection for B efficiency could readily identify superior germplasm for the low B soils in North and North East Thailand (Rattanarat et al., 1994; Rerkasem, 1994). In addition to M1, two green gram genotypes (KPS1, VC2755) were rated as B efficient. The efficient genotypes might be sensitive to B toxicity because grain yield of these genotypes was depressed in high B. Therefore, these B-efficient genotypes should not be planted in areas with high soil B. Boron deficiency particularly limited processes related to pod setting in inefficient genotypes. It was shown previously that B deficiency reduces grain yield by reduces number of pod per plant.

In this study the seedling score from experiment 1 and seed yield in low B solution in experiment 2 were closely correlated (Figure 4). The genotypes which produced normal seedlings in low B also produced high grain yield in low B. The efficient and moderately efficient genotypes from experiment 1 were not affected by B deficiency in experiment 2. Therefore, screening for B efficiency based on visual symptoms in seedlings, 3 weeks after germination in low B sand culture appears to be effective in identifying B-efficient mungbeans. However, the screening method has to consider in seed B concentration because low B concentration in black gram seed depresses vigor of seedling (Rerkasem et al., 1990).

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Table 1. Scoring criteria for mungbean seedlings at 3 weeks after germination

Symptom	Score
Apical necrosis and plant mortality within 3 weeks from germination	1
Apical necrosis and main shoot missing above the unifoliate leaves	2
Main shoot missing above the first trifoliate leaf. Trifoliate leaf fails to extend, misshapen	3
Main shoot missing above the first trifoliate leaf. Trifoliate leaf fully extended but misshapen	4
Rosette of leaves above the unifoliate leaves	5
Second trifoliate leaf misshapen	6
Third trifoliate leaf misshapen	7
Normal seedling: 2-3 sets of trifoliate leaves and active apical growth	8

Table 2. Effect of B supply on B concentration in the YFEL (mg Bkg^{-1} dry wt) at the R3 growth stage

Genotype	Solution B concentration (μM)			
	0	0.5	3	5
Black gram				
M1	16.7 a B	26.9 b B	42.9 c B	43.0 c BC
Regur	10.0 a A	21.1 b B	38.9 c B	42.0 c ABC
CPI79563	8.3 a A	14.5 b A	38.3 c B	45.0 d BC
Green gram				
KPS1	6.4 a A	16.2 b A	41.5 c B	47.8 d C
VC2755	8.7 a A	12.7 a A	39.6 b B	41.4 b AB
VC1163	8.8 a A	16.5 b A	28.8 c A	36.1 d A
F test	G**	B**	GxB**	
$LSD_{0.05}$	3.0	2.4	6.0	

Values within a row are significantly different ($P<0.05$) unless followed by the same lower case letter. Values within a column are significantly different ($P<0.05$) unless followed by the same capital letter

B=Boron level, G=genotype, BxG=interaction between B and G

Table 3. Effect of B supply on shoot dry matter (g pot^{-1}) in six mungbean genotypes at two growth stages

Genotype	Solution B concentration (μM)				Mean
	0	0.5	3	5	
			R3 stage		
Black gram					
M1	5.8	6.2	4.2	3.8	5.0 A
Regur	5.4	11.1	10.4	17.1	11.0 B
CPI79563	10.8	16.8	20.4	14.3	15.6 C
Green gram					
KPS1	12.9	10.0	13.7	9.4	11.5 B
VC2755	11.8	13.5	15.7	13.0	13.5 BC
VC1163	5.2	9.0	13.0	13.0	10.1 B
F test	B^{NS}	G**	GxB^{NS}		
$LSD_{0.05}$	-	4	-		
			Seed maturity		
Black gram					
M1	60.1 b	29.2 a	12.5 a	16.4 a	29.5
Regur	30.9 a	41.2 ab	38.0 ab	61.5 b	42.9
CPI79563	47.4 a	89.2 b	84.6 b	100.4 b	80.4
Green gram					
KPS1	46.2 b	40.2 ab	39.9 ab	18.1 a	36.1
VC2755	42.6 a	45.3 a	54.0 a	33.2 a	43.8
VC1163	16.9 a	40.1 a	21.2 a	28.1 a	26.6
F test	B^{NS}	G**	BxG**		
$LSD_{0.05}$	-	13.0	25.9		

Values within a row are significantly different ($P<0.05$) unless followed by the same lower case letter. Values within a column are significantly different ($P<0.05$) unless followed by the same capital letter

B=Boron level, G=genotype, BxG=interaction between B and G

Table 4. Effect of B supply on relative yield (yield as % of yield in sufficient B) and relative pod number (pod number as % of pod number in sufficient B) in six mungbean genotypes

Genotype	Solution B concentration (μM)			
	0	0.5	3	5
		Relative yield		
Black gram				
M1	90.2 ab C	100.0 b B	44.6 a A	52.3 a ABC
Regur	9.0 a A	58.7 b AB	100.0 b B	91.7 b BC
CPI79563	0.3 a A	38.5 a A	86.9 b AB	100.0 b C
Green gram				
KPS1	89.2 b C	93.6 b B	100.0 b B	33.3 a A
VC2755	61.6 ab BC	81.3 ab AB	100.0 b B	48.5 a AB
VC1163	32.2 a AB	100.0 b B	75.6 ab AB	92.0 b BC
F test	B**	G^{NS}	BxG**	
LSD0.05	21.9	-	46.6	
		Relative pod number		
Black gram				
M1	100.0 b D	95.2 b B	48.3 a A	44.4 a A
Regur	10.0 a AB	63.7 b AB	88.6 b B	100.0 b B
CPI79563	0.3 a A	51.9 b A	78.5 bc AB	100.0 c B
Green gram				
KPS1	100.0 b D	72.1 b AB	74.3 b AB	30.2 a A
VC2755	68.6 ab CD	73.3 ab AB	100.0 b B	49.5 a A
VC1163	42.5 a BC	100.0 b B	69.8 ab AB	87.7 b B
F test	B*	G^{NS}	BxG**	
$LSD_{0.05}$	15.1	-	37.0	

Values within a row are significantly different (P<0.05) unless followed by the same lower case letter. Values within a column are significantly different (P<0.05) unless followed by the same capital letter.

B=Boron level, G=genotype, BxG=interaction between B and G

Table 5. Effect of B supply on 1000 seed weight and seed B concentration in six mungbean genotypes

Genotype	Solution B concentration (μM)			
	0	0.5	3	5
	1000 seed weight (g)			
Black gram				
M1	34.48 a	30.65 a	33.15 a	35.94 a
Regur	55.89 c	40.61 b	45.70 b	36.62 a
CPI79563	37.79 c	32.76 bc	27.52 ab	22.25 a
Green gram				
KPS1	46.50 a	49.49 a	49.12 a	53.71 a
VC2755	54.24 a	52.52 a	51.65 a	56.90 a
VC1163	62.56 b	54.25 a	59.24 ab	59.23 ab
F test	B*	G**	BxG**	
$LSD_{0.05}$	3.34	4.09	8.16	
	Seed B concentration (mg B kg^{-1})			
Black gram				
M1	6.2 a AB	13.8 b C	18.0 c A	17.4 c A
Regur	4.9 a AB	9.4 b B	17.6 c A	17.1 c A
CPI79563	24.3 d C	4.6 a A	18.1 b A	18.5 b AB
Green gram				
KPS1	4.3 a A	11.0 b B	17.7 c A	20.7 d BC
VC2755	5.3 a AB	11.0 b B	22.0 c B	22.4 c C
VC1163	6.9 a B	11.1 b B	17.2 c A	18.2 c A
F test	B**	G**	GxB**	
$LSD_{0.05}$	0.96	1.17	2.34	

Values within a row are significantly different ($P<0.05$) unless followed by the same lower case letter. Values within a column are significantly different ($P<0.05$) unless followed by the same capital letter.

B=Boron level, G=genotype, BxG=interaction between B and G

Figure 1. Seedling scores in green gram and black gram genotypes after three weeks growth in sand culture without added B.

Seedling score 1-2 = inefficient

Seedling score 3-4 = moderately inefficient

Seedling score 5-6 = moderately efficient

Seedling score 7-8 = efficient

(For detailed criteria for scores see Table 1)

Figure 2. The relationship between seed B concentration and seedling score in black gram (a) and green gram genotypes (b).

Figure 3. The relationship between relative pod number (pod number in B0 as % of pod number insufficient B) and relative yield (seed yield in B0 as % of seed yield in sufficient B).

Figure 4. The relationship between seedling score form in experiment 1 and relative yield (seed yield in B0 as % of seed yield in sufficient B) from experiment 2

(For detailed criteria for seedling scores see Table 1)

Figure 1

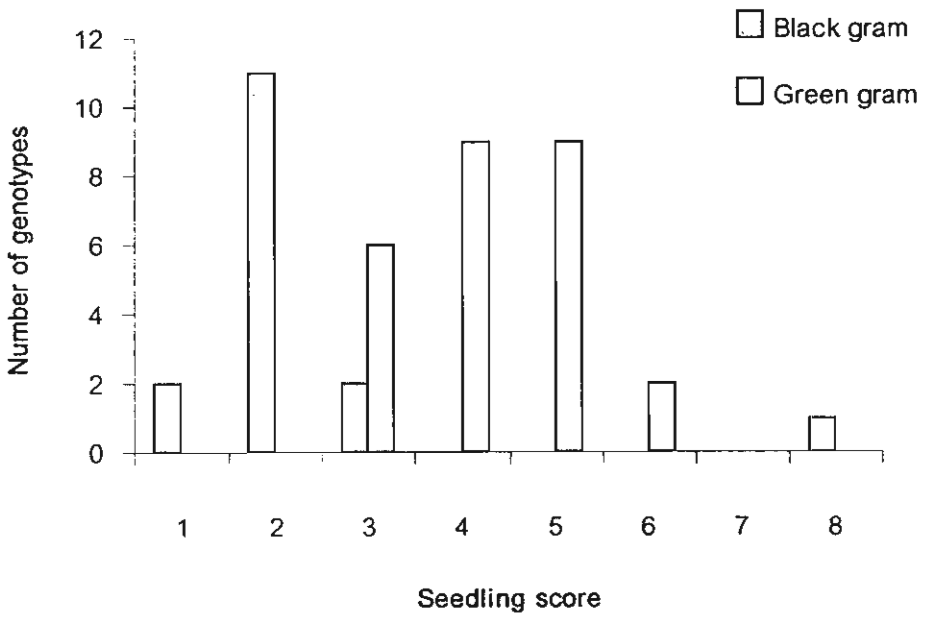
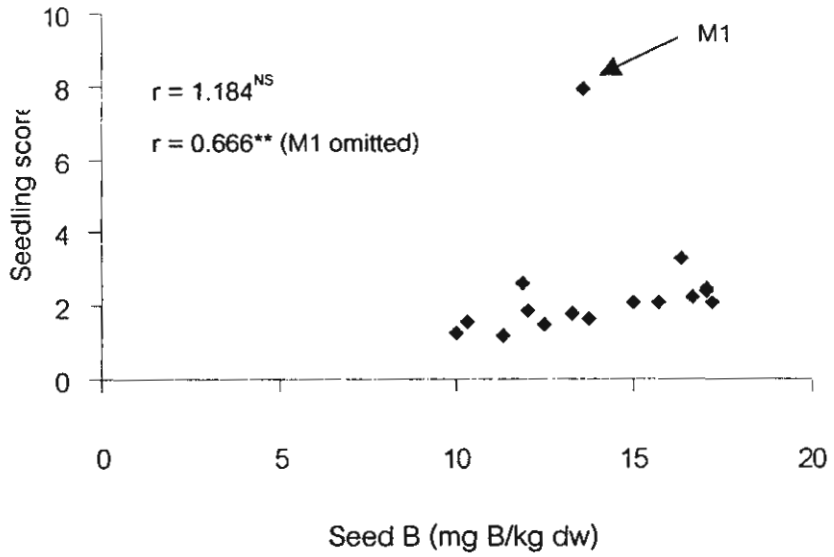

Black gram
Green gram
Number of genotypes
12
10
8
6
4
2
0
1
2
3
4
5
6
7
8
Seedling score

Figure 2

(a)


10
8
6
4
2
0
Seedling score
r = 1.184NS
r = 0.666** (M1 omitted)
M1
0
5
10
15
20
Seed B (mg B/kg dw)

(b)

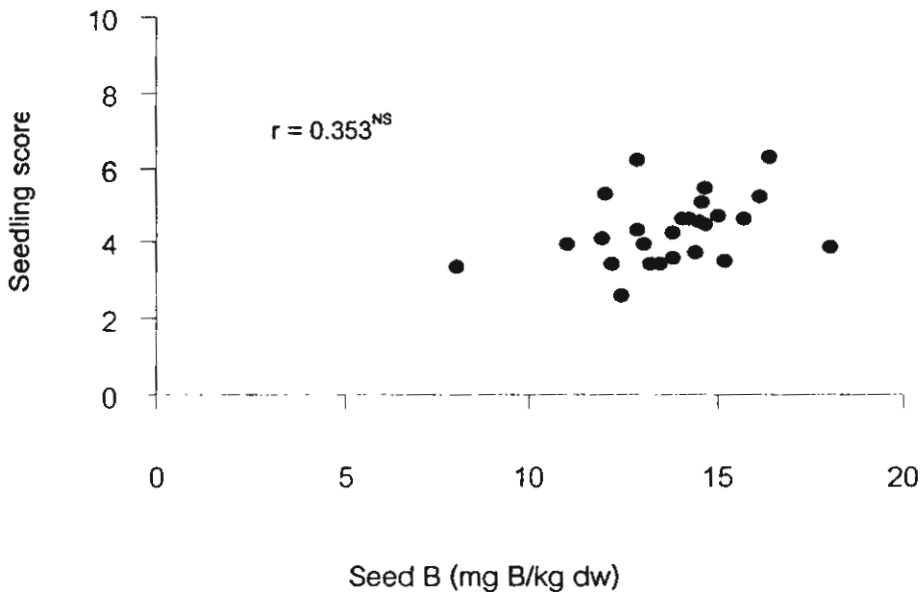

10
8
6
4
2
0
Seedling score
r = 0.353NS
0
5
10
15
20
Seed B (mg B/kg dw)

Figure 3

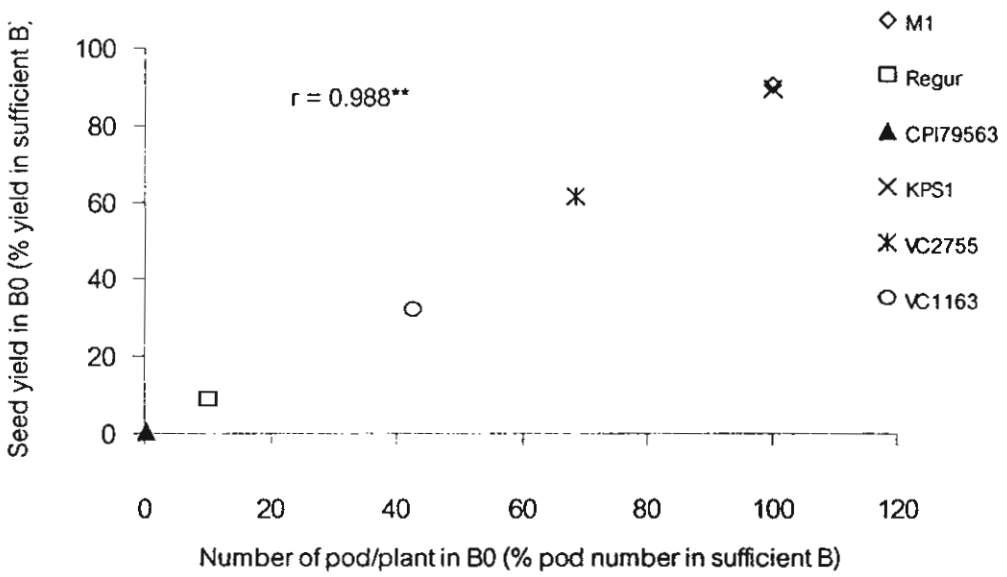
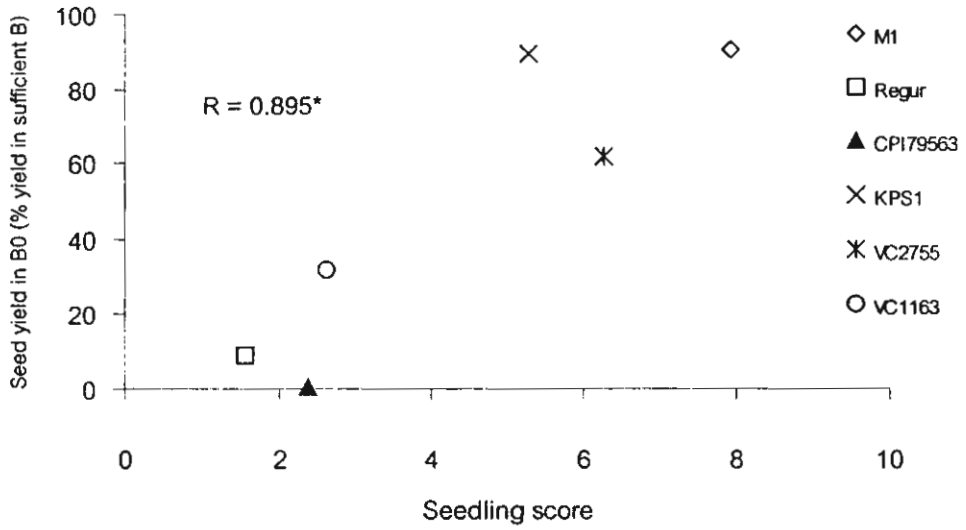

Seed yield in B0 (% yield in sufficient B)
100
80
60
40
20
0
r = 0.988**
0
20
40
60
80
100
120
Number of pod/plant in B0 (% pod number in sufficient B)
M1
Regur
CPI79563
KPS1
VC2755
VC1163

Figure 4


Seed yield in B0 (% yield in sufficient B)
100
80
60
40
20
0
R = 0.895*
0
2
4
6
8
10
Seedling score
M1
Regur
CPI79563
KPS1
VC2755
VC1163

Do Boron Deficiency and Toxicity Responses Correlate in Wheat Genotypes?

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Abstract

There is a wide range of genotypic variation in responses to boron (B) deficiency and toxicity in wheat. Yield reductions in cultivated area occur because of either B deficiency or toxicity. The relationship between B deficiency and toxicity responses in wheat is not understood. The objectives of this study were to measure the responses between B deficiency and toxicity in wheat genotypes and examine relationship between them. Two experiments, with nine genotypes known to differ in response to B deficiency (Fang 60, CMU 88-9, SW 41, Bonza) and toxicity (Turkey 1473, BT-Schomburgk, Schomburgk, Tatiara, Kenya Farmer), were undertaken. The response to B deficiency was evaluated in sand culture with two levels of applied B (0 and 10 μM B) in the nutrient solution. After maturity, grain set index (GSI; percentage of the 20 basal florets from 10 spikelets with grain), grain weight spike^{-1}, tiller plant^{-1} and straw yield were measured. B toxicity response was assessed in solution culture with three levels of B added (0, 100, 150 mg B L^{-1}). After 12 days, root and shoot length were measured. Tissue B analysis was conducted to compare B utilization in Fang 60, Bonza and Turkey 1473 by growing in sand culture with three B added (0, 10, 50 mg B L^{-1}) for 21 days.

In low B sand, GSI and grain weight spike^{-1} of all genotypes were depressed, except in Fang 60 (B-efficient), but tiller plant^{-1} and straw yield were not affected. At toxic levels B, root and shoot length reduction occurred in all genotypes. The tolerant genotypes, Turkey 1473 and Bonza, maintained the longest root length. However shoot length did not differ between genotypes. When grown without added B, deficiency tolerant Fang 60 did not differ significantly in B concentration in the whole plant and specific parts including YEB and YEB+1 from deficiency sensitive Bonza

and Turkey 1473. When grown at 50 mg B L^{-1}, efficient genotype, Fang 60 had higher B concentration in all parts than inefficient genotype, Bonza and Turkey 1473. Tissue B in the three genotypes was closely related to their toxicity response but not their deficiency response. These results suggested that sensitivity to B toxicity in Fang 60 be due to its tendency ability to accumulate more B in its plant part resulting in more severity symptom and root length reduction. In contrast, Bonza and Turkey1473 tolerant to B toxicity because they accumulated less B in their tissue.

We are postulating that there may be four types of the relationship between B deficiency and toxicity responses in wheat genotypes, on the basis of GSI and relative root length comparisons. The genotypes studied fell into three groups: (1) efficient (E) genotypes sensitive to high B i.e. Fang 60 (high GSI with short root length), (2) tolerant genotypes (T) sensitive to low B such as Turkey 1473 and Bonza (long root length with low GSI), and (3) inefficient genotypes sensitive to high B and low B such as BT-Schomburgk, Shomburgk, Tatiara, Kenya Farmer, SW 41 and CMU 88-9 (low GSI and short root length). The fourth possible type may be those genotypes that are tolerant to both B deficiency and toxicity, although none has yet been found so far.

Keywords: Boron deficiency, Boron toxicity, Wheat

Introduction

Boron (B) is an essential micronutrient for crop growth and there is a narrow range of deficiency and toxicity for growth (Reisenauer et al., 1973) and the sufficient range is narrow (Mahalakshmi et al., 1995).

Yield reductions in cultivated area occur because of either boron (B) deficiency or toxicity. Low B in soils contributes to male sterility in wheat and can depress grain yield. This problem has been reported in many countries in Asia including Nepal (Subedi, 1992), India (Tandon and Naqvi, 1992), Bangaladesh (Ahmed and Hossain, 1997), China (Yang, 1992) and Thailand (Rerkasem et al., 1989). The application of B fertilizer can ameliorate yield loss on low B soils (Rerkasem and Jamjod, 1997b), but the use of B-efficient genotypes is recommended (Jamjod et al., 2000). High B in soils causes necrosis and chlorosis of vegetative organs resulting in reduced grain

yield in wheat and also affects the growth at all stages of development as found in South Australia (Cartwright et al., 1984) and Turkey (Kalayci et al., 1998).

There is a wide range of genotypic variation in responses to B deficiency (Rerkasem and Jamjod, 1997b) and toxicity (Paull et al. 1991) in wheat. Boron efficiency is an ability of plant to grow well in soil, which is deficient for standard genotype. Boron efficiency mechanisms might be due to the ability to acquire B from soil, the way that B is distributed, and its utilisation within plant, while B tolerance mechanism is the ability to maintain lower B by B restriction in plant. It is as yet unclear how mechanisms governing tolerance to B deficiency and toxicity are related in wheat. This study set out to relate responses to B deficiency and toxicity in wheat genotypes covering a wide range of tolerance to measure the responses between B deficiency and toxicity in wheat genotypes and examine relationship between them.

Materials and methods

Genetic material

Nine standard wheat genotypes were evaluated in sand and solution culture.

Group 1 Genotypes known the range of response to B deficiency (Rerkasem and Jamjod, 1997b).

(1) Fang 60 (E; Efficient)

(2) CMU 88-9 (ME; Moderately efficient)

(3) SW 41 (MI; Moderately inefficient)

(4) Bonza (I; Inefficient)

Group 2 Genotypes known the range of response to B toxicity (Chantachume et al., 1995).

(1) Turkey 1473 (T; Tolerant)

(2) BT-Schomburgk (MT; Moderately tolerant)

(3) Schomburgk and Tatiara (MS; Moderately sensitive)

(4) Kenya Farmer (VS; Very sensitive)

Experiment 1: Sand culture experiment.

Nine wheat genotypes were grown in 0.3 m diameter earthenware pots containing washed river quartz sand with ten seeds of each genotype. The pots were watered twice daily with complete nutrient solution at two levels of B added (0 and 10 μM B),

referred to B0 and B10, respectively. The complete nutrient solution, adapted from Broughton and Dilworth (1971), consisted of: $CoSO_4$ (0.1 µM) Na_2MoO_2 (0.1 µM) $CuSO_4$ (0.2 µM) $ZnSO_4$ (0.5 µM) $MnSO_4$ (2 µM) FeEDTA (10 µM) K_2SO_4 (250 µM) $MgSO_4$ (250 µM) KH_2PO_4 (500 µM) $CaCl_2$ (1,000 µM) and KNO_3 (5,000 µM). Genotypes and B treatments were arranged randomly in blocks with four replications. After maturity, tiller plant^{-1}, straw yield, Grain Set Index (GSI) (measured as percentage of the 20 basal florets from 10 spikelets with grain) (Rerkasem and Loneragan, 1994) and grain weight spike^{-1} were measured.

Experiment 2: Solution culture experiment.

Nine wheat genotypes were assessed by the aerated solution culture method adapted from Campbell et al. (1998) with three levels of B concentrations (0, 100 and 150 mg BL^{-1}) assigned as B0, B100 and B150, respectively, prepared from boric acid (H_3BO_3), $ZnSO_4 \cdot 7H_2O$ (2.5 µM) (Webb and Loneragan, 1990) and $Ca(NO_3)_2 \cdot 4H_2O$ (500 µM) (Haynes and Robbins, 1948). The B treatments and genotypes were arranged factorially with two replications. Plastic mesh stuck to the underside of a foam sheet which had a row of holes punched was used in this experimental apparatus. Foam sheet was placed on plastic box that had the same size of length and width (0.37x0.23 m) and used the hose of an air pump to pass the air through into the solution (it was necessary to maintain growth of seedlings).

Seeds of the nine wheat genotypes were germinated in Petridishes for two days at 18 °C. The germinants were transferred to small plastic mesh containers inserted into foam sheet floating on the surface of a solution in plastic boxes on a laboratory bench at room temperature. Root and shoot length were measured after 12 days and the severity of symptoms of B toxicity was by evaluating the percentage of necrosis (necrosis (%) = (necrosis length/ length of that leaf) x 100). Root length was measured as the longest seminal root at B100 and B150, relative to B0 (relative root length; RRL). Likewise, shoot length was measured as the coleoptile length at B100 and B150, relative to B0 (relative shoot length; RSL).

Experiment 3: Tissue boron analysis.

Fang 60, Bonza and Turkey 1473 were grown in sand culture to compare B utilization with three levels of B (0, 10, 50 mg B L^{-1}) referred to B0, B10, B50 respectively added to nutrient solution adapted from Broughton and Dilworth (1971).

Genotypes and B treatments were arranged factorially with three replications. After 21 days, plants were collected to analyze tissue B concentration by azomethine-H method (Lohse, 1982) in YEB, YEB+1 and whole plant. Root and shoot length, root and shoot dry weight, symptom of B toxicity in YEB and YEB+1 were measured.

Statistical analysis

Data were analyzed by analysis of variance (AOV). Significant differences between means were calculated by the LSD test at 95% probabilities. Few data were transformed by square root arcsine transformation and square root transformation.

Results

Response to boron deficiency

There were significant differences between genotypes and boron treatments for GSI (Figure 1) and grain weight spike^{-1}, but not for tiller plant^{-1} and straw yield (Table 1), in experiment 1. Boron deficiency in wheat (B0) depressed GSI of all genotype compared with B10 except in Fang 60 (92.2 % GSI at B0). At B10, GSI of Fang 60 was not different from B0 (94.9 % GSI). Further, the GSI of Turkey 1473 (T), BT-Schomburgk (MT) and Schomburgk (MS) was more severely decreased at B0 than in B-efficient genotypes (GSI<40%). Genotypes that were more susceptible to B toxicity were also more sensitive to B deficiency (Figure 1). Tatiara (MS) and Kenya Farmer (VS) had very low GSI<20% at B0) but Tatiara set grain less than Kenya Farmer.

Grain weight spike^{-1} was affected by B0 in the same way as GSI in all genotypes (Table 1). Fang 60 had more grain weight spike^{-1} than sensitive ones at both B levels. For tillering and straw yield, all genotypes were not affected in these characters by B levels. Tiller plant^{-1} and straw yield were genotype dependent.

Response to boron toxicity

In experiment 2, higher B concentration affected root and shoot length of wheat genotypes differently (Figure 2). High B affected root length more than shoot length. The clearest differences in response to B toxicity occurred at B100 and B150 (Table 2). At B100, Bonza showed the least root length reduction (RRL = 70.7%) followed by Turkey 1473 (RRL = 68.9%) and BT-Schomburgk (RRL = 51.2%), whereas Kenya Farmer, Tatiara and Fang 60 showed the most reduction in root length (RRL

range 39.4-50.3%). At B150, Turkey 1473 and Bonza still had less root length reduction than other genotypes, whereas Fang 60 and Tatiara had the most root length reduction.

For shoot length, high B supply reduced shoot length (range 75.2-94.0%) but there was no significant interaction between genotypes and B treatments when assessed by RSL (% of B0) (Table 2). Leaf necrosis (%) at B100 and B150, was severe in sensitive genotypes such as Fang 60, Kenya Farmer and SW 41 (necrosis (%) = 47.6, 46.4, 45.7, respectively) (Table 3). Bonza and Turkey 1473 showed less severe symptoms (26.6 and 30.7%, respectively).

Tissue boron analysis

Boron levels did not affect on root and shoot length, root and shoot dry weight of wheat genotypes at 21 days after sowing but affected on necrosis (%) significantly between genotypes (Figure 3). Bonza had the least toxicity symptoms in both YEB and YEB+1 whereas Fang 60 had the most.

When grown without added B, Fang 60 did not differ significantly in B concentration in the whole plant and specific parts including YEB and YEB+1 from Bonza and Turkey 1473 (Table 4). At 50 mg B L^{-1}, Fang 60 had higher B concentration in all parts of its plant than Bonza and Turkey 1473. Whole plant B concentration of Fang 60 was 806.55 mg B kg^{-1} and 678.19, 655.97 mg B kg^{-1} in Bonza and Turkey 1473 respectively. Furthermore, B concentration in YEB and YEB+1 of Fang 60 was higher than Bonza and Turkey 1473 that was 180.08, 131.82, 142.28 mg B kg^{-1} respectively in YEB and 273.66, 226.85, 226.17 mg B kg^{-1} respectively in YEB+1.

Discussion

From these studies, there had the relationship between B deficiency and toxicity responses categorized into four groups by assessing GSI (for B deficiency response) and relative root length (for B toxicity response) (Figure 4):

(1) Genotypes are efficient to B deficiency but sensitive to B toxicity i.e. Fang 60.

(2) Genotypes are inefficient to B deficiency and sensitive to B toxicity i.e. CMU 88-9, SW 41, BT-Schomburgk, Schomburgk, Tatiara, Kenya Farmer.

(3) Genotypes are inefficient to B deficiency but tolerant to B toxicity i.e. Bonza and Turkey 1473.

(4) Genotypes are efficient to B deficiency and tolerant to B toxicity, have not been found yet. However, such genotypes have so far not been identified.

Relationship between B deficiency and toxicity in wheat in this study was resemblance with the response in barley. In case of efficient genotype, it has one or more efficient mechanisms such as the ability to acquire B, the way that B is distributed, and its utilization within the plant (Rerkasem and Jamjod, 1997a). Besides, phloem mobility is one of efficient mechanism in efficient genotype whereas *genotype that is unable to translocate B in phloem is found in genotype that tolerate to* B toxicity (Brown and Shelp, 1997). So, genotype that had ability to translocate B in phloem will susceptible to B toxicity (Brown and Hu, 1996). Nable (1992) reported that there has a general trend for species more tolerance of high B concentrations to be more prone to B deficiency such as tobacco, *Eucalyptus* and barley.

In the first experiment, the significant interaction between genotype and B treatment for GSI and grain weight spike^{-1} confirms that genetic variation for B efficiency occurs in wheat and B deficiency impairs reproductive growth. So that GSI is an appropriate index to compare the effect of B on grain set (Anantawiroon et al., 1997) by avoiding effects from spike type, spike size and it was used for B efficiency screening by growing wheat in B deficient condition without comparing with B sufficient condition. Fang 60 still efficient to B deficiency because of high GSI but not in CMU 88-9. SW 41 and Bonza that were classed in the same range as the study from Rerkasem and Jamjod (1997a). Besides this, Turkey 1473, BT-Schombirgk, Schomburgk, Tatiara and Kenya Farmer were sensitive to B deficiency. In addition to this, B deficiency has no effect on tiller plant^{-1} and straw yield since B deficiency affects on reproductive growth more than on vegetative growth in wheat (Rerkasem and Loneragan, 1994).

From the results in experiment two, higher B concentrations affected both root and shoot length of all genotypes, but B toxicity reduced root length more than shoot length. Bonza had long root length as same as Turkey 1473 when grown at higher B levels which ought to classified as B toxicity tolerance as Chantachume et al. (1995) have mentioned. By contrast, Fang 60, CMU 88-9, SW 41, BT-Schomburgk, Schomburgk, Tatiara and Kenya Farmer had short root length which could be suggested that they were not tolerant to B toxicity. In addition to this, Holloway and Alston (1992) found that high B concentration will restrict root growth of wheat and decrease yield (Cartwright et al., 1984) and tolerant genotype had longer root length

than sensitive genotype. Furthermore, susceptible genotypes had more symptoms of necrosis than tolerant genotypes when grown at higher B concentrations. Therefore, root length is an appropriate index for selecting or screening tolerance genotype because of quick and easy method (Campbell et al., 1998; Chantachume et al., 1995).

For tissue B analysis, deficiency tolerant Fang 60 did not differ in B concentration in the whole plant, YEB and YEB+1 from deficiency sensitive Bonza and Turkey 1473 when grown at 0 mg B L^{-1}. Therefore genotypic variation for B efficiency did not measure by tissue B analysis. At 50 mg B L^{-1}, Fang 60 had higher B concentration in any parts of its plant than Bonza and Turkey 1473. Tissue B in the three genotypes was closely related to their toxicity response (necrosis and chlorosis) but not their deficiency response. It also demonstrated that Fang 60 was not tolerant to B toxicity due to maintain more B in any parts at high B with resulted in more severity of B toxicity symptom. In contrast, Bonza and Turkey 1473 remained tolerant to B toxicity due to ability to maintain less B in any parts at high B. Nable (1988) stated that barley and wheat cultivars examined displayed a large range of resistance to B toxicity that was governed in both species by the ability of cultivars to restrict B accumulation in the plant. This mechanism is called exclusion. In addition, Nable et al. (1988) found that tolerant barley genotype was susceptible to B deficiency. Tolerant genotype accumulated less B concentration than sensitive genotype in both root and shoot. He concluded that resistance to B toxicity was governed by the ability of cultivars to restrict B accumulation in the plant. Fang 60 exemplifies the highest tolerance to B deficiency and Bonza and Turkey 1473 the highest tolerance to B toxicity. Tissue B data indicated that their may be some association between responses to the two extremes of B supply.

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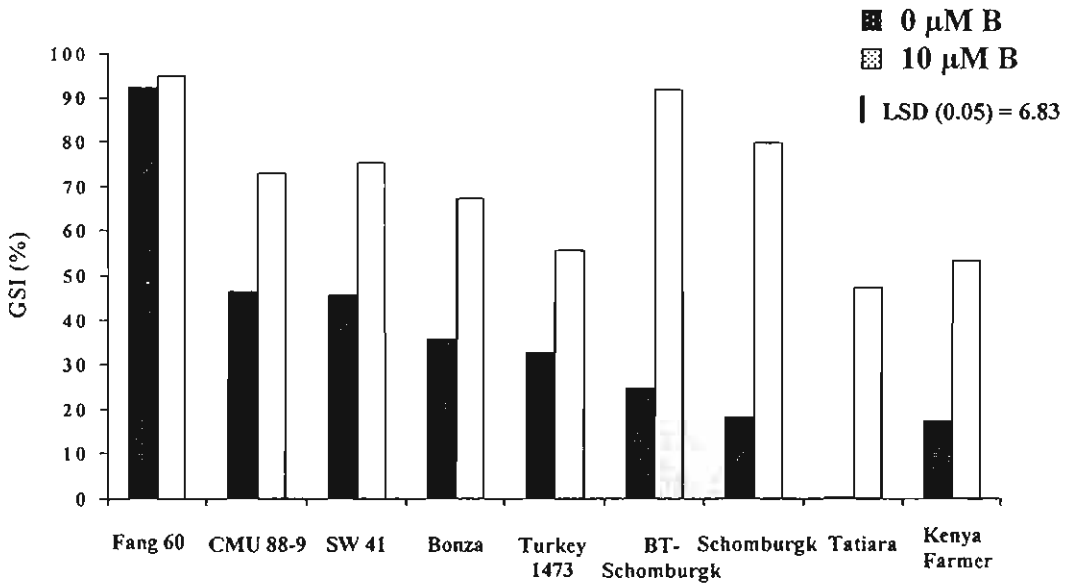

Figure 1 Effect of B supply on grain set index (GSI; %) of nine wheat genotypes grown in sand culture. (Experiment 1)

Table 1 Effects of B supply on grain weight spike^{-1} (g), tiller plant^{-1} and straw yield (g plant^{-1}) of nine wheat genotypes grown in sand culture. (Experiment 1)

Genotype	Grain weight spike^{-1}			Tiller plant^{-1}			Straw yield		
	B supply		*Mean*	B supply		*Mean*	B supply		*Mean*
	B0	B10		B0	B10		B0	B10	
Fang 60	0.87 aA	1.01 aA	*0.94*	7.3	7.3	*7.3 D*	9.38	9.36	*9.37 D*
CMU 88-9	0.52 bBC	0.97 aA	*0.74*	6.7	6.3	*6.5 DE*	10.38	10.26	*10.32 CD*
SW 41	0.57 bB	0.73 aB	*0.65*	6.9	6.7	*6.8 DE*	10.86	8.88	*9.87 D*
Bonza	0.37 bC	0.59 aBC	*0.48*	8.7	9.0	*8.9 BC*	15.27	14.11	*14.69 A*
Turkey 1473	0.39 aC	0.49 aCD	*0.44*	5.9	6.4	*6.1 E*	11.80	14.03	*12.92 ABC*
BT-Schomburgk	0.19 bD	0.62 aBC	*0.41*	10.9	10.8	*10.8 A*	11.07	9.81	*10.44 CD*
Schomburgk	0.14 bDE	0.48 aCD	*0.31*	10.3	9.0	*9.6 B*	13.29	13.16	*13.22 AB*
Tatiara	0.00 bE	0.35 aD	*0.18*	8.1	8.8	*8.5 C*	11.97	11.69	*11.83 BCD*
Kenya Farmer	0.19 bD	0.37 aD	*0.28*	7.4	6.3	*6.8 DE*	13.50	9.13	*11.32 BCD*
Mean	*0.36*	*0.62*	*0.49*	*8.0*	*7.8*	*7.9*	*11.95*	*11.16*	*11.55*
F-test	B**	G**	BxG**	B^{ns}	G**	BxG^{ns}	B^{ns}	G**	BxG^{ns}
$LSD_{0.05}$	0.05	0.11	0.15	-	1.03	-	-	2.62	-
CV (%)	21.83			12.92			22.57		

^{ns} not significant ($p<0.05$), ** significant at $p<0.01$.

Means within a row with the same lowercase letter and within a column with the same uppercase letter do not differ significantly at 5% with LSD.

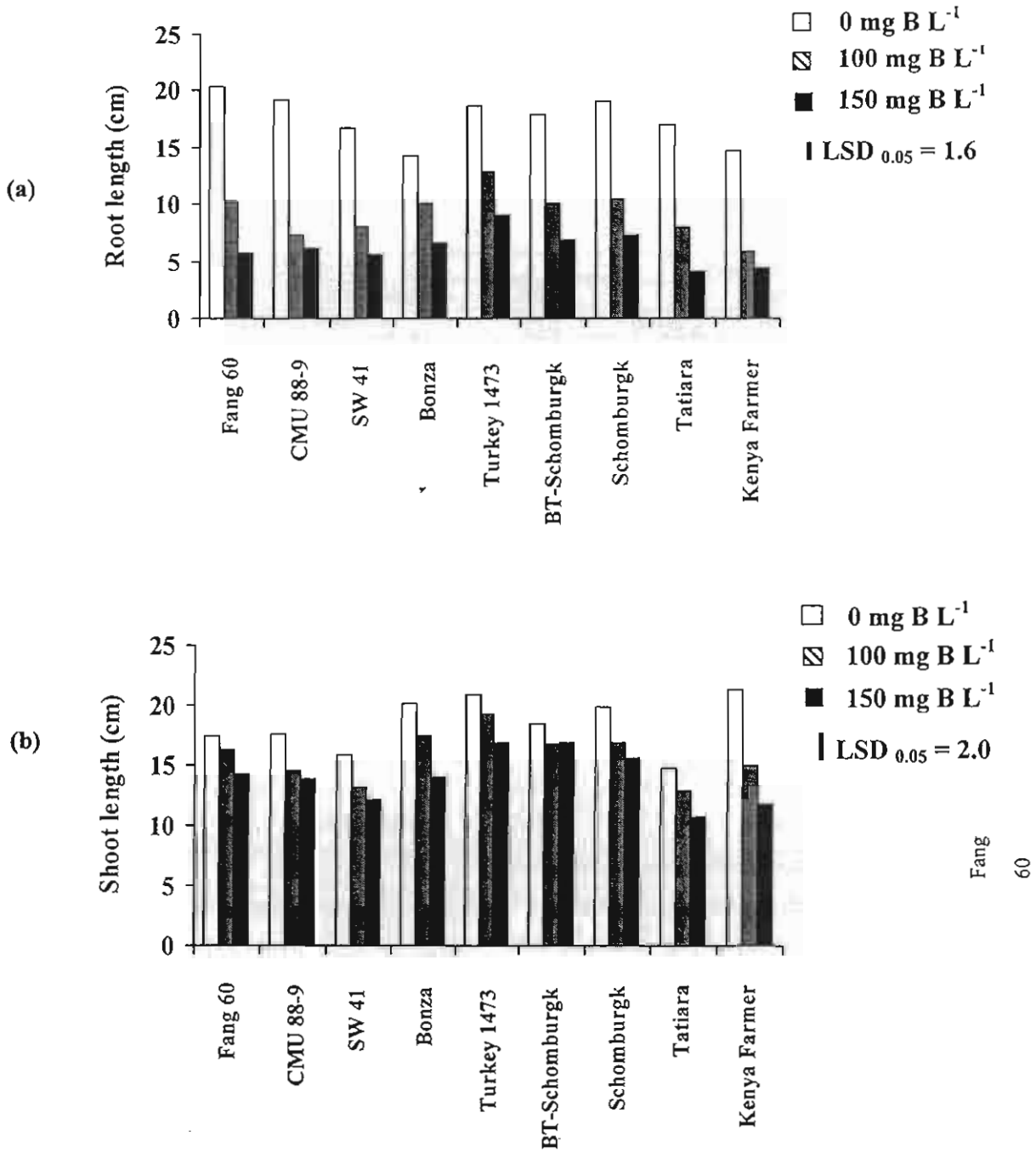

Figure 2 Root and shoot length of nine wheat genotypes grown in solution culture with three levels of B concentrations. (a) root length (cm.) (b) shoot length (cm.). (Experimet 2)

Table 2 Relative root length (RRL; % of B0) and relative shoot length (RSL; % of B0) of nine standard genotypes grown in solution culture with three B supplies. (Statistical value was transformed by square root arcsine transformation based on the data) (Experiment 2)

Genotype	B supply			*Mean*	B supply			*Mean*
	RRL				**RSL**			
	B0	B100	B150		B0	B100	B150	
Fang 60	100 aA	50.3 bCD	28.1 cDE	*59.5*	100	93.1	81.6	*91.6 AB*
CMU 88-9	100 aA	38.5 bF	32.5 bCD	*57.0*	100	83.1	78.8	*87.3 AB*
SW 41	100 aA	48.1 bD	33.2 cCD	*60.4*	100	82.1	75.9	*86.0 B*
Bonza	100 aA	70.7 bA	46.3 cAB	*72.3*	100	86.8	69.2	*85.3 B*
Turkey 1473	100 aA	68.9 bAB	48.7 cA	*72.6*	100	93.0	81.1	*91.4 AB*
BT-Schomburgk	100 aA	57.2 bBC	38.3 cBC	*65.2*	100	90.7	91.3	*94.0 A*
Schomburgk	100 aA	55.1 bCD	38.4 cBC	*64.5*	100	85.8	79.4	*88.4 AB*
Tatiara	100 aA	47.1 bDE	24.6 cE	*57.2*	100	87.5	73.3	*87.0 AB*
Kenya Farmer	100 aA	39.4 bEF	30.1 bDE	*56.5*	100	70.8	54.9	*75.2 C*
Mean	*100*	*52.8*	*35.6*	*62.8*	*100*	*85.9*	*76.2*	*87.4*
F-test	B**	G**	BxG**		B**	G**	BxG^{ns}	
$LSD_{0.05}$	0.023	0.039	0.068		0.039	0.068	-	
CV (%)	3.81				5.39			

RRL = (root length at B+/root length at B0) x 100

RSL = (shoot length at B+/shoot length at B0) x 100

^{ns} not significant ($p<0.05$), * significant at $p<0.05$, ** significant at $p<0.01$

Means within a column with the same letter do not differ significantly at 5% with LSD.

Table 3 Symptom of B toxicity (% of necrosis) of the oldest leaf of nine standard genotypes grown in solution culture with two levels of B supplies. (Statistical value was transformed by square root transformation based on the data in this table) (Experiment 2)

Genotype	B treatment		*Mean*	*Rank*
	B100	B150		
Fang 60	40.9	54.4	*47.6 A*	*9*
CMU 88-9	36.5	41.2	*38.9 ABC*	*6*
SW 41	37.5	54.0	*45.7 AB*	*7*
Bonza	20.3	32.9	*26.6 E*	*1*
Turkey 1473	27.0	34.4	*30.7 DE*	*2*
BT-Schomburgk	31.5	40.4	*35.9 CD*	*4*
Schomburgk	37.1	40.4	*38.7 BC*	*5*
Tatiara	32.1	37.9	*35.0 CD*	*3*
Kenya Farmer	38.6	54.1	*46.4 AB*	*8*
Mean	*33.5 b*	*43.3 a*	*38.39*	
F-test	B**	G**	BxG^{ns}	
$LSD_{0.05}$	0.033	0.071	-	
CV (%)	7.61			

%necrosis = (length of necrosis/length of that leaf) x 100

^{ns} not significant ($p<0.05$), ** significant at $p<0.01$

Means within a row with the same lowercase letter and within a column with the same uppercase letter do not differ significantly at 5% with LSD.

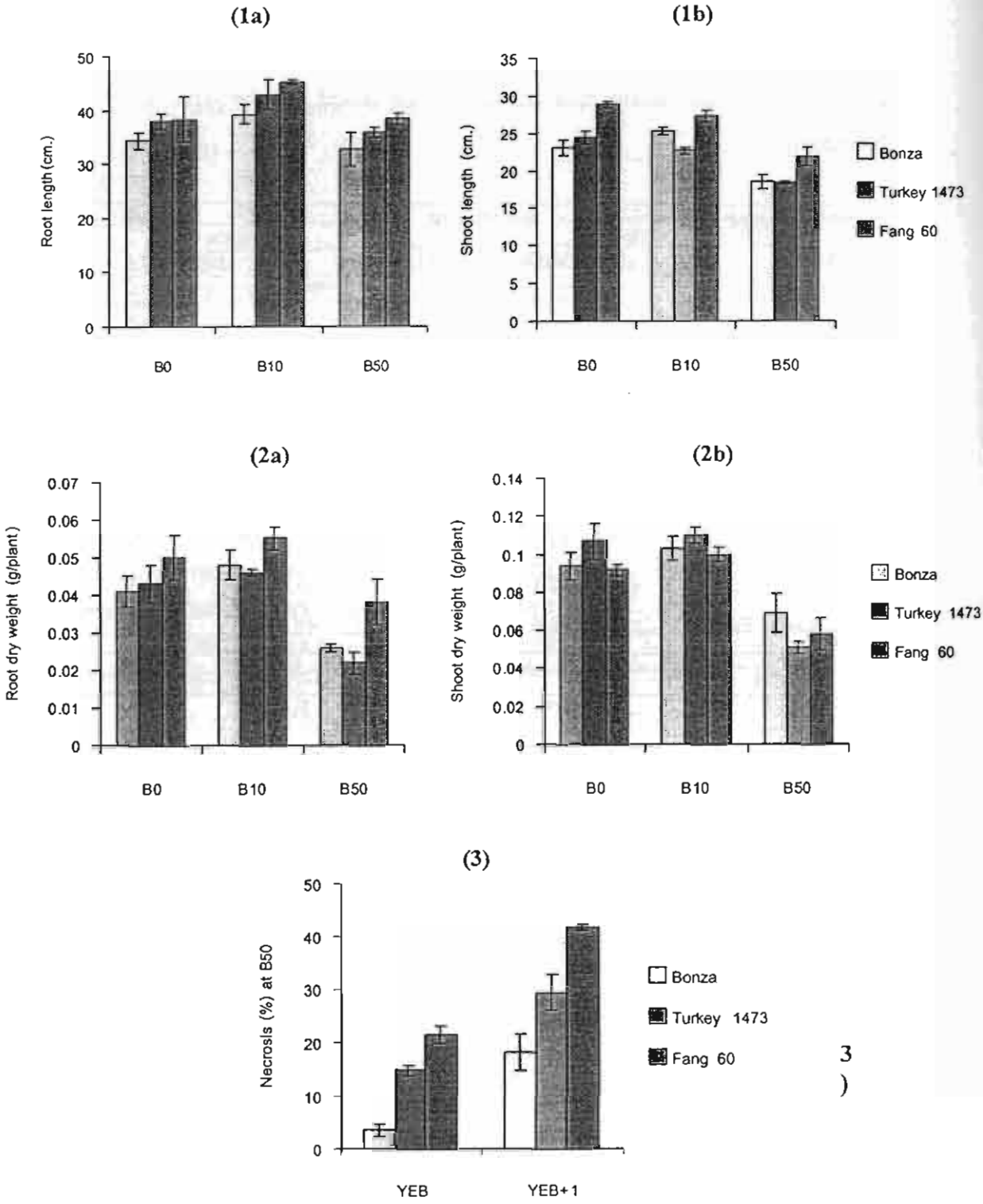

Figure 3 Root and shoot length (1a, 1b), root and shoot dry weight (2a, 2b) and necrosis (%) of YEB and YEB+1 (3) of three wheat genotypes grown in sand culture with three B supplies at 21 days after sowing. (Vertical bars presented as standard error of three replications) (Experiment 3)

Table 4 Effects of B supply on B concentration (mg B kg^{-1}) in YEB, YEB+1 and whole plant of three wheat genotypes grown in sand culture 21 days after sowing. (Statistical value was transformed by square root transformation based on the data in this table) (Experiment 3)

Genotypes	B supply			*Mean*
	B0	B10	B50	
YEB				
Fang 60 (E)	1.60 (1.26) bA	2.05 (1.43) bA	180.08 (13.41) aA	*61.24 (5.37)*
Bonza (I)	2.41 (1.55) bA	2.34 (1.53) bA	131.82 (11.48) aB	*45.53 (4.85)*
Turkey 1473 (T)	2.01 (1.40) bA	3.44 (1.85) bA	142.28 (11.87) aB	*49.24 (5.04)*
Mean	*2.01 (1.41)*	*2.61 (1.60)*	*151.40 (12.25)*	*52.00 (2.00)*
F-test	B**	G^{ns}	BxG**	
$LSD_{0.05}$	0.53	-	0.92	
CV (%)	10.58			
YEB+1				
Fang 60 (E)	7.92 (2.81) bA	8.04 (2.84) bA	273.66 (16.53) aA	*96.54 (7.39)*
Bonza (I)	7.65 (2.76) bA	7.80 (2.79) bA	226.85 (15.06) aB	*80.77 (6.87)*
Turkey 1473 (T)	1.65 (1.29) cB	7.69 (2.77) bA	226.17 (15.02) aB	*78.50 (6.36)*
Mean	*5.74 (2.29)*	*7.84 (2.80)*	*242.23 (15.54)*	*85.31 (6.87)*
F-test	B**	G**	BxG**	
$LSD_{0.05}$	0.44	0.44	0.77	
CV (%)	6.49			
Whole plant				
Fang 60 (E)	22.18 (4.71) cA	28.38 (5.33) bA	806.55 (28.40) aA	*285.70 (12.81)*
Bonza (I)	22.06 (4.69) bA	25.18 (5.02) bA	678.19 (26.04) aB	*241.81 (11.92)*
Turkey 1473 (T)	14.86 (3.85) cB	28.84 (5.37) bA	655.97 (25.60) aB	*233.22 (11.61)*
Mean	*19.70 (4.42)*	*27.47 (5.24)*	*713.57 (26.68)*	*253.58 (12.11)*
F-test	B**	G**	BxG**	
$LSD_{0.05}$	0.33	0.33	0.58	
CV (%)	2.78			

^{ns} not significant ($p<0.05$), ** significant at $p<0.01$

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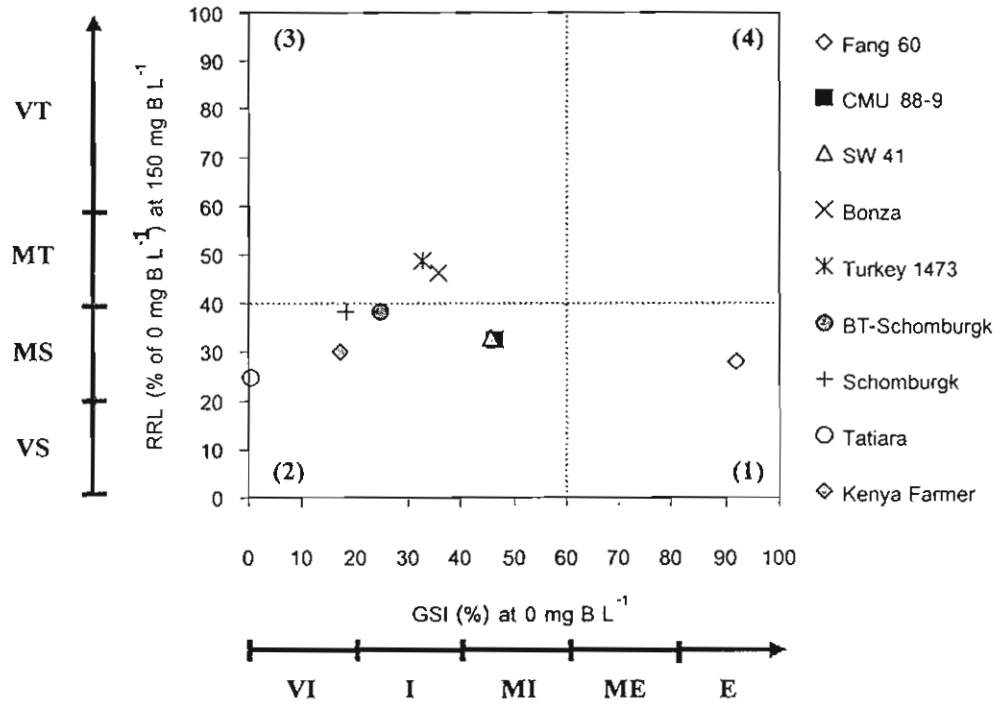

Figure 4 Relationship between RRL (at 150 mg BL^{-1}) and GSI (at 0 mg BL^{-1}) of nine standard wheat genotypes that could be categorized into three groups:

(1) GSI>60%, RRL<40% Tolerant to B deficiency but sensitive to B toxicity.

(2) GSI<60%, RRL<40% Sensitive to B deficiency and toxicity.

(3) GSI<60%, RRL>40% Sensitive to B deficiency but tolerant to B toxicity.

and the fourth possible group were:

(4) GSI>60%, RRL>40% Tolerant to B deficiency and toxicity that have not been found yet.

Iron in the Grain of High and Low Iron Density Rice Grown in Different Water Regimes

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Abstract

Throughout the rice growing areas of the world, water supply may range from intermittent rains, irrigation with relatively constant soil saturation, or to flooding several meters deep. This study sets out to measure the effect of water supply on Fe accumulation in the rice grain. Two rice genotypes, one with high (IR68144) and one with low (KDML105) grain Fe content, were grown in 4 water regimes (well-drained, W00; early drainage, from transplanting to anthesis, W0+; waterlogged, W++; late drainage, from anthesis to harvesting, W+0). Grain Fe concentration and content in IR68144 were generally higher than in KDML105. The water regimes affected both grain yield and grain Fe in the two genotypes differently. . In IR68144, grain Fe concentration in W00 and W++ were lower than in W0+ and W+0 whereas in KDML105, grain Fe concentrarion in W+0 was lower than in W00, W0+ and W++. By contrast, in IR68144, grain Fe content in W++ was lower than in W0+, but there was not differed from in W00 and in W+0. In KDML105, grain Fe content in W++ was higher than in W00 and W0+, but there was not differed from W+0. However, a very small fraction of the Fe was uptake from the shoot into the grain. In IR68144, grain Fe content in W00, W0+, W++ and W+0 were 2.9, 2.8, 1.8, and 2.3% respectively of Fe in the whole shoot, whereas, in KDML105, 0.7, 0.4, 1.0 and 0.4 respectively, it was lower Fe in shoots allocated to the

grain than in IR68144. In IR68144, the grain yield was not affected by water regimes whereas, in KDML105, the grain yield in W++ and W+0 were higher than in W00 and W0+. The grain Fe concentration and content was depended on rice genotype and water supply to the root.

Keyword: *Orysa sativa*, rice, water supply, grain Fe, transportation

Introduction

It is now generally agreed that increasing grain Fe concentration can help to solve problems associated with Fe-deficiency anemia (Senadhira et al., 1998; Welch and Graham, 1999). Previous studies found that grain Fe varied widely among rice genotypes and environmental conditions (Senadhira et al., 1998; Prom-u-thai and Rerkasem, 2001; Lauguet et al., 2001). Throughout the rice growing areas of the world, water supply may range from intermittent rains, irrigation with relatively constant soil saturation, or to flooding several meters deep (Naklang et al., 1996; Lauguet et al., 2001; Dingkuhn and Le Gal, 1996). Rainfed rice crops are commonly grown in either lowland paddies or upland fields in tropical Asia. Under rainfed, lowland conditions the use of the bunds and puddling of soils helps retain standing water, whereas aerobic soil conditions are usually maintained for upland crops (Naklang et al., 1996). Rice yield is highly responsive to water deficit during reproductive development and grain filling. The most sensitive stage is flowering, followed by gametogenesis (booting stage) and grain filling (O' Toole, 1982). Dingkhun and Le Gal (1996) found that early drainage, 3 to 4 days after flowering, reduced grain yield when compared to late drainage. Rice plants growing in flooded soil contain much higher levels of Fe then those growing in dry-land soil condition (Beyrouty et al., 1994). It is not known how grain Fe is influenced by such difference in Fe uptake

into the rice plant. The literature also lacks data on the distribution of Fe between the shoot and grain, as well as comparative information across genotypes. This paper documents how grain Fe is influenced by variation in Fe supply to the root by varying the water regimes in rice genotypes with high (IR68144) and low (KDML105) grain Fe content.

Materials and Methods

Two rice genotypes with high (IR68144 a improved rice genotype from IRRI) and low grain Fe content (KDML105 a popular genotype from Thailand) were grown under four soil conditions, in four replications. Five rice plants were grown in each black plastic bag containing 12 kg of soil (San Sai Series). The soil conditions were W00 (well-drained soil through out), W0+ (early drainage, the black plastic bag was completely drained 10 days after sowing and then submerged in a 10 L container of water after the anthesis stage), W++ (waterlogging through out) and W+0 (late drainage, the black plastic bag was submerged in a 10 L container of water and completely drained after anthesis). Basal fertilizer was applied at the rate of 0.707 g N/pot, 0.497 g P_2O_5/pot and 0.497 g K_2O/pot and 0.707 g N/pot, 0.497 g P_2O_5/pot and 0.497 g K_2O/pot four weeks later. Iron concentration was determined in mature grain (unhusked and brown rice), straw by dry-ashing and atomic absorption spectrometry (Emmanuel *et al.*, 1984).

Results

The Water regimes affected grain yield and both grain Fe concentration and content differently in two genotypes. In IR68144, grain Fe concentration in W00 and W++ were lower than in W0+ and W+0 whereas in KDML105, grain Fe concentrarion in

W+0 was lower than in W00, W0+ and W++ (Fig. 1). By contrast, in IR68144, grain Fe content in W++ was lower than in W0+, but there was not differed from in W00 and in W+0. In KDML105, grain Fe content in W++ was higher than in W00 and W0+, but there was not differed from W+0 (Table 1). Grain Fe concentration and content in IR68144 was higher than in KDML105 in 4 water regimes (Fig. 1 and Table 1). The effect of water regimes to grain Fe concentration and content were different from the percent empty grain and grain yield of two genotypes. In IR68144, the percent of empty grain in W00 and W+0 were higher than in W0+ and W++ , but in KDML105, the percent of empty grain in W0+ and W00 were higher than in W++ and W+0 (Table 2). These was affected to the grain yield of two genotypes grown in four water regimes. In IR68144, the grain yield was not affected by water regimes whereas, in KDML105, the grain yield in W++ and W+0 were higher than in W00 and W0+ (Table 2).

There was no effect of water regimes to Fe concentration in the whole shoot of two genotypes. The genotype was affected to Fe concentration in the whole shoot. These were differed from the effect of water regimes to grain Fe concentration in two genotypes. In IR68144, the Fe concentration in the whole shoot was 389.7 mg Fe/kg whereas in KDML105 the Fe concentration in the whole shoot was 555.6 mg Fe/kg. However, the Fe concentration in the grain was only a fraction of that in the whole shoot (Fig. 1). The Fe content of the whole shoot was affected by genotype and water regime (Table 2). But, there was no interaction between genotype and water regimes to shoot Fe content. The Fe content in the whole shoot of KDML105 was higher than IR68144 (Table 2). The Fe content of the whole shoot in W0+ and W+0 were higher than in W00, but there was not differed from W++ (Table 2). However, the grain accounted for a very small fraction of the whole shoot Fe in both genotypes. There was very little percent of Fe from the shoot was transported into the grain of two genotypes. In IR68144, grain Fe content in

W00, W0+, W++ and W+0 were 2.9, 2.8, 1.8, and 2.3% respectively of Fe in the whole shoot, whereas, in KDML105, 0.7, 0.4, 1.0 and 0.4% respectively, it was lower Fe in shoots allocated to the grain than in IR68144. There was no relationship between the grain and shoot and Fe concentration and content in two rice genotypes grown in four water regimes.

Discussion

Previous study found that Fe in soil solution increases to concentrations as high as 600 ppm within 1-3 weeks of submergence and later show a steep, roughly exponential, decrease to levels of 50-100 ppm, which persist of several months (Cho and Ponnamperuma, 1971) and in calcareous soil the concentration of water-soluble Fe rarely exceeds 20 ppm (Ponnamperuma, 1972).

The Fe uptake from the root into the whole shoot was affected by genotype and water regimes. There was not interacted between genotype and water regime. The Fe uptake into the whole shoot of two genotypes in W++ was higher than in W00 in this study. These were supproted the previous studies that when soils are flooded, the concentration of Fe^{+2} in the soil solution increases to several times that in aerated soil (Ponnamperuma, 1972). Furthermore, rice plants growing in flooded soil have been reported to contain Fe at many times those growing in well-drained soil (Beyrouty et al., 1994). However, The Fe uptake in the whole shoot in W++ was not differed from in W0+ and W+0. Trust, the Fe uptake into the whole shoot was affected by the stage of rice growing in different water regimes. The water can be supply to the rice plant before or after anthesis stage instead of waterlogged throughout. There was no previous result supported the Fe uptake of rice in different water regimes. However, Fe is an important

minerals for chlorophyll and enzyme synthesis process in plant function (Marschner, 1995). Therefore, the Fe uptake in rice plant was related to the growth stage of rice in different water regime may depending on the function of plant on that time. Moreover, Fe uptake was also affected by rice genotype in four water regimes. The Fe uptake in KDML105 was higher than in IR68144 in four water regimes. These were related to the grain Fe concentration and grain yield of two genotypes. The grain Fe concentration in IR68144 was low in W00 and W++ but the grain yield was not affected by water regimes. By contrast, the grain Fe concentration in KDML105 was low in W+0 but there was high grain yield in W++ and W+0.

Rice grain is the edible part of rice plant. Therefore, Fe uptake from the plant into the grain need to be discuss. In IR68144, the Fe transportation from the shoot into the grain much higher than in KDML105 in 4 water regimes. There was differed effect from the uptake of Fe in the whole shoot. In IR68144, Fe transportation from the shoot into the grain in W0+ was higher than in W++ but there was not differed in W00 and W+0 Whereas, in KDML105 in W++ was higher than in W00 and W0+ but there was not differed in W+0. The effect of water regimes to Fe uptake into the grain of two genotypes was not related to the previous studies about Fe in the soil solution ((Ponnamperuma, 1972). Clearly, The effect of water regimes to Fe uptake from the shoot into rice grain of two genotypes was differed from the uptake of Fe from the soil solution into the whole plant. However, there was a very small fraction of Fe from the shoot was transported into the grain in two genotypes. In IR68144, the distribution of Fe in the grain as percent of total Fe in W00, W0+, W++ and W+0 were 2.9, 2.7, 1.8 and 2.2% respectively, whereas in KDML105 were 0.9, 0.3, 0.9 and 0.4% respectively.

The Fe distribution in the grain is clearly depending on the rice genotype and water regimes. Previous study found that grain Fe in rice was varied widely among genotype

and water condition (Prom-u-thai and Rerkasem, 2001). Grain Fe was increased among the Fe supply into the soil, e.g. the suppling of nitrogen fertilizer (Senadhira et al., 1998; Prom-u-thai and Rerkasem, unpublish datas). Therefore, to solve the Fe-deficiency anemia problem by consuming the Fe from rice grain. High grain Fe content can be managed by genotype and supplying of Fe into the soil. The supplying of Fe into the soil was also correlated with the growth stage of rice.

Acknowledgement

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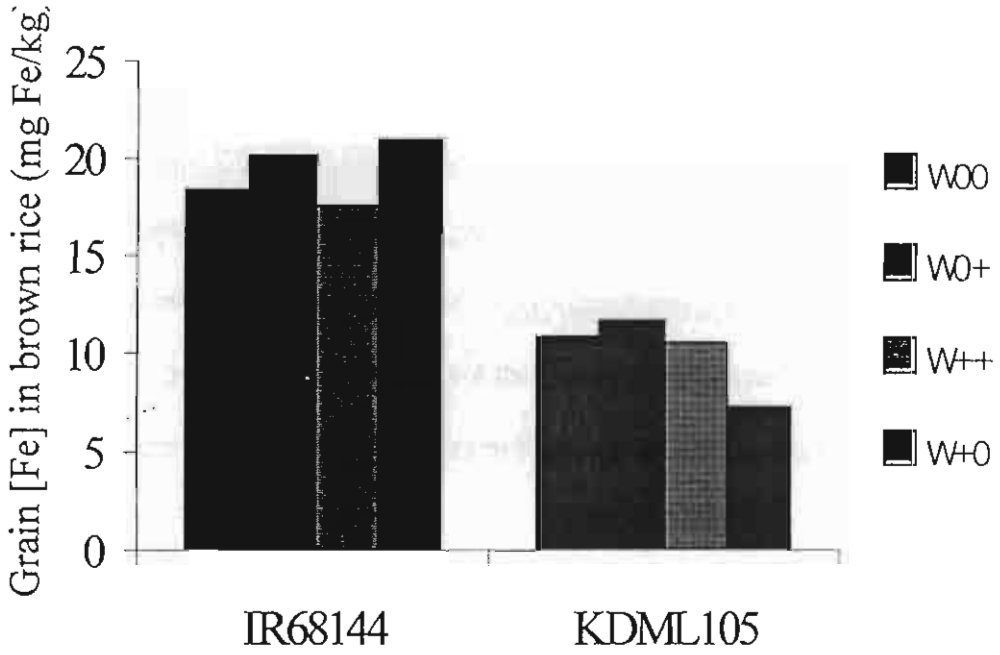

Fig. 1 Grain Fe concentration in brown rice of two rice genotypes grown under four water conditions (LSD=1.8)

Table 1 The Fe content in shoot and grain of two genotypes grown under four water regimes

Genotype	Water condition	Fe content (mg Fe/pot)	
		Shoot	Grain
IR68144	W00	20.4	0.6 cd
	W0+	25.5	0.7 d
	W++	28.2	0.5 bc
	W+0	26.9	0.6 cd
KDML5	W00	23.1	0.2 a
	W0+	66.8	0.2 a
	W++	44.1	0.4 b
	W+0	72.0	0.3 ab
Analysis of variance			
p (Genotypes)		**	***
p (Water)		*	ns
p (G X W)		ns	**

Table 1 The dry weight of grain and straw and percent of empty grain of two rice genotypes grown in different water regimes

Genotype	Water condition	Dry weight (g/pot)		% Empty grain
		Grain	Straw	
IR68144	W00	31.6 b	40.1 ab	25 b
	W0+	35.1 bc	44.4 b	10 a
	W++	29.9 b	32.1a	9 a
	W+0	28.5 b	29.6a	16 ab
KDML105	W00	14.5 a	58.1c	62 d
	W0+	20.9 a	67.1d	52 d
	W++	40.7 c	63.8 cd	18 ab
	W+0	37.2 c	63.4 c	33 c
Analysis of variance				
p (Genotypes)		*	**	**
p (Water)		**	*	**
p (G X W)		**	*	**

Lower case used for comparison between each columns

Response of F_2 population derived from boron efficient (Fang 60) x boron inefficient (Bonza) wheat (*Triticum aestivum* L.) genotypes to boron levels

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Abstract

Responses of a F_2 population between boron (B) efficient (Fang 60) and B inefficient (Bonza) wheat (*Triticum aestivum* L.) parents to levels of B were studied in two experiments. The three B levels; nil (B0), limed at the rate 1 t ha^{-1} (BL) and boron at the rate 10 kg borax ha^{-1} (B+), were applied to three populations, the two parents and their F_2. Response to B, i.e. number of grains $spikelet^{-1}$, grain set index (GSI) and grain yield, were found to differ among populations when grown in low B (BL and B0). Mean grain sets of F_2 in low B were intermediate between the two parents but closer to the more efficient parent, Fang 60. This suggests that B efficiency was expressed as a dominant trait. Segregation of the F_2 fit 15 B efficient plus intermediate: 1 B inefficient ratio, indicating that B efficiency was controlled by two genes. From each B level, 24 F_2 plants with the highest grain set and grain yield were selected and their F_3 progenies were evaluated in sand culture without B in the second experiment. Segregation for response to B was found within F_2-derived F_3 families selected from all B treatments. Populations selected from low B (BL and B0) displayed a higher proportion of B efficient genotypes than those from sufficient B (B+). F_2 populations selected from BL and B0 comprised B efficient, homozygous and heterozygous genotypes but no B inefficient genotype was found. Both B efficient and inefficient genotypes were found within populations selected under B+ condition, indicating that selecting for B efficiency in BL and B0 is more effective than in B+. In conclusion, B efficiency was qualitatively inherited in wheat. This character can be improved in breeding programme by backcrossing. As dominant gene action was involved, progeny testing method should be employed in selection for B efficient genotype.

Introduction

Low boron (B) soils are widespread in many wheat growing, subtropical areas (Sillanpaa, 1982). These include the northern and northeastern regions of Thailand, where wheat is being promoted (Rerkasem et al., 1988; Keerati-Kasikorn et al., 1987). Boron deficiency causes yield reduction by inducing male sterility, resulting in grain set failure (Cheng and Rerkasem, 1993). Wide range of genotypic variation for response to low B has been identified and genotypes were classified into four distinct groups, namely, efficient, moderately efficient, moderately inefficient and inefficient (Rerkasem and Jamjod, 1997). At low B, the inefficient genotypes were completely sterile and set only a few or no grain, while the efficient genotypes set grain normally. Evidence of genotypic variation offers a solution to B deficiency through selection and breeding for B efficient cultivars. In this study, the B efficient (Fang 60) and inefficient (Bonza) genotypes were used as parents to produce F_2 generation. Response of F_2 population to B levels and their genetic control are described. Understanding response of segregating population and genetic control will facilitate selection and breeding for B efficiency.

Materials and methods

Genetic materials

Fang 60 (B efficient, Jamjod et al., 1992) and Bonza (B inefficient, Rerkasem and Jamjod, 1997) were used as parents. F_1 plants were sown in B sufficient soil to produce the F_2 generation. The F_2 population was tested at 3 levels of B in the soil in

Experiment 1. Seventy-two F_2 plants were selected and multiplied. Selected F_3 families were tested in sand culture in Experiment 2.

Experiment 1: *Evaluation of F_2 response to B levels*

Parents and F_2 were sown in a low B soil at Chiang Mai University. The experiment was arranged as a split plot design with 3 replications. Three B levels assigned to main plots were nil (B0), limed at the rate 1 t ha^{-1} (BL) and B at the rate 10 kg borax ha^{-1} (B+), applied to the soil and the three populations, two parents (Fang 60 and Bonza) and their F_2, were sown in sub plots. In each plot, 10 plants each of Fang 60 and Bonza, and 120 F_2 plants were sown. At booting, the first two emerged ears from each plant were bagged to prevent outcrossing. At maturity, the bagged ears were harvested and analysed for number of spikelets ear^{-1}, grains $spikelet^{-1}$ and Grain Set Index (GSI, percentage of the 20 basal lorets from 10 central spikelets with grain; Rerkasem and Loneragan, 1994). All ears from each plant were counted, pooled, threshed and determined for grain yield. Responses to B of parents and the F_2 population were compared by LSD. Chi-square tests were used to examine the segregation ratio of F_2 population for each B treatment.

Experiment 2: *Evaluation of selected F_2-derived F_3 families*

Twenty-four F_2 plants which had the highest grain yield and gain set were selected from each B level, and seeds harvested from these plants represented F_2-derived F_3 families selected from BL, B0 and B+. All families were grown in trays containing washed river quartz sand with no detectable available B. Families were grown in rows, 12 plant row^{-1}, with a spacing of 6 cm between plants and 6 cm between rows. Grid rows of Fang 60 and SW 41 parents were included every 6 rows. Trays were watered twice daily with a

complete nutrient solution without added B. At booting, two ears from each plant were bagged and at maturity the bagged ears were harvested and GSI determined. For each F_3 family, mean and within family variance were calculated and compared to both parents.

Results and discussion

Parents used in this study displayed genotypic differences for response to B (Table 1). Severe reduction in number of grains spikelet^{-1}, grain yield and GSI were found in Bonza while those of Fang 60 parent were not affected, compared to B+. However, B had no effect on number of ears plant^{-1} and spikelets ear^{-1} of both parents and their F_2. These findings were consistent to those reported by Jamjod et al. (1992) and Rerkasem and Jamjod (1997) for Fang 60 which is B efficient and Bonza which is B inefficient.

At B+, mean grain set and grain yield of the F_2 population and both parents were similar while in low B the F_2 population means were intermediate between the two parents but closer to Fang 60 (Table 1). F_2 distribution for GSI were used to study the segregation pattern of F_2 compared to parents in response to low B (Figure 1). No segregation of individual F_2 plants was found when grown in B+. However, when grown in low B, most of F_2 plants fell into the range of the efficient parent, Fang 60. This type of segregation suggested that B efficiency was controlled by dominant gene action. In addition, low B treatments in this study allow genetic variability to be expressed and could be used to screen other segregating populations.

As B efficiency was controlled by dominant gene action, the F_2 segregation ratio was calculated by the following criteria. If the cross was segregating at a single gene, the F_2 population was expected to segregate in a ratio of 3 efficient : 1 inefficient. If the cross was segregating at two genes, the population was expected to segregate in a ratio of 15 (efficient + intermediate) : 1 inefficient. In Figure 1, the GSI of Bonza and Fang 60 grown in BL were 2.1 and 96.8 % and in B0 were 8.6 and 97.0 % respectively. The mean GSI of each parent plus one standard deviation was used to classified the response of F_2 plants. For example, F_2 plants grown in BL having GSI less than 10.9 % were classified as B inefficient. According to this classification, it was found that the segregation ratio of the F_2 population grown in BL and B0 fit with 15 efficient plus intermediate : 1 inefficient ratio (Table 2). This indicates that Fang 60 and Bonza differed by two genes for B efficiency.

If B efficiency was dominant to inefficiency and controlled by two independent loci, *A* and *B*, then it is expected that genotype of Fang 60 in term of response to B should be *AABB* and Bonza should be *aabb*. Genotypes of F_2 plants that fell into the range of Fang 60 when grown in BL and B0 were likely to be *A-B-* (i.e. *AABB*, *AABb*, *AaBB* and *AaBb*) and those in the range of Bonza were all *aabb*. Genotypes of F_2 plants classified as intermediate were likely to be *A-bb* (*AAbb* and *Aabb*) and *aaB-* (*aaBB* and *aaBb*). Selection for B efficiency base on phenotype will not effective because it is not possible to distinguish between heterozygous (e.g. *AaBb*) and homozygous efficient genotypes.

The value of each F_2 individual was the expression of its phenotype, which included both genotypic and environmental effects. The measurement of B response of

F_2 derived F_3 families allowed the genotype of the F_2 to be identified. Twenty-four F_2 plants with the highest grain yield and grain set were selected from each B treatments. Their F_3 progenies were tested in low B and assigned into homozygous efficient, segregating or homozygous inefficient to B by comparing the family's mean and variance to the parents. Bonza parental check set no grain while mean GSI of Fang 60 were between 80-90% and variances were <1000 (Figure 2). Although all selected F_2 plants had GSI >95%, most of their progenies were segregating when grown in low B. The segregation within the F_3 families selected from BL and B0 confirmed the dominant gene action of B efficiency while segregation of families selected from B+ resulted from random selection for B efficient genes. It is suggested that progeny testing should be employed in selection for B efficiency.

High proportions of B efficient alleles were found from populations selected under low B, compared to those selected from B sufficient (Table 3). Four families or 8 % of selected populations from BL and B0 were homozygous efficient but none were homozygous inefficient. In contrast, in B+ treatment where B efficient genes were randomly selected, no homozygous efficient and 8 % homozygous inefficient were found. This indicates that low B in this study exerted selection pressure for B efficiency and high yield. Moreover, populations selected from non B stress condition were likely to contain a high proportion of inefficient genotypes (for example, 46 % compared to 29 % of those selected from BL, Table 3). In breeding programmes, genotypes or breeding materials should be screened for response to B prior to release or promote in low B areas.

Most cereal breeding programmes devote a considerable proportion of their resources to selection for grain yield *per se*. This involves sowing yield trials at several contrasting locations within the one target region and retaining those selections with a comparatively high mean yield. Advanced lines from CIMMYT germplasm, #144, #1510 and #1015, which are all sister lines, outyielded National trials during the early 1980s. Line #1015 was released as Fang 60 from Fang Rice and Winter Cereals Research Station, Chiang Mai, low B site, in 1987, and has shown outstanding yield performance until now. High correlation ($r = 0.81$) between GSI and grain yield was found when wheat and barley genotypes were grown in low B but no correlation was found when plants were grown in B sufficient conditions (Jamjod and Rerkasem, 1999). B efficient genes in Fang 60 might having been unconsciously selected by selecting for grain yield.

The results of this study demonstrated that B efficiency is qualitatively inherited. This character can be improved in breeding programmes by backcrossing. As complete dominant gene action was involved, progeny testing method should be employed in selection for B efficient genotype.

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Table 1. Response of Fang 60 (E, efficient), Bonza (I, inefficient) and F_2 grown at nil boron (B) plus lime (BL), nil B (B0) and 10 kg B ha^{-1} (B+) (Experiment 1).

	B treatment		
Characters/population	BL	B0	B+
Ears plant^{-1}			
Bonza (I)	9.1	11.7	9.4
F_2	10.0	7.5	9.3
Fang 60 (E)	5.4	8.1	8.5
LSD(0.05) B x G ns			
Spikelets ear^{-1}			
Bonza (I)	15.3	16.1	17.2
F_2	17.2	16.8	17.4
Fang 60 (E)	16.0	16.7	17.0
LSD(0.05) B x G ns			
Grains spikelet^{-1}			
Bonza (I)	0.1	0.4	1.9
F_2	1.6	1.7	2.2
Fang 60 (E)	2.8	2.9	3.0
LSD(0.05) B x G 0.3			
Grain yield (g plant^{-1})			
Bonza (I)	0.2	0.8	6.6
F_2	6.3	4.6	6.0
Fang 60 (E)	5.6	8.8	8.1
LSD(0.05) B x G 3.2			
GSI (%)			
Bonza (I)	2.1	8.6	89.9
F_2	69.9	79.1	87.6
Fang 60 (E)	96.8	97.0	99.3
LSD(0.05) B x G 8.3			

Table 2. Response of F_2 population from Fang 60 (B efficient) x Bonza (B inefficient) grown in 3 levels of B (Experiment 1).

B		Number of F_2 plants				
		Model[a]	Efficient + Intermediate	Inefficient	χ^2	P
BL	Expected	3:1	130.5	43.5	26.67	<0.01
	Expected	15:1	163.1	10.9	0.96	0.33
	Observed		160.0	14.0		
B0	Expected	3:1	146.2	48.7	33.03	<0.01
	Expected	15:1	182.9	12.1	0.29	0.61
	Observed		181.0	14.0		
B+	Expected	3:1	127.5	42.5	-	-
	Expected	15:1	159.4	10.6	-	-
	Observed		No segregation observed			

[a] Expected ratio for single gene was efficient : inefficient = 3:1 and for two genes was efficient + intermediate : inefficient = 15:1.

Table 3. Variance of F_2-derived F_3 families selected from BL (limed soil), B0 (no added B) and B+ (10 kg B ha^{-1}) then grown in sand culture without added B(Experiment 2). Selections were categorized by GSI.

	Number of family (%)					
	Variance					
Mean	0	1-500	>500-1000	>1000-1500	>1500	*Total*
			BL selection			
0-25			17	13		*29*
>25-50				17	21	*38*
>50-75				13	12	*25*
>75-100		8				*8*
Total	*0*	*8*	*17*	*43*	*33*	
			B0 selection			
0-25		4	13	17		*33*
>25-50				8	25	*33*
>50-75				8	17	*25*
>75-100		4	4			*8*
Total	*0*	*8*	*21*	*33*	*42*	
			B+ selection			
0-25	8	4	25	8		*46*
>25-50				17	21	*38*
>50-75				4	13	*17*
>75-100						*0*
Total	*8*	*4*	*25*	*29*	*44*	

Figure 1

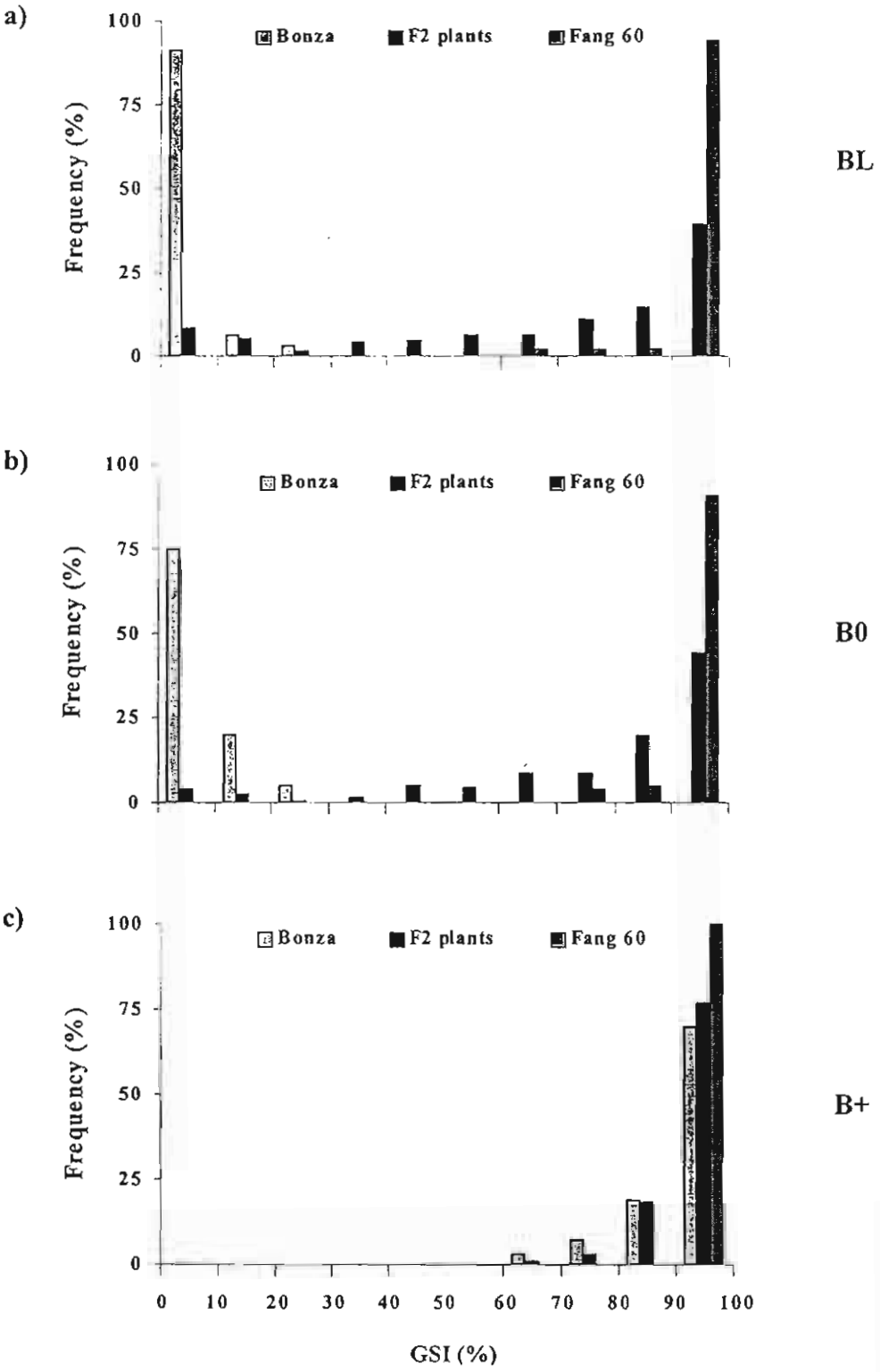
a)
b)
c)
Bonza
F2 plants
Fang 60
Frequency (%)
100
75
50
25
0
BL
B0
B+
0
10
20
30
40
50
60
70
80
90
100
GSI (%)

Figure 2

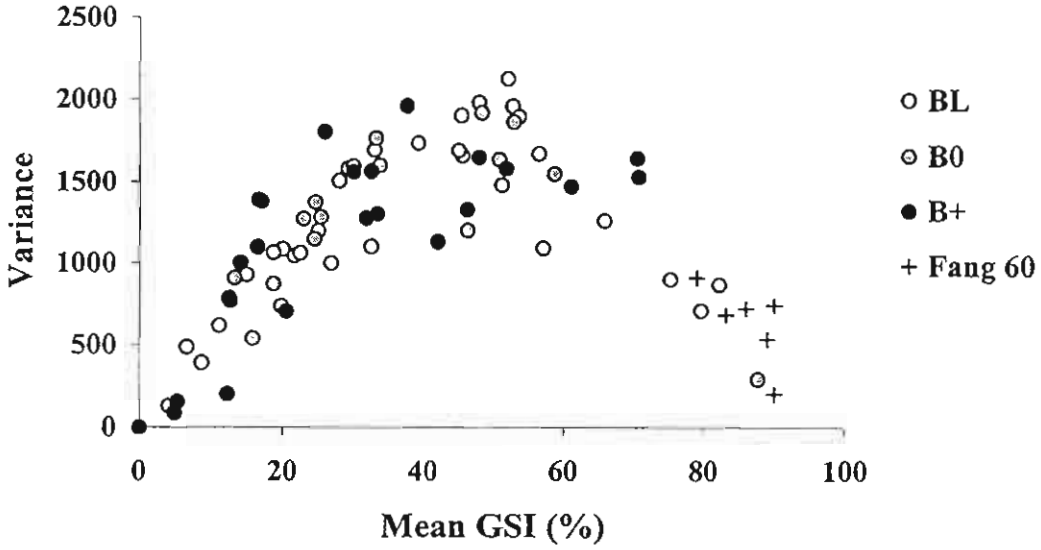
2500
2000
1500
1000
500
0
Variance
0
20
40
60
80
100
Mean GSI (%)
BL
B0
B+
Fang 60

Figure 1. Grain Set Index (GSI, %) of parents and F_2 plants of (Fang 60 x Bonza) grown in:

BL: mean (sd) of Bonza, F_2 population and Fang 60 were 2.1 (8.8), 69.9 (32.8) and 96.8 (9.8), respectively.

B0: mean (sd) of Bonza, F_2 population and Fang 60 were 5.6 (9.0), 79.1 (25.3) and 97.0 (5.1), respectively.

B+: mean (sd) of Bonza, F_2 population and Fang 60 were 89.9 (12.9), 87.6 (7.8) and 99.3 (1.4), respectively.

Figure 2. Mean and variance of F_2-derived F_3 families selected from BL (limed soil), B0 (no added B) and B+ (10 kg B ha^{-1}) and of Fang 60 parent grown in sand culture without B (Experiment 2). Note: Mean GSI and variance of Bonza parent were both 0 and obscured by F_3 families' data. GSI of all selected F_2 plants when grown in Experiment 1 were 95-100%.

Boron Deficiency in Wheat: a Review

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ABSTRACT

Although cereals are generally considered to be insensitive to boron (B) deficiency, incidences of B deficiency have been reported from many of the world's wheat growing countries since the 1960's. The most extensive region of B deficiency in wheat so far reported is the adjoining area of eastern Nepal, northeastern India and northwestern Bangladesh, through to southwestern China. Wheat is more prone to B deficiency than rice and maize, and some dicotyledons including soybean and mungbean. Although it has been reported to adversely affect many processes of wheat growth and development, B deficiency depresses commercial wheat yield primarily through grain set failure, which is in turn governed by male fertility. The function of wheat anthers has been found to be impaired when their B concentration per unit dry weight was 8-10 times that found limiting for vegetative growth. Wheat genotypes vary greatly in their adaptation to low B soils, B efficient genotypes may grow and yield normally on low B soils in which inefficient genotypes are so adversely affected by B deficiency that they set no grain at all. International germplasm from the International Maize and Wheat Improvement Centre (CIMMYT) on which most developing countries depend on for their new wheat cultivars is largely B inefficient. Increasing B efficiency in such internationally important germplasm should boost production in the world's growing areas on low B soils.

1. Incidences of boron deficiency in wheat

Boron (B) was shown to be essential to plant growth in 1923 (Warington, 1923). Among the micronutrients, deficiency of B is the most frequently encountered in the field (Gupta, 1979). However, along with other cereals, wheat has generally been considered to have a low requirement for B (Marten and Westermann, 1991). Lack of reports of deficiency in wheat and other small grains from areas where B deficiency in other crop species is otherwise widespread such as the USA (Lamb, 1967) further reinforced the perception of wheat being relatively free of B deficiency problem. Boron deficiency in field grown wheat was first observed almost concurrently on

different sides of the world following the spread of semi-dwarf, 'green revolution' wheat in the 1960's. Grain set failure associated with male sterility was observed in wheat in Brazil in 1962 (da Silva and de Andrade, 1980). Diagnosis of B deficiency was confirmed by positive responses to B application. The same was observed in Nepal in 1964, among introduced high-yielding Mexican and Indian wheat germplasm (Misra et al., 1992). Boron deficiency was found to be the cause of almost complete crop failure in some 40,000 ha of wheat in Heilongjian Province in the north of China in 1972 and 1973 (Li et al., 1978).

Countries where B deficiency, based on responses to B application, in wheat has been reported included Bangladesh, Brazil, Bulgaria, China, Finland, India, Madagascar, Nepal, Pakistan, South Africa, Sweden, Tanzania, Thailand, USA, USSR, Yugoslavia, Zambia (Shorrocks, 1997). Reports of B deficiency in wheat continue to come out of India (Singh et al., 1976; Ganguly, 1979; Sarkar and Chakraborty, 1980; Mandal and Das, 1988; Dwivedi et al, 1990.). Most of these were from the northeastern states of Bihar, West Bengal, Orissa, Meghalaya and Assam. It was common local knowledge in the 1980's that the problem does not stop at the international borders, but extends into neighboring areas of Bangladesh and Nepal (Reuter, 1987). "Wheat sterility", depressed percentage of florets with grain, has been reported from many parts of Nepal, with B deficiency, low temperature stress during reproductive development (Subedi, 1992), waterlogging at flowering, low soil nitrogen and hot dry wind (Misra et al, 1992) suggested as possible causes. An imprecise way in which the term "sterility" is used may sometimes lead to inaccurate diagnosis for the causal factor (see below). Except at higher altitudes, responses to B application have identified B deficiency as the cause of grain set failure in wheat in Nepal (Sthapit, 1988; Subedi et al, 1992). Boron deficiency was also found to be the cause of massive sterility observed in the northern wheat zone of Bangladesh. Application of B increased wheat yield in farmers' field by 8.5% to 14% (an equivalent of approximately 60% of the yield gains due to plant breeding in the past 20 years (D.A. Saunders, pers. comm.). Recent studies have confirmed widespread problem of B deficiency in wheat in this part of Asia (Kataki et al., 2001).

The adjoining areas of India, Nepal and Bangladesh is probably the world's most extensive area of B deficient wheat so far reported, covering at least several hundred thousand hectares. The problem of B deficiency affects wheat farmers of area, who are some the world's poorest, in two ways. Firstly, they continue to suffer grain set failure and yield loss each year. Secondly, they are prevented from realizing benefits from new improved wheat varieties with greater yield potential and better resistance to important diseases, which turned out to be poorly adapted to low B soils. Boron deficient wheat has also been found in northern Thailand (Rerkasem et al., 1989) and southwestern China to the Myanmar border (Yang, 1992; Rerkasem, 1996). Any attempt to improve wheat production in Myanmar should keep a close watch on B deficiency especially with introduced germplasm of semi-dwarf wheat from CIMMYT (Rerkasem et al., 2003 and see also section on adaptation to low B soils below).

2. Responses to low boron

2.1 Vegetative growth

The most rapid response to B deficiency in higher plants is the cessation of root elongation (Dugger, 1983; Marschner, 1995; Shelp, 1993; Dell and Huang, 1997), but this has rarely been seen in wheat. Boron deficiency in early vegetative growth is much less readily inducible in wheat than in dicots. For example, Snowball and Robson (1983) found that after a transfer to a solution culture to which no B had been added wheat root continued growing normally for a considerable time, while root growth in subterranean clover (*Trifolium subterraneum* L.) stopped immediately. In earlier studies, B deficiency was induced in vegetative growth in wheat only after B in the nutrient solution had been depleted by plant uptake. Characteristic symptoms in young wheat plants made B deficient in this way include a longitudinal splitting of the newer leaves close to the midrib and the development of a saw tooth effect on young leaves reflecting abnormal cellular development (Snowball and Robson, 1983).

Other evidence of lower requirement for B and lower sensitivity to B deficiency in wheat has all been based on early vegetative growth. Wheat has been shown to grow almost normally in a nutrient solution without added B in which various legumes were adversely affected by B deficiency in a comparison made on 30 days of early vegetative growth (Chapman et al., 1997). Similarly, the lower external and internal requirement for B in wheat than sunflower and marri (*Corymbia calophylla*) were judged on the basis of an early vegetative growth of 10-20 days (Asad et al., 2001). The young wheat plants grew well and were free of B deficiency symptoms in a nutrient solution with ≤ 0.13 μM B in which vegetative growth of the two dicots, marri and sunflower, was severely depressed by B deficiency. Maximum dry weight was attained in wheat with ≥ 0.6 μM B in the nutrient solution, compared with ≥ 1.2 μM B for Marri and sunflower. The difference was even greater in the B concentration in the young open leaf associated with maximum growth, referred by the authors as internal requirement. Ten days old wheat achieved maximum dry weight with ≥ 1.2 mg B kg^{-1} DW, whereas marri and sunflower did not until they had exceeded 18-20 mg B kg^{-1} DW. The lower B requirement in graminaceous species than dicotyledonous species is said to be related to their different cell wall composition (Marschner, 1995). Their shoots have been shown to contain 4-7 mg B kg^{-1} cell wall (CW) compared with 20-40 mg B kg^{-1} CW in dicotyledonous plants (Matoh, 1997).

These early vegetative responses to B in wheat, however, may or may not correlate with whole plant responses. None of the effects of low B on early vegetative growth cited above has ever been observed in the field. An exception is the longitudinal split along the mid-rib observed in solution culture (Snowball and Robson, 1983) which is common the field in Thailand, Bangladesh and Nepal (Rerkasem unpublished). In the field, however, the symptom is extremely ubiquitous and not restricted only to fields or plants that are otherwise proved to be B deficient.

2.2 Reproductive development

The first symptom of B deficiency in field grown wheat is seen during anthesis, when florets remain open longer than normal. When viewed from a distance of 3-4 m against the light, the ears have a translucent appearance, like paper lamps. Examination of the florets just before or during anthesis show poorly developed pollen and sometimes anthers, leading to the association between male sterility and B deficiency (Li et al., 1978; da Silva and de Andrade, 1983; Rerkasem et al., 1989).

A simple staining with iodine (in a KI/I_2 solution) may be used for pollen examination (Cheng et al., 1992). Dead pollen shows up misshapened, shrivelled and un-stained by iodine. However, pollen with starch deposits that stain blue black with iodine is not always viable. A more precise assessment of pollen viability may be made with a fluorochromatic (FCR) test or staining with 4'-6-Diamidino-2-phenylindole2HCl (DAPI). Pollen that exhibited an adverse effect of B deficiency in a 30-70% depression in viability by the FCR test was indistinguishable from B sufficient pollen by the iodine stain (Nachiangmai et al., 2002). The adverse effect of B deficiency on pollen viability was also shown in the absence of one or more of the nuclei by the DAPI test. In addition to male fertility, B deficiency has also been shown to depress the fertilization process (Cheng et al., 1993). Grain set was partially restored when B deficient female wheat flowers were fertilized with B sufficient pollen (Rerkasem et al., 1993) and further enhanced by an application of B to the stigma (Rerkasem and Jamjod, 1997).

That male sterility is the primary effect of B deficiency on grain set in wheat has been demonstrated by an increase in grain set in B deficient plants by hand pollinating with fertile pollen (Rerkasem et al., 1993). Anthers and carpel account for a much larger proportion of B content of the ear of wheat relative to their dry weight (Rerkasem and Lordkaew, 1996). Wheat anthers and carpel contain several times the B concentration of the whole ear (Table 2). Grain set failure was associated with less than 10 mg B kg^{-1} in the anthers and 8 mg B kg^{-1} in the carpel (Rerkasem et al., 1997). In contrast, the critical B deficiency concentration for vegetative growth in wheat has been estimated at 1 mg B kg^{-1} dry weight in the youngest open leaf (Huang et al., 1996; Asad et al., 2001) and 3 mg B kg^{-1} dry weight in the whole shoot (Reuter et al., 1997; Asad et al., 2001).

At present it is still unclear what function B is required for in the development of anthers, pollen and carpel that is different from that for somatic tissues including the secondary sexual part of the ear such as rachis, glumes and lemmas. Anthers with lower B contents appeared to have normal tapetum and lignified endothecium (Rerkasem et al., 1997). These were different from Cu deficient anthers, with their amoeboid tapetal cells (Jewell et al., 1988) and absent lignification of the endothecium (Dell, 1981). Pollen abortion has been found to take place some time after uninucleate vacuolar stage, microsporogenesis in B deficient wheat having proceeded normally prior to this (Rerkasem et al., 1997). This indicates the B requirement for the later stage of pollen development after meiotic and at least the earlier stage of mitotic cell division had occurred.

2.3 Whole plant response

To understand whole plant response to a nutrient deficiency, and thus to apply the understanding to field grown crops, it is necessary to consider responses of different growth processes in relation to one another as well as the response of individual processes. The relationship may be in the chronological order in which the processes occur in the life cycle of the plant, and in their relative sensitivity to the deficiency. Irreversible adverse effects that occur earlier may over-ride effects on more sensitive processes or organs that occur later. Boron deficiency causes flower buds to shed in some species, e.g. in apple (*Malus domestica*) (Dong et al., 1997); black gram

(Noppakoonwong et al., 1997) and sunflower (Blamey, 1987). In such cases it may be irrelevant if the development of the male and female gametes are more sensitive to B deficiency if the flower buds had been lost even before meiosis. On the other hand, a greater sensitivity of the development the stamen or carpel or the fertilization process may make one of them the limiting-step if the B deficiency is not severe enough cause prior irreversible damages. A key to understanding B deficiency in wheat appears to be the relative sensitivity of its reproductive process. Published accounts of responses to low B in field grown wheat invariably reported on the effect of B deficiency on male fertility, grain set and grain yield (Table 1). Evidence of adverse effects of low B on vegetative parameters such as straw yield, tiller number, and secondary reproductive organs such as number of spikelets ear^{-1} is rare. In contrast to the effect on male fertility and grain set, B deficiency tended to increase the weight of individual grains. Barley and triticale (x*Triticosecale* Wittmack) are different from wheat in one respect. As well as the grain set failure, B deficient barley and triticale have been reported to have shorter ears (fewer spikelets ear^{-1}), and also delayed ear emergence in the case of barley (Jamjod and Rerkasem, 1999; Pasook, 2000; Wongmo, 2001).

In wheat (Subedi et al., 1997; Pant et al., 1998), along with barley (Ambak and Tandao, 1991; Jamjod and Rerkasem, 1999), the greater requirement for B for reproductive growth than vegetative growth may be indicated by the effect of B deficiency that actually increased tillering while at the same time depressing male fertility and grain set. In addition to the greater functional requirement for B in the anthers and carpel as discussed above, sensitivity to B deficiency of reproductive development in wheat, and the other Triticeae cereals, may be related to B supply to these organs during critical time. Boron is transported from plant roots via the xylem, driven by water potential gradient created by transpiration. The site of the reproductive process most sensitive to B deficiency in wheat along with barley, durum (*Triticum durum* Dest.) and triticale is in the non-transpiring ear, while it develops inside the leaf sheath. The effect of B deficiency on male fertility in wheat may therefore be expected to operate through interrupted supply of B for anthers and pollen development. On the other hand, it is as yet unclear how wheat avoids the effect of B deficiency on terminal spikelets development that causes depression in the number of spikelets ear^{-1} and the rat-tail symptom barley and triticale.

A greater requirement for B in reproductive than vegetative growth has been shown in canola and sunflower (Asad et al., 2002). In these species, however, B deficiency depressed dry weight of vegetative parts along with the flowers, and stamens that were determined in canola. Similarly in maize, adverse effects of B deficiency on vegetative growth were observed along with those on the pollen and anthers (Agarwala et al., 1981). Wheat is different in that male sterility and the associated grain set failure may be the only observable effect of B deficiency. It offers a unique model through which the effect of B deficiency on the primary sexual process may be studied without the confounding effects on other organs and processes.

2.4 Wheat in comparison to other species

Wheat may be judged to be relatively insensitive to B deficiency on the evidence of its early vegetative growth (see above). In farmers' fields, however, wheat is more prone to B deficiency than rice, maize and even some dicotyledons such as soybean

and mungbean. Cases of B deficiency in wheat in south Asia reviewed above were generally reported from areas growing rice-wheat, the region's most common cropping system. Yet B deficiency has never been observed in the associated rice crop. One of the earliest reports of B deficiency in wheat was made on rice-wheat and soybean-wheat cropping systems, in which neither rice nor soybean were deficient (da Silva and de Andrade, 1983). The wheat crop in a rice-wheat cropping system recorded grain set failure and yield losses of 30% to 70% over 3 consecutive years (Rerkasem and Loneragan, 1994). No adverse effect of B deficiency was ever observed in the rice crops in between the wheat seasons.

This difference between wheat and other crops may be based on relative tolerance to low B of the species. It may also reflect seasonal effects on plant response to soil B, since wheat in the subtropics is grown in the coolest months normally to be avoided for rice, soybean, maize and green gram. In non-alkaline soils wheat grain set and grain yield were depressed by the same level of hot water soluble (HWS) B that affected black gram (*Vigna mungo* (L). Hepper), peanut (*Arachis hypogaea* L.) and sunflower (*Helianthus annuus*) (Bell, 1997). This level of soil B, < 0.12 mg HWS B kg^{-1}, had no adverse effect on rice, soybean, green gram (Bell et al., 1990), maize and sorghum (Rerkasem, unpublished). However, the other Triticeae cereals, including barley (*Hordeum vulgare* L.), have shown responses to B in the same order as wheat (Jamjod and Rerkasem, 1999; Rerkasem and Jamjod, 2001).

2.5 Variation due to the environment

The variable nature of plant responses to B is well known and evidence of B deficiency being accentuated by suboptimal environmental conditions such temperature (too low as well as too high), water stress and high light intensity has been reviewed by Shorrocks (1997), adding to management difficulties. Variation in the response to low B among wheat genotypes is well established. On the same soil, some wheat genotypes may set no grain at all because of B deficiency while others set grain normally (see section on genotypic variation below). Waterlogging (Pintasen et al., 1997) and drought (Pant et al., 1998) have both been shown to accentuate B deficiency in wheat. Researchers in Bangladesh have induced "sterility" by shading, waterlogging or fogging (decreasing water vapour deficit), but the symptoms appeared to be very different from those observed in farmers' fields (Saifuzzaman and Meisner, 1996). No evidence was presented to show if these treatments had caused "sterility" by inducing B deficiency. An experiment in controlled environment showed that the effect of B deficiency in wheat was amplified by low light intensity but not high humidity (Rawson and Noppakoonwong, 1996). Many observations indicating an involvement of B in frost resistance have been reviewed, but it is still unclear if these are simply the effect of B deficiency being accentuated by low temperature stress (Shorrocks, 1997). On the other hand, the wheat sterility problem that occurs regularly at high altitudes in Nepal has not responded to B application (Sthapit, 1988; Subedi, 1992).

3. Diagnosis and measuring effects of B deficiency in wheat

A combination of methods including plant symptoms, soil and plant analysis and plant response to applied B has been employed for diagnosis of B deficiency (Bell, 1997). Vegetative symptoms are not very useful in wheat as they are hardly ever seen

in the field. Male sterility, with florets that stay open for many days at anthesis, followed by grain set failure, are the most common symptoms seen in field grown B deficient wheat (Li et al., 1978; da Silva and de Andrade, 1980; Sthapit 1988; Rerkasem et al., 1989; Rerkasem and Loneragan, 1994). However, similar symptoms associated with male sterility are also caused by Cu deficiency (Graham, 1975). In wheat Cu deficiency also causes the rat-tail symptom of the ear which B deficiency does not. It is however necessary to keep in mind that B deficiency does cause the rat-tail symptom in barley and triticale. Further evidence may be found in local knowledge of the history of B deficiency in the area. As it is now clear that wheat can be as prone to B deficiency as some legumes and other dicots, the history of B deficiency in other crops is also useful. In many crop species, however, genotypes have been observed to vary widely in their sensitivity to B deficiency, making the choice genotypes for indicator plants critical. The problem of B deficiency would never have been suspected in Nepal by the appearance and yield of two local lentil varieties 'Simal' and 'Simrik', although it almost completely destroyed an introduced germplasm of some 500 entries (Srivastava et al., 2000). Locally adapted wheat varieties such as Sonora 64 and Fang 60 are not very good indicators because they are extremely well adapted to low B soils (Anantawiroon et al., 1997; Rerkasem et al., 2003).

Available soil B levels found associated with B deficiency in wheat ranged from about 0.1 mg HWS B kg^{-1} in Thailand (Rerkasem and Loneragan, 1994) to 0.3 – 0.4 mg HWS B kg^{-1} in China (Li et al., 1978). As in other crops, the critical level of available soil B is likely to be highly variable. It is influenced by soil characteristics such as pH, moisture and texture (Shorrocks, 1992; Sims and Johnson, 1991), above ground conditions of light, humidity and temperature (Shorrocks, 1997) and genotypes (see below). Incidences of B deficiency in wheat in Bangladesh have been reported to be completely unrelated to the level of HWS B in the soil (Kataki et al., 2001). Wheat has been found to respond to B in areas dominated by soils with toxic levels B such as Pakistan (Rashid et al., 2001). Response to B has been observed in durum wheat in Turkey (Topal et al., 2001), where pockets of low B soils have also be found amongst toxicity levels B (Gezgin et al., 2001).

The critical B concentration for early vegetative growth in wheat is reported to be about 1 mg B kg^{-1} DW (Asad et al., 2001). In contrast, grain set failure in wheat has been found associated with less than 2 mg B kg^{-1} DW in the ear (Rerkasem and Lordkaew, 1992) and 3 mg B kg^{-1} in the flag leaf at boot stage (Rerkasem and Loneragan, 1994). At these concentrations the flag leaf and ear themselves appeared normal. The leaf and ear B concentration are all somewhat imprecise for diagnosis for B deficiency in wheat, for two reasons. The reproductive organs affected by deficiency, the anthers and carpel, account for only 4% of the whole ear dry weight at anthesis, and 10% of its B content (Rerkasem, 1996). Furthermore, the critical B deficiency concentration for the carpel and anthers, at 10-12 mg B kg^{-1} (Rerkasem et al., 1997), are several times the values for these vegetative and secondary reproductive tissues such as the lemma, palae and rachis.

Diagnosis for B deficiency with tissue analysis may be made with the most precision by analysing for B in the anthers. However, sampling for anthers is logistically impossible for use in farmers' fields. It is extremely time consuming, especially with the samples (larger amounts of B) needed for analysis by the colorimetric method

with Azomethine-H of Loshe (1982). The final verification of B deficiency is plant response to apply B. Thus after an observation of massive sterility in wheat in Bangladesh in 1986/87, widespread B deficiency was verified by the average 14% on-farm yield increase by B application in 1987/88 and 10% in 1988/89 (D.A. Saunders, pers. comm.). Although not as effective as B applied to the soil, foliar B may increase grain set significantly (Rerkasem and Jamjod 1988) and may be sufficient for the purpose of confirming B deficiency. A source of error in B response trials is "contamination". Large amounts of B have been found in common N, P and K fertilizers in Asia (Bell et al., 1990; Lordkaew, 1995). Thus B deficiency may be overcome even in the nil B treatment.

The occurrence of wheat sterility in farmer's field in Nepal (Sthapit, 1988; Misra et al., 1992; Tiwari, 1996) and Bangladesh (Saifuzzaman and Meisner, 1996) has often been reported to be highly variable. Confirmation of B deficiency as the cause, however, has sometimes been hindered by imprecise definition of "sterility". Percentage of florets without grain measures the combined success of two different processes, florets development (photosynthetic capacity) and fertilization (grain set). Boron deficiency, on the other hand, specifically affects grain set only (see above). Unless there is a B sufficiency control, grain set failure is more precisely measured with the grain set index (GSI). The GSI is defined as the percentage grain bearing in two basal florets of 10 central spikelets (Rerkasem and Loneragan, 1994). Among florets of a wheat spikelet, the two basal florets are the first to develop, while development of terminal florets is dependent on the supply of photosynthate. The absence of a grain in either or both of the basal florets of a spikelet is therefore indicative of grain set failure. Focusing on central spikelets removes the possibility of a confounding effect of incompletely developed basal and terminal spikelets. Without the need for a B sufficiency control, the GSI is very useful to evaluate responses to low B in nurseries with large entry numbers (Rerkasem and Jamjod, 1997a; Anantawiroon et al., 1997). The extent of B deficiency in the screening environment may be indicated by inclusion of a set of check genotypes covering a range of responses to low B. The GSI is also useful to quantify the problem of grain set failure in wheat, triticale and barley under a wide range of on-farm environmental conditions. The presence of common varieties with known susceptibility to B deficiency allows verification of B deficiency as the likely limiting factor.

4. Adaptation to low B soils

4.1 Genotypic variation

The ability of a genotype to grow and yield well in soils too deficient in a particular nutrient for a standard genotype has been defined as 'nutrient efficiency' (Graham, 1984). This simple definition enables performances of genotypes to be compared experimentally even when the mechanism behind their differences is yet to be explained. Without inferring a mechanism, the ability of a genotype to perform well in soils too deficient in B for other genotypes has been termed B efficiency (Rerkasem and Jamjod, 1997b). Germplasms of oilseed rape have successfully been evaluated for B efficiency based on their performance in low B relative to sufficient B (Xue et al, 1998; Stangoulis et al, 2000).).

Reports of B deficiency in wheat, from Brazil (da Silva and de Andrade, 1983), China (Li et al., 1978), to India (Ganguly, 1979), Nepal (Subedi et al., 1997) and Thailand (Rerkasem et al., 1989), have invariably noted large genotypic variations in the response to B. Variation in B efficiency in wheat is probably the widest possible of any species in response to a deficiency in any nutrient element. Wheat genotypes growing in the same low B condition may range from the most inefficient that set no grain at all to the most efficient that set grain normally (Rerkasem and Jamjod, 1997a; Rerkasem et al., 2003). Boron efficient and inefficient genotypes have been identified in different countries (Table 3). Some of these, which have shown consistent responses to low B, have been used as standard B efficiency checks.

Wheat genotypes have been ranked according to their adaptation to low B soils in into 5 different B efficiency classes (Rerkasem and Jamjod, 1997). The most efficient and most inefficient classes appear to be readily distinguishable by their tissue B concentrations. Growing in the same low B conditions, B concentration in the flag leaf and ear of the very inefficient Tatiara were only about half of those of B efficient Fang 60 (Wongmo et al., 2003). Those belonging to closer B efficiency classes, however, are less readily distinguishable by the concentration of B in their flag leaf (Rerkasem and Loneragan, 1994; Subedi et al., 1999) or ear (Rerkasem and Lordkaew, 1992). Male fertility and grain set are more closely correlated with B concentration in the anthers than in the leaf or secondary reproductive tissues such as the palea or lemmas (Rerkasem et al., 1997). Boron efficient genotypes appear to have escaped male sterility by maintaining anther B above the critical deficiency concentration (Figure 1).

The ability to recycle B from old tissues is a mechanism that enables some plant species to escape deficiency when external supply is low. Unique among the essential plant nutrients, B is freely mobile in the phloem of some species while having restricted mobility in other species, (Brown and Shelp, 1997). Some have suggested that certain wheat genotypes may be more tolerant to B deficiency than others because they are able to meet reproductive demand by their ability to recycle B into growing ears (Rawson, 1996; Subedi et al., 1999; Huang et al., 2001). No evidence of B remobilization has been found in the B efficient Fang 60 which had escaped B deficiency caused by withholding B for five days between premeiotic interphase and young microspore stage (Nachiangmai et al., 2003). The authors were able to trace B supply to the ear by first providing adequate B supply with ^{11}B at 10 μM and then labeling the much lowered supply at 0.1 μM with ^{10}B. They clearly demonstrated that with the lowered external supply to 0.1 μM, inefficient SW41 was unable to maintain adequate B supply to the ear, and so its pollen viability was depressed by 40-70% by B deficiency. In contrast, Fang 60 was unaffected by B deficiency because it was able to meet the demand for pollen development with the 0.1 μM ^{10}B.

4.2 Genetics of B efficiency

Genetic control of B efficiency has been reported for many species (Rerkasem and Jamjod, 1997). For wheat, analysis of B efficiency in F1s from seven crosses of genotypes with different adaptation to low B soils led to a suggestion of additive and dominant gene actions in the control of B efficiency (Jamjod et al., 1992). The F1s by B efficient Fang 60 as male parent and very inefficient female parents showed adaptation to low B soil that was almost identical to Fang 60 (Figure 2). The F2

populations of a Fang 60 x Bonza cross were found to fit the 1:15 ratio of B inefficient (similar to Bonza) to efficient (more efficient than Bonza to similar to Fang 60), suggesting two dominant genes controlling B efficiency (Ngorian, 2000).

For triticale, durum wheat and barley, a transfer of relevant genes from B efficient bread wheat such as Fang 60 will probably be essential. As it is present in the more B efficient bread wheat but not in the less B efficient durum wheat, triticale and barley, the D genome is of great interest as a possible source of genes for increasing B efficiency.

4.3 Boosting wheat production on low boron soils with B efficiency

The world's largest single source of wheat germplasm is the International Maize and Wheat Improvement Centre (CIMMYT). Thousands of advanced breeding lines are introduced into developing countries each year in various yield trials, screening and observation nurseries. Evidence of B inefficiency in the germplasm relative to B efficient Fang 60 (PI/FD//PI/MZ/3/MXP) or Sonora 64 was seen in lines after lines of male sterile genotypes in the various screening nurseries (e.g. the International Bread Wheat Screening Nursery, Semi-Arid Areas Wheat Screening Nursery) and yield trials (e.g. High Temperature Wheat Yield Trial, Elite Selection Wheat Yield Trial) in stations on low B soils of the Asian subtropics such as Nashipur in Bangladesh, Chiang Mai in Thailand and Yunnan in China (Rerkasem unpublished, C.E. Mann and D.A. Saunders, Pers. Comm.). This has been confirmed experimentally (Rerkasem and Jamjod, 2001; Rerkasem et al., 2003.). Some 30-40% of the germplasm set only 1-2 grains ear^{-1} or none at all in the same low B condition in which Fang 60 set grain normally. Most developing countries, including Nepal and Bangladesh, depend on CIMMYT for their new improved wheat cultivars. It is therefore not surprising that wheat varieties and advanced breeding lines from Nepal (Subedi et al., 1997) and Bangladesh (Ahmed et al., 2002) are mostly B inefficient. Similarly, promising lines selected in Thailand that turned out to be susceptible to B deficiency-induced male sterility when they reached on farm trials included ARTC87001 (Junco 'S'/Buc 'S', CM64478, from the 4th Hot Climate Wheat Screening Nursery) and SMGBW88001 (Rerkasem, 1996).

By screening the F2s in low B the author demonstrated the ease of transfer of the B efficiency genes. There is real scope for genetic improvement. The source of genes for B efficiency already exists in bread wheat, especially in advanced breeding lines already incorporating high yielding, disease resistance and other desirable characteristics. Screening can be done in the field on soil with low B or in a simple sand culture (Anatawiroon et al., 1997; Rerkasem et al., 2003). Many of the B efficient genotypes identified were advanced breeding lines, i.e. ready to be released as cultivars, that were included in CIMMYT international yield nurseries such as the 4HTWYT and 17ESWYT.

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Table 1. Responses to boron in wheat.

Responsive Parameters	% max†	Non-responsive parameters	References
Seed yield	51-61	Straw yield	Rerkasem et al (1989)
Grains spikelet^{-1}	25-73	Ears m^{-2}	
mg seed^{-1}	106-121‡	Spikelets ear^{-1}	
Seed yield	25-65	Straw yield	Rerkasem and
Grains spikelet^{-1}	21-57	Ears m^{-2}	Loneragan (1994)
Grain set index	31-73	Spikelets ear^{-1}	
mg seed^{-1}	123-141‡		
Seed yield	3-75	-	Subedi et al. (1997)
Grains ear^{-1}	9-79		
mg seed^{-1}	121-164‡		
Ears m^{-2}	95-161‡		
Seed yield	62-88	Above ground	Pant et al. (1998)
% ears with grain	63-79	biomass	
Grains ear^{-1}	40-85	Plant height	
Grain set index	66-75	Spikelets ear^{-1}	
mg seed^{-1}	120-130‡		
Ears m^{-2}	99-116‡		
Grains ear^{-1}	9-67	Florets ear^{-1}	Subedi et al. (1999)
Pollen viability	15-78	Dry weight of roots, stems, leaves	

† Relative to performance in B sufficiency

‡ Increased in low B

Table 2. Boron concentration in different parts of the wheat ear at ear emergence and anthesis in five wheat cultivars.

Genotype	Just emerged		Anthesis	
	Whole ear	Anthers	Whole ear	Carpel
	mg B kg^{-1}			
SW41	2.6	14.0	2.6	6.8
Glenaro 81	3.7	14.3	2.7	9.2
Glennson	2.9	18.0	2.5	8.9
Nesser	3.4	16.7	3.8	10.9
Seri 82	3.5	15.3	2.7	6.7
SE	0.6	5.2	0.7	2.0

Each number is mean of samples from three replicated plots of field grown plants.
Source: Rerkasem (1995).

Table 3. Boron efficiency of selected Asian wheat varieties and genotypes.

Country of origin	Efficiency	Reference
Bangladesh	Efficient: **(Fang 60)**[1]	Ahmed et al., 2002
	Inefficient: Kanchan, Gourab, E12, Sourav, **(SW41)**[2]	
	Inefficient: Ananda, Aghrani, Balaka, Inia 66, Kanchan, Kalyasona, Sonalika, Veery	Rerkasem unpublished
China	Inefficient: Saric F70, Tanori F71, Chapingo, Spring 980[3]	Yang, 1992
	Efficient: **Sonora 64**	
India	Inefficient: Janak, UP262, BW5, BW11, BW43	Reuter, 1987
	Inefficient: HP1102, HP1209, HD2285, HUW206	Tandon and Naqvi, 1992
	Efficient: HD2307, HDR77, C 306	
Nepal	Inefficient: **(SW41)**, BL1022, SW23	Subedi et al., 1993
	Efficient: **(Fang 60, Sonora 64)**	
	Inefficient: BL1022, Annapurna 4, Annapurna 3, BL1135, RR21, **(SW41)**	Subedi et al., 1999
	Efficient: BL1249, Nepal 297, **(Fang 60)**	
Thailand	Inefficient: Seri, Kauz, **SW41**, SW23	Jamjod et al., 1992
	Efficient: **Fang 60**, #144[4]	
	Inefficient: **SW41**	Rerkasem and Loneragan, 1994
	Efficient: **Sonora 64**	
	Inefficient: **SW41**, Bonza[5]	Wongmo, 2001
	Efficient: **Fang 60**	

[1]Boron efficicent check (PI/FD//PI/MZ/3/MXP), locally known as 1015 before release as Fang 60 in 1987 in Thailand.
[2] Boron inefficient check (Baya/Emu)
[3]Ald/Pci
[4]Another selection from PI/FD//PI/MZ/3/MXP
[5] Australian variety

Table 4. Effects of boron fertilizer on wheat line SW41

Boron Treatment†	Seed yield (kg ha^{-1})	Ears m^{-2}	Spikelets ear^{-1}	Grains spikelet^{-1}	Grain weight (mg)	Harvest Index (%)
Nil	531	270	15.5	0.49	42	10.4
Soil	2913	290	15.1	2.36	35	44.8
Foliar(31)‡	906	272	15.1	1.26	41	19.2
Foliar(39)	1144	290	14.3	1.23	43	22.3
Foliar(49)	1325	312	14.8	1.47	40	22.1
Foliar(52)	838	304	14.8	0.97	41	17.1
Foliar(54)	863	314	15.5	10.8	41	16.8
Foliar(57)	1238	316	14.6	1.18	41	20.2
LSD ($p < 0.05$)	594	NS	NS	0.4	3	9.0

† Soil application before sowing, with borax at 1 kg B ha^{-1}. Foliar application of at 50 g B ha^{-1} (as borax in 0.05% solution, w/v)

‡ Time of foliar application in brackets, in days from sowing: 31, tillering; 39, stem elongation; 49, flag leaf visible; 52, flag leaf emerged; 54, boot stage; 57, anthesis.

Source: Rerkasem and Jamjod, 1989.

Table 5. B efficiency in F3 populations from Fang 60 x Bonza crosses selected under B deficiency and sufficiency.

GSI in B0†	Selected in		
	BL	B0	B+
= Bonza	25.0	20.8	41.7
> Bonza	75.0	79.2	58.3
= Fang	29.2	29.2	16.7
Fang 60	85.9	78.9	81.9
Bonza	0	0	0

† $P < 0.05$

Source Ngorian (2000)

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Contents

Boron in Plants: Requirements and Function