

CHAPTER 3

Variation in boron responses in wheat (*Triticum aestivum* L.) genotypes during vegetative and reproductive growth

3.1 Introduction

Boron deficiency in wheat causes grain set failure, through male sterility, but the level of grain set at low B varies among cultivars. Rerkasem and Jamjod, (1997) have found responses of 64 genotypes in low B soil at Chiang Mai to range from complete male sterility through those partially affected to no deficiency symptoms in anthers at all. In the same study, the range of grain set index varied from 0-100% among the genotypes. They classified the genotypes by their GSI in sand culture without added B into five classes of efficiency namely: very inefficient (0-20%), inefficient (21-50%), moderately inefficient (51-70%), moderately efficient (71-85%) and efficient (> 85%).

Variation in B response amongst 12 genotypes during vegetative growth did not correlate with the variation in B efficiency determined from GSI (Rerkasem *et al.*, 1993). Most research since then has focused on the success of the reproductive growth in low soil B as measured by grain set. However, there is evidence of B response in wheat to low B during vegetative growth (Chapman *et al.*, 1997; Asad *et al.*, 2000) and of genotypic variation in vegetative response (Rerkasem *et al.*, 1993). In Rerkasem *et al.* (1993), leaf elongation rate was depressed after 12 days growth in

low B solution culture and relative leaf elongation ranged from 0.84 to 0.92 indicating some cultivar variation although not a wide range, compared to the variation in GSI in the same cultivars. Moreover, there was no correlation between vegetative and reproductive efficiency. Since the effect of B on yield could best be explained by variation in reproductive efficiency, further consideration has been given to the significance of vegetative response to low B in wheat. By contrast, in barley, low B causes varied responses in vegetative growth amongst different cultivars (Jamjod and Rerkasem, 1999). Differences in B efficiency during vegetative growth were important in ranking overall B efficiency in barley cultivars. In other species, such as oil seed rape, screening for B efficiency has been proposed based entirely on vegetative responses assessed as relative root elongation of seedlings in solution culture at 10 days (Stangoulis *et al.*, 2000b). Hence, there seems to be a case for further examination of the role of B efficiency during vegetative growth of wheat in the overall B efficiency ranking of cultivars. The aim of the present chapter was to identify the variation in vegetative response of wheat cultivars with known variation in B efficiency as measured by their grain set index (GSI).

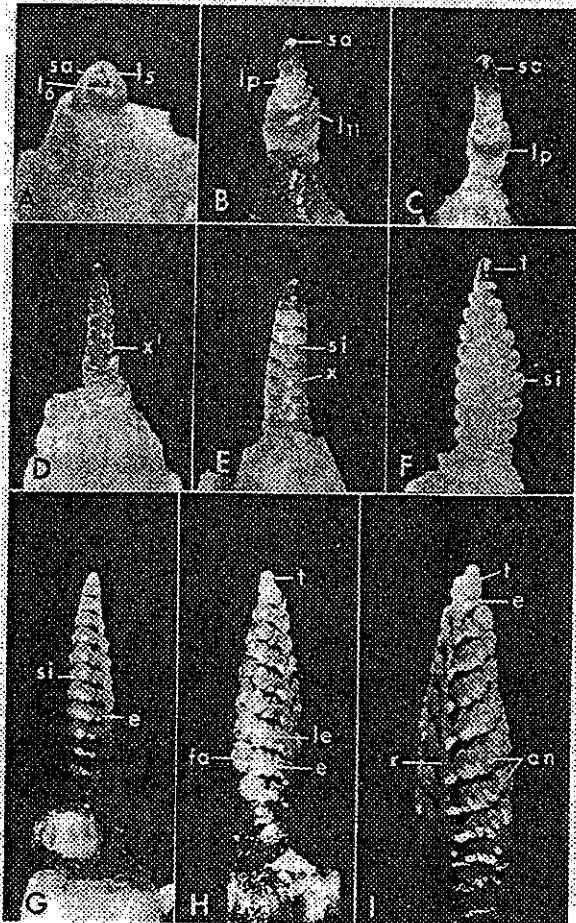
3.2 Materials and Methods

3.2.1 Sand culture experiment

Six spring wheat genotypes were selected from the efficient, inefficient and very inefficient classes of B efficiency determined by Rerkasem and Jamjod (1997): B efficient Fang 60; inefficient SW 41 and Schomburgk; very inefficient 922-211, 922-267 and Kite, were grown at two levels of added B, (0 and 10 μM). There were three replicate pots per treatment. Twenty 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. Pots were supplied twice daily with complete nutrient solution with either of two levels of added B (0 and 10 μM). The nutrient solution, adapted from Broughton and Dilworth (1971), contained (in μM): KNO_3 , 5000; CaCl_2 , 1000; KH_2PO_4 , 500; MgSO_4 , 250; K_2SO_4 , 250; FeEDTA , 10; MnSO_4 , 2; ZnSO_4 , 0.5; CuSO_4 , 0.2; CoSO_4 , 0.1 and Na_2MoO_2 , 0.1. Genotypes and B levels were arranged factorially with three replications.

Duration of plant growth from floral initiation in the main stem shoot apex through double ridge to terminal spikelet (Figure 3.1) was recorded by dissection of extra plants under a stereo microscope. The number of leaves per plant was recorded at 14, 25, 31 and 39 days after sowing. At mid boot and late boot stage, the flag leaves were taken and oven-dried (70 °C) for 3 days and analysed for B concentration by dry ashing and azomethine-H (Lohse, 1982). At the mature stage, the number of spikelets spike⁻¹, the number of grains spike⁻¹ and the number of grains spikelet⁻¹ were

determined and grain set index (GSI) assessed (defined as the percentage of the 20 basal florets from 10 central spikelets with grain) (Rerkasem and Lonergan 1994).



(Fig. 1)

Figure 3.1 Spike initiation and development .

A. Leaf primordia and shoot apex of a two-leaved wheat plant, B. Shoot apex from the main stem of a volunteer plant of winter wheat.

C. Elongated shoot apex just before spikelet initiation.

D. Beginning of spikelet formation show by double ridges on the spike.

E. Early stage of spikelet formation.

F. Spikelet-forming branches just before the differentiation of the spikelet parts.

G. Beginning of the differentiation of the empty glumes.

H. The basal florets have been initiated in the middle of the spike.

I. The florets of all of the spikelets haven initiated.

(an = stamen primordia; e = empty glume; fa = floret apex; le = lemma; lp= leaf primordium; l₅ = primordium of fifth leaf; l₆ = primordium of sixth leaf; l₁₁ = primordium of eleventh leaf; r = rachis; sa= shoot apex; si = spikelet primordia; t= terminal spikelet; x = upper ridge; x' = lower ridge)

3.2.2 Solution culture experiment

Experimental design

The experiment was conducted in glasshouse at Murdoch University, Perth, Australia. A short-term solution culture trial was undertaken with the boron supply being buffered by the B-specific resin, Amberlite IRA 743. A randomized complete block design consisting of 5 rates of boron (μM): 0.1, 0.25, 0.5, 1, 10, 2 cultivars of wheat (SW 41(B efficient) and Fang 60 (B inefficient) and 3 replicates was arranged.

Resin preparation

Amberlite IRA 743, (Sigma Chemical Co.), diameter 0.4-0.7 mm, was washed by soaking in one volume of 10% H_2SO_4 followed by one volume of 4% NaOH and rinsed with B-free water (Kunin and Preuss, 1964). This process was repeated 3 times until the pH was 6 and then the washed resin was stored at 0-4 °C in an air tight plastic bottle.

Treatment preparation

Analytical grade chemicals were used to make up the nutrient solutions. The nutrient solutions were prepared with B-free water and further purified by exposure to the washed resin.

The B-loaded resin was prepared by placing 40 moist cleaned resin beads into 1 L of TDI water containing 1, 2, 5, 10, 50 mg B for 72 hours, with manual shaking 3-

4 times per day. The solutions were sampled at the start and the end of this period to calculate the net amount of boron sorbed by the resin. At the end of 72 hours, the resin was separated from the solution by filtering with Whatman paper 1.

The amount of B in the resin was measured by soaking 0.5 g resin beads from each solution in 10% H₂SO₄ and analysis by inductively coupled plasma atomic emission spectrometry (ICP-AES).

Plant material

Seeds of wheats (*Triticum aestivum* cvv. Fang 60 and SW 41) were imbibed in aerated 0.2 mM CaSO₄ in the dark at 25 C for 48 hours. After germination, the seedlings were transferred into trays containing basal solution and 10 (MH₃BO₃ with 5mM MES(2-[N-Morpholino] ethanesulfonic acid). Solution pH was adjusted to 6.0 ± 0.2 everyday with 1 M KOH.

Pot trial

The full-strength basal nutrient solution used in this experiment contained (μM) KNO₃ 2800; NH₄NO₃ 2000; Ca(NO₃)₂ 1600; MgSO₄ 1000; KH₂PO₄ 100; K₂HPO₄ 100; FeEDTA 100; NaCl 8; ZnSO₄.7H₂O 2; MnSO₄.H₂O 2; CuSO₄.5H₂O 0.5, Na₂MoO₄.2H₂O 0.08. Each plastic pot lined with a polythene bag was filled with 5 L basal solution containing 5 mM MES. An acid-washed cotton bag containing 2 grams of B-loaded resin was added to each pot and the solutions were equilibrated for at least 2 days before transferring the seedlings. The pots were sampled for the

determination of equilibrium B concentrations in the culture solutions (Huang *et al.*, 1998).

Four days after germination, seedlings (10 per pot) were transferred (0 DAT) into pots containing 5 L of complete nutrient solution when their roots were 10 cm long and after their roots had been washed three times in 5 mM $\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$. Plants were thinned to 8 per pot on day 4. The pots were randomly distributed in root tanks, which maintained the temperature at 21 ± 1 °C, and rotated to minimize positional effects on plant growth every two days. The pH was adjusted to 6 ± 0.2 with 1M KOH or 10% H_2SO_4 . Nutrient solutions were continuously aerated with filtered air. For B analysis of nutrient solutions, 10 ml samples were collected on 0 and 10 DAT.

Programmed nutrient addition was used to maintain nutrients in solution (Asher and Blamey, 1987). The amount of nutrients needed was calculated from the dry weight increment of extra plants.

Harvesting

After 16 days growth in solution culture, plants were harvested and oven-dried (70 °C) for 3 days. Dry matter of root and shoot were recorded. Plant deficiency symptoms were observed throughout the experiment.

3.3 Results

3.3.1 Sand culture experiment

3.3.1.1 Duration of apical development

There was no effect of B supply on the time taken for the spike to develop from floral initiation to terminal spikelet stage (Table 3.1) and, likewise, the time taken for the spike from double ridge to terminal spikelet stage (Table 3.2). The duration of floral bud development were not significantly affected by B supply. However, cultivars differed significantly in the duration of floral bud development with an overall variation of 10 days from Schomburgk to Kite, which took the longest (Tables 3.1 and 3.2). The appearance of the shoot apex throughout, including floral initiation to terminal spikelet stage, was normal for all cultivars regardless of B supply.

3.3.1.2 Leaf number

Boron had no effect on the number of leaves after 14 days (D14), 25 days (D25) and 39 days (D39) growth, respectively (Table 3.3). The number of leaves at D14, D25 and D39 was the lowest in Fang 60 and highest in 922-211. The rest of the genotypes were intermediate. On the other hand, there was a highly significant interaction between boron and genotype in their effect on the number of leaves at D31 (Table 3.4). In B0, the number of leaves at D31 was highest in Kite and lowest in

922-267. Boron increased the number of leaves in 922-267 from 4.9 to 5.8 leaves, but it had no effect in the rest of the genotypes.

Table 3.1 The effect of B (0 μ M B (B0), 10 μ M B (B10)) on the time taken (the number of days) for the spike to develop from floral initiation to terminal spikelet stage.

Genotype	Duration of apical development (number of days)		
	B0	B10	mean
Fang 60	21	22	22 cd ¹
922-211	26	25	26 b
Schomburgk	20	20	20 d
SW 41	23	21	22 c
922-267	26	26	26 b
Kite	32	29	30 a

F-test: Geontype (G)**, Boron (B)^{ns}, G \times B^{ns}

¹different letters indicate significant difference at $p < 0.05$

^{ns} not significant at $p < 0.05$

** highly significant at $p < 0.01$

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Table 3.2 The effect of B (0 μ M B (B0), 10 μ M B (B10)) on the time taken (the number of days) for the spike to develop from double ridge to terminal spikelet stage.

Genotype	Duration of apical development (number of days)		
	B0	B10	mean
Fang 60	8	8	8 b ¹
922-211	11	10	11 a
Schomburgk	6	7	6 b
SW 41	7	8	7 b
922-267	14	10	12 a
Kite	14	10	12 a

F-test: Genotype (G)**, Boron (B)^{ns}, G \times B^{ns}

¹different letters indicate significant difference at $p < 0.05$

^{ns} not significant at $p < 0.05$

**highly significant at $p < 0.01$

Table 3.3 The effect of B (0 μ M B (B0), 10 μ M B (B10)) on the number of leaves per plant after 14 (D14), 25 (D25) and 39 (D39) days growth.

Genotype	Leaf number								
	D14			D25			D39		
	B0	B10	mean	B0	B10	mean	B0	B10	mean
Fang 60	2.1	2.0	2.0 c	4.2	4.1	4.1 c	6.0	6.0	6.0 d ¹
922-211	2.3	2.4	2.3 a	4.7	4.8	4.7 a	6.6	6.6	6.6 ab
Schomburgk	2.0	2.0	2.0 c	4.6	4.5	4.6 b	6.2	6.4	6.3 c
SW 41	2.1	2.0	2.0 c	4.7	4.5	4.6 b	6.6	6.7	6.7 a
922-267	2.0	2.0	2.0 c	4.6	4.6	4.6 b	6.4	6.5	6.4 bc
Kite	2.2	2.2	2.2 b	4.6	4.7	4.6 b	6.6	6.6	6.6 ab
F-test:									
Genotype (G)	**			**			**		
Boron (B)	ns			ns			ns		
G \times B	ns			ns			ns		

¹different letters indicate significant difference at $p < 0.05$

^{ns} not significant at $p < 0.05$

^{**} highly significant at $p < 0.01$

Table 3.4 The effect of B (0 μ M B (B0), 10 μ M B (B10)) on the number of leaves per plant after 31 (D31) days growth.

Genotype	Leaf number (D31)	
	B0	B10
Fang 60	5.3 cd	5.3 cd ¹
922-211	5.8 ab	5.8 ab
Schomburgk	5.0 cd	5.4 bc
SW 41	5.8 ab	5.8 ab
922-267	4.9 d	5.8 ab
Kite	5.9 a	5.8 ab

F-test: Genotype (G)**, Boron (B)**, G \times B**

¹different letters indicate significant difference at $P < 0.05$

** highly significant at $P < 0.01$

3.3.1.3 Flag leaf B concentration

There was a highly significant interaction between B and genotype in their effect on B concentration in the flag leaves at both mid and late boot stages (Table 3.5). At mid boot, in B0, B concentrations did not differ between genotypes. Boron increased B concentration in the flag leaves in 922-211, 922-267, Schomburgk, SW 41 Fang 60, but not in Kite. In B10, on the other hand, B in the flag leaves was highest in Fang 60 and SW 41 and lowest in Kite: 922-211, Schomburgk and 922-267

were intermediate in flag leaf B concentrations (Table 3.5). At late booting, in B0, B in the flag leaf was highest in Fang 60 and lowest in Kite. Boron supply increased the B concentration in the flag leaves most strongly in Kite and also in 922-267, 922-211, Schomburgk and Fang 60, but not in SW 41. In B10, B in the flag leaves was highest in Kite and lowest in SW 41; 922-211, 922-267, Schomburgk and Fang 60 were intermediate (Table 3.5).

Table 3.5 The effect of B (0 μM B (B0), 10 μM B (B10)) on B concentration (mg kg^{-1}) in the flag leaves at mid boot and full boot stages.

Genotype	Flag leaf boron concentration (mg kg^{-1})			
	Mid boot		Full boot	
	B0	B10	B0	B10
Fang 60	6.0 cd	11.5 a	5.5 cd	9.0 b ¹
922-211	5.9 cd	8.5 b	3.5 de	7.2 bc
Schomburgk	5.2 d	6.9 bc	3.5 de	7.2 bc
SW 41	6.0 cd	10.4 a	3.9 de	6.0 cd
922-267	4.9 d	7.5 bc	3.3 de	9.9 ab
Kite	4.9 d	6.4 cd	1.9 e	12.6 a
F-test				
Genotype (G)		ns		ns
Boron (B)		ns		ns
G \times B		**		**

¹different letters indicate significant difference at $p < 0.05$

**highly significant at $p < 0.01$

3.3.1.4 The number of spikelet spike⁻¹

There was no interaction between B and the genotype in their effect on the number of spikelets spike⁻¹ (Table 3.6). Boron had no effect on the number of spikelets spike⁻¹, on the other hand the genotype did. Cultivars 922-211, Kite and 922-267 had the higher number of spikelets than the others. The number of spikelets was lowest in Schomburgk and intermediate in Fang 60 and SW 41.

Table 3.6 The effect of B (0 μ M B (B0), 10 μ M B (B10)) on the number of spikelet spike⁻¹.

Genotype	Spikelets spike ⁻¹		
	B0	B10	mean
Fang 60	17	17	17 b
922-211	21	21	21 a
Schomburgk	15	15	15 c
SW 41	19	17	18 b
922-267	22	21	21 a
Kite	21	22	22 a

F-test:

Genotype (G)**, Boron (B)^{ns}, G \times B^{ns}

¹different letters indicate significant difference at $p < 0.05$

^{ns} not significant at $p < 0.05$

** highly significant at $p < 0.01$

3.3.1.5 Grain set

There was an interaction between B and the genotype in their effect on grain set index (GSI) (Table 3.7). In B0, GSI was highest in Fang 60 and lowest in Kite. Boron increased GSI in all genotypes, but most strongly in Kite. In B10, the GSI did not differ significantly among all six genotypes.

Table 3.7 The effect of B (0 μ M B (B0), 10 μ M B (B10)) on grain set.

Genotype	Grains spike ⁻¹		Grains spikelet ⁻¹		Grain set index (%)	
	B0	B10	B0	B10	B0	B10
Fang 60	24 cd	33 b	1.3 de	1.9 ab	73 b	91 a ¹
922-211	18 d	33 b	0.8 fg	1.6 bcd	50 c	87 ab
Schomburgk	6 e	27 bc	0.5 gh	1.7 abc	23 d	90 a
SW 41	6 e	26 c	0.5 gh	1.5 cde	16 de	87 ab
922-267	5 e	24 c	0.2 hi	1.2 ef	15 de	78 ab
Kite	0.3 e	43 a	0.02 i	1.9 a	0.6e	92 a
F-test						
Genotype (G)	**		**		**	**
Boron (B)	**		**		**	**
G \times B	**		**		**	**

¹different letters indicate significant difference at $p < 0.05$

^{ns} not significant at $p < 0.05$

** highly significant at $p < 0.01$

There was an interaction between B and the genotype in their effect on the number of grain spike⁻¹ (Table 3.7). In B0, the number of grain was highest in Fang 60. Boron supply increased the number of grain in all genotypes, but most strongly in Kite. In B10, the number of grain spike⁻¹ was highest in Kite. There was an interaction between B and the genotype in their effect on the number of grain spikelet⁻¹ (Table 3.7). In B0, the number of grain spikelet⁻¹ was highest in Fang 60 and lowest in Kite. Boron increased the number of grain spikelet⁻¹ most strongly in Kite and also in the remainder. In B10, the number of grain spikelet⁻¹ was highest in Kite and Fang 60, and lowest in 922-267.

3.3.1.6 Relative response of grain set to B

The interaction between B and genotype on the number of grains spike⁻¹ and grains spikelet⁻¹ are more clearly seen from the relative response to B, measured in B0 as a percentage of the genotype's performance in B10 (Table 3.8). The relative response to B for the number of grains spike⁻¹ was 72% in Fang 60; 55% in 922-211; 21-23% in Schomburgk, SW41 and 922-267 and only 1% in Kite. Similarly, the relative response to B for the number of grains spikelet⁻¹ was 70% in Fang 60; 50% in 922-211; 17-33% in Schomburgk, SW41 and 922-267 and only 1% in Kite.

Table 3.8 Relative responses of grain set to low B

Genotype	Grains spike ⁻¹	Grains spikelet ⁻¹
	% B0/B10	% B0/B10
Fang 60	72.7	68.4
922-211	54.5	50.0
Schomburgk	22.2	29.4
SW 41	23.1	33.3
922-267	20.8	16.7
Kite	0.7	1.1

3.3.2 Solution culture experiment

3.3.2.1 Deficiency symptoms

The plants were generally healthy throughout the experiment and did not show any symptoms of B deficiency. However, mild interveinal chlorosis resembling iron deficiency was observed in the leaves of plants grown at 0.1 μM B for a few days after transplanting. The symptoms disappeared a week after transplanting.

3.3.2.2 Plant growth

Boron supply did not affect total shoot dry weight, on the other hand root dry weight was affected by B supply in the solution (Figure 3.2). Genotypic variation was observed on root dry weight. At B 0.1, root dry weight in Fang 60 was higher than that in SW 41. Boron supply increased root dry weight in SW 41 at B 0.25 and had

no further effect with increase in B, while root dry weight in Fang 60 did not respond to B supply at all.

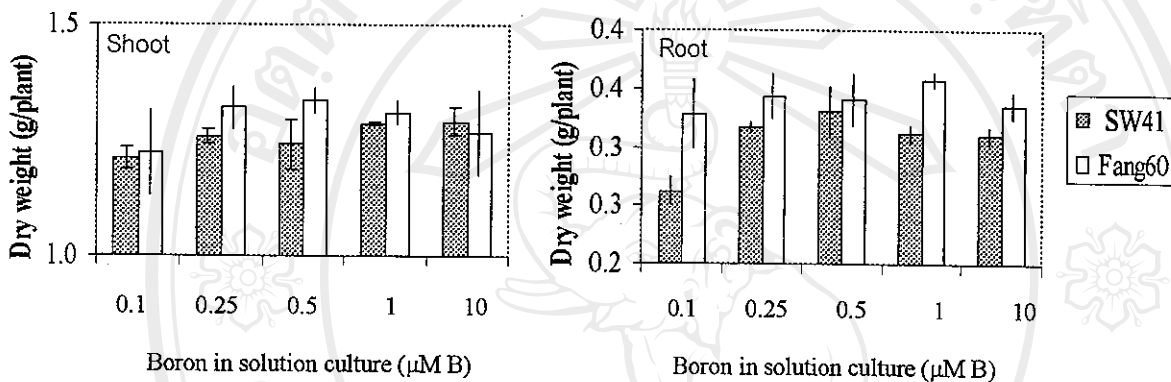


Figure 3.2 The effect of B supply on total shoot and root dry weight in two genotypes of wheat grown for 16 days in solution culture. Bars represent means of 3 replications \pm se.

3.4 Discussion

3.4.1 Classifying wheat genotypes for boron efficiency

The reproductive response to B varied markedly among wheat genotypes, as previously reported (Rerkasem and Jamjod 1997). Based on their GSI without added B (Rerkasem and Jamjod 1997), the six wheat genotypes in this study will be grouped into 3 classes. Results from this study have clearly shown that B efficiency

classification in wheat genotypes may be improved by considering other parameters as well as the GSI. I propose that the genotypes are classified into 4 B efficiency groups. These are efficient (E: Fang 60), moderately inefficient (MI: 922-211), inefficient (I: Schomburgk, SW41 and 922-276) and very inefficient (VI: Kite), respectively. Furthermore, the ranking of genotypes in their number of grain spike⁻¹ and their number of grain spikelet⁻¹ were closely related to their GSI response. These results support an extensive body of research that variation in B efficiency was associated with the effect of B deficiency on reproductive processes, such as pollen development or/and fertilisation (Rerkasem and Jamjod 1997; Dell *et al.* 2002). Impairment of reproductive processes under B deficiency has been suggested to limit wheat yield by causing grain set failure owing to pollen sterility (Cheng and Rerkasem 1992).

At low B, Fang 60 generally maintained higher flag leaf B concentrations than the same leaf in other cultivars. Kite, the least B efficient cultivar, generally contained the lowest B concentration in the flag leaf. Hence, there is a general correlation between the GSI and flag leaf B concentration at booting. However, the B concentration in flag leaf of SW 41 was the same as Fang 60 at mid boot stage despite its much lower GSI. Previous studies (Rerkasem and Loneragan 1994; Subedi *et al.*, 1999) reported that differential response to low B between wheat genotypes could not be indicated by their flag leaf B concentration. However, I have shown conclusively that, at low external B, Kite and Fang 60 were readily distinguished by their flag leaf

B. Furthermore, there was a decreasing trend in flag leaf B concentration at full boot stage from the most B efficient Fang 60 to Kite and the other 4 cultivars in between. The finding that flag leaf B concentration in the other cultivars, including SW41, was not significantly different from either Fang 60 or Kite when grown at low B, suggests that leaf B responses in wheat only segregate the most efficient from the least efficient cultivars.

Among the six cultivars there is four B efficiency groups, the only responsive vegetative parameter measured was leaf number. At day 31, cultivar 922-267 had significantly reduced leaf number at low B, however no other cultivars showed a response in leaf number to low B at this time and at day 14, 25 and 39 leaf number was unaffected by B treatment.

Others have reported that B deficiency delayed ear emergence and depressed the number of spikelets spike⁻¹ in barley but not in wheat (Wongmo *et al.*, 2003). The lack of response to low B in spikelet number spike⁻¹ is here again confirmed. I have also established that B deficiency has no effect on rate of reproductive development in wheat including the time different cultivars took to reach floral initiation at the terminal spikelet stage and the number of days to develop to the double ridge stage.

In addition to the GSI, the response to low B in these six wheat cultivars may be distinguished in terms of grains spike⁻¹ and grains spikelet⁻¹. Many authors have reported plant responses to low B expressed as the relative B response, the measurement of plant performance in low B relative to that in sufficient B (e.g. Asad

et al., 2001; Stangoulis 1998). Thus, the relative performance at low B for both the number of grains spike⁻¹ and grains spikelet⁻¹ was only about 1 % in Kite compared with some 70 % in Fang 60, about 50 % in 922-211 and 20-30 % in the other 3 cultivars.

The GSI is a simple and rapid method for assessing B efficiency in wheat. It may be used to screen for adaptation to low B soils of large numbers of genotypes without the B-sufficient control (Anantawiroon *et al.*, 1997). However, sometimes it may be too insensitive to distinguish between genotypes from similar efficiency classes, e.g. between Kite and SW41 or Schomburgk in this study. In such cases, other measurements of plant performance and a B sufficient control may be necessary. Thus, from the combination of the GSI, flag leaf B at the boot stage and relative B response in the number of grains spike⁻¹, grains spikelets⁻¹, the six wheat cultivars evaluated may be classed into 4 B efficiency groups. Kite is determined to be very inefficient (VI), followed by 922-211 as inefficient (I), Schomburgk, SW41 and 922-267 as moderately inefficient (MI) and Fang 60 as efficient (E).

3.4.2 Fang 60 vs SW41

The ranking of Fang 60 and SW 41 in their GSI response to low B was found to relate with their vegetative root dry matter response. By contrast, in a previous report vegetative and reproductive responses were not correlated (Rerkasem *et al.*, 1993). In the study of Rerkasem *et al.* (1993) the vegetative response to low B was

measured by leaf elongation over a 12 day period. The present result also showed no differences between Fang 60 and SW 41 in the shoot response to low B. Root growth appeared to be the more sensitive indicator of vegetative response to low B in wheat. Hence, the conclusion by Rerkasem *et al.* (1993) may have been different had they examined root responses to low B. In oilseed rape, root length was a rapid and sensitive indicator of boron efficiency during vegetative growth. Root length after 10 days during early vegetative growth was correlated with B efficiency for yield at low B in oilseed rape (Stangoulis *et al.*, 2000 a,b). By contrast, in studies with wheat in B buffered solution culture, shoot response to low B was more sensitive than root response at 10 and 20 days after treatment with increasing level of B (Asad *et al.*, 2000). Root dry matter was decreased by low solution B at 20 days but not at 10 days. Hence, between different studies the sensitivity of root and shoot responses to low B were inconsistent. The wheat cultivar grown by Asad *et al.*, (2000) was Wilgoyne.

In conclusion, four B efficiency groups were identified among the six wheat cultivars evaluated: efficient (E: Fang 60), moderately inefficient (MI: 922-211), inefficient (I: Schomburgk, SW41 and 922-276) and very inefficient (VI: Kite). Some variation in B efficiency may exist between Fang 60 and SW 41 during vegetative growth. In the following two chapters, variation in B mobility and uptake are explored as possible mechanisms for B efficiency in wheat during reproductive growth.