CHAPTER 4

The effect of boron supply on boron uptake and distribution in wheat (*Triticum aestivum* L.) genotypes.

4.1 Introduction

In wheat, pollen development in B-inefficient cultivars is impaired by B limitation resulting in pollen grains that are small and misshapen and do not accumulate starch (Rerkasem *et al.*, 1987; Anantawiroon *et al.*, 1997; Subedi *et al.*, 1997). It has been suggested that the critical phase of anther development is a period of a few days surrounding pollen meiosis (Rawson, 1996), especially the period from premeiotic interphase through meiosis to late tetrad development (Huang *et al.*, 2000; Dell and Huang, 2002). However, the mechanisms underlying cultivar differences in B efficiency in wheat remain unknown, but clearly they are mostly related to B supply to the spike during critical stages of microsporogenesis. Furthermore a wide range of B efficiency has been found among wheat genotypes (Rerkasem and Jamjod, 1997). The mechanisms responsible for different degrees of B efficiency may also be different.

Huang *et al.* (2001) showed that little of the ^{10}B sequestered in vegetative plant parts following absorption from the external solution, was later partitioned to the spike of wheat following transfer from adequate to low external B supply. Thus there was no evidence for significant retranslocation of ^{10}B from leaves in the phloem.

Since a B-inefficient cultivar, Wilgoyne (Rerkasem unpublished), was used by Huang *et al.* (2001), a possibility remains that the capacity to partition or retranslocate B into the spike may differ across cultivars, and that this difference may be a mechanism for B efficiency in wheat.

It is hypothesised that avoidance of male sterility in B-efficient wheat cultivars involves the ability to supply B adequately into the anthers of non-transpiring spikes during the critical stages of microsporogenesis. To test this hypothesis, we examined B uptake and distribution in five cultivars grown to maturity with 4 levels of B in sand culture.

4.2 Materials and methods

Five wheat cultivars chosen were Fang 60, SW 41, CMU 88-9, Bonza and Sonora. Twenty seeds of each genotype were sown in freely drained, earthernware pots (0.3 m diameter and 0.3 m deep) containing washed river quartz sand. The pots were supplied twice daily, one liter each, with complete nutrient solution with four levels of B (0, 0.1, 0.33 and 10 μM H_3BO_3). The nutrient solution, adapted from Broughton and Dilworth (1971), as described in Chapter 3. Genotypes and B levels were arranged factorially with three replications. At full boot stage, spikes from the main stem of all plants of each of three replicate plots were harvested, dried at 80 °C, dry ashed at 500 °C for 8 hrs and their B concentrations were determined using the azomethine-H method (Lohse, 1982). At maturity, all remaining spikes in each

replicate pot were harvested and the number of grains spike^{-1}, spikelets spike^{-1}, tillers plant^{-1}, spikes plant^{-1} and grains spikelet^{-1} were determined. Grain set index (defined as the percentage of the 20 basal florets from 10 central spikelets with grain) was also determined on these spikes, to distinguish effects on grain set from those on grain filling (Rerkasem *et al.*, 1991). Grain weight from the main stem and tiller for each pot were separately determined. Straw dry weight for each pot were determined.

Data were analyzed statistically by analysis of variance. Significantly different means were separated at the 0.05 probability level.

4.3 Results

4.3.1 Yield, yield components and GSI

Boron deficiency depressed grain yield from the main stem, tillers and the total grain yield (Figure 4.1) most strongly in Bonza, significantly in SW 41 and CMU 88-9 but not at all in Fang 60 and Sonora 64. At 0 μM B, only Bonza produced no grain yield on the main stem: it also produced almost no grain in tillers. Even at 0.1μM B, Bonza produced almost no grain. In the remaining cultivars, even in those that had grain yield reduced by B deficiency, significant grain yield was produced at 0 and 0.1 μM B. The minimum external B supply to achieve maximum yield varied from 10 μM B in Bonza to 0.33 μM B in CMU 88-9 and SW 41, and 0 μM B in Sonora 64 and Fang 60.

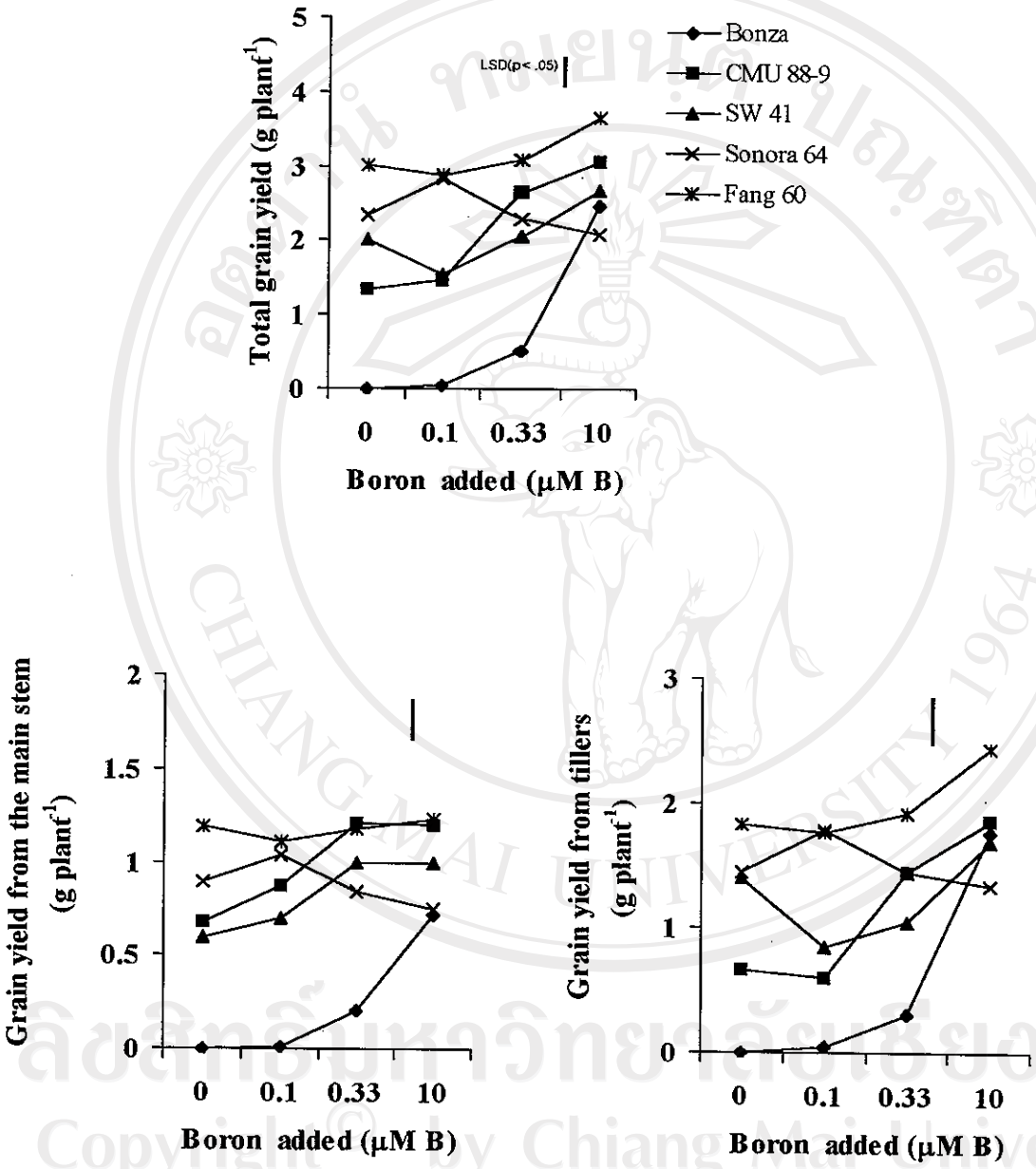

Figure 4.1 The effect of B on total grain yield, grain yield from the main stem and from tillers in five wheat genotypes.

Unlike grain yield, GSI in Fang 60 and Sonora 64 were decreased at low B (Table 4.1). In Fang 60, GSI was depressed only at 0 μM B. In Sonora 64, GSI at 0 and 0.1 μM B were significantly decreased compared to 10 μM B. GSI response to B supply in CMU 88-9 and Bonza was similar to their grain yield response. In SW 41, maximum GSI required 10 μM B whereas maximum grain yield was achieved at only 0.33 μM B. At 0 μM B, GSI increased from 0 in Bonza to 71 % in Fang 60. At 0.1 μM B, the ranking of cultivars according to GSI was the same as at 0 μM B and the range of GSI was from 0.3 % in Bonza to 88 % in Fang 60. At 10 μM B, all cultivars had a GSI of 69 % or greater. At 0.33 μM B, SW 41, CMU 88-9 and Sonora 64 could not be distinguished according to GSI. In summary, GSI was a more sensitive indicator of cultivar differences in response to B supply than grain yield.

Table 4.1. The effect of B on grain set index (%) in five wheat genotypes.

Genotype	B added in sand culture (μM B)			
	0	0.1	0.33	10
Bonza	0.0	0.3	9.1	75.5
CMU 88-9	26.6	35.3	63.3	69.1
SW 41	41.2	45.7	56.0	74.1
Sonora 64	65.6	68.2	71.2	79.5
Fang 60	71.0	88.2	84.4	89.1

F-test:
G (Genotype)** B (Boron)** G×B** ($LSD_{(0.05)}$ = 8.6)

**highly significant at $p < 0.01$

Variation in GSI was associated with either variation in grain spike^{-1} or grain spikelet^{-1} (Figure 4.2). SW 41 outperformed CMU 88-9 in GSI at 0.1 μM B, but had similar number of grain spike^{-1} and grain spikelet^{-1}. In Fang 60, maximum GSI was achieved at 0.1 μM B but grain spike^{-1} and grain spikelet^{-1} both required 0.33 μM B for maximum grain set.

Straw yield, top dry weight, number of spikelets plant^{-1}, the number of tillers plant^{-1} and the day of full spike emergence were not affected by B supply in any of the cultivars (Table 4.2).

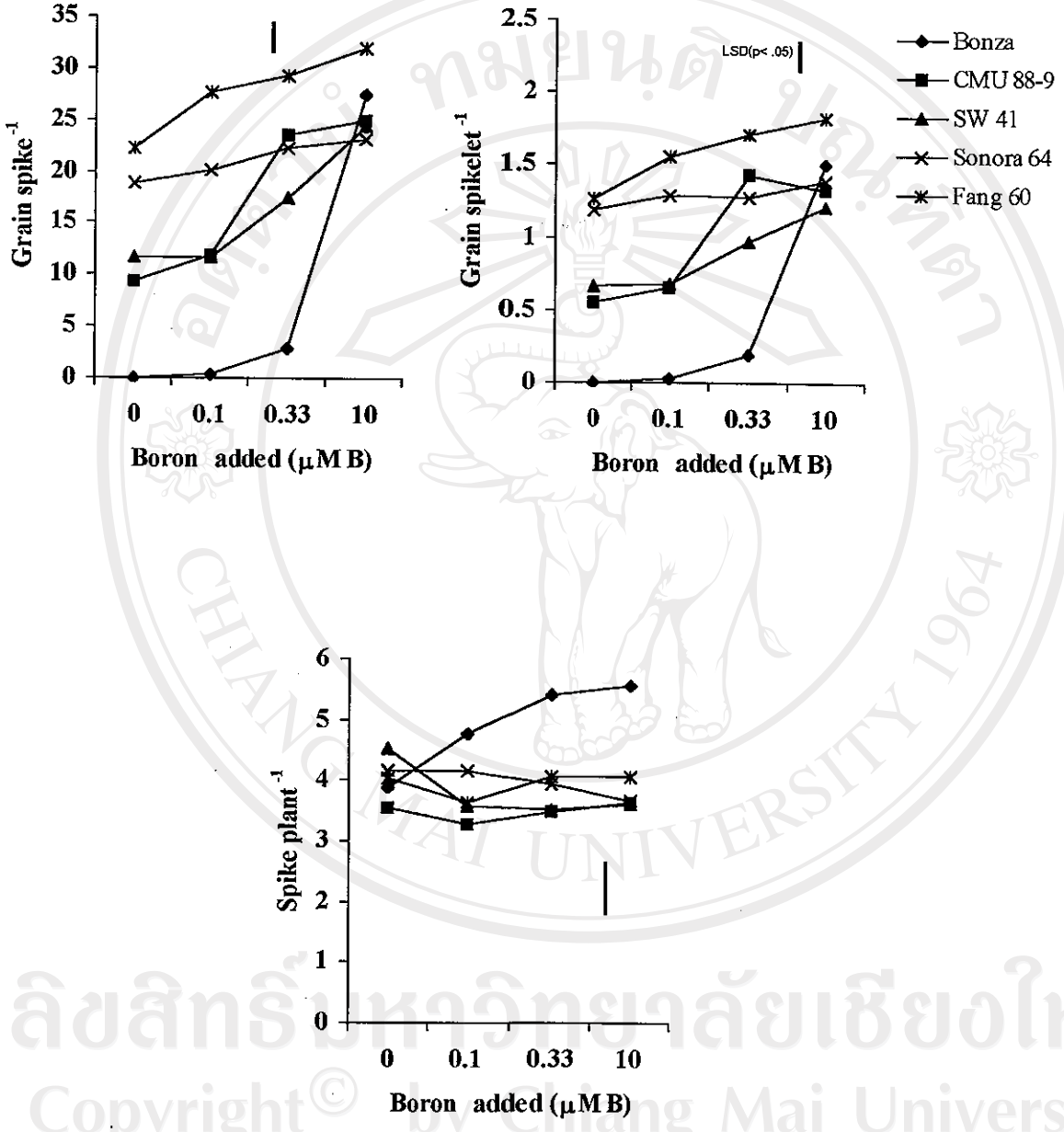

Figure 4.2 The effect of B on grain spike^{-1}, grain spikelet^{-1} and spike plant^{-1} in five wheat genotypes.

Table 4.2 Day of full ear emergence, tiller plant^{-1}, spikelet plant^{-1}, top dry weight and straw yield of wheat genotypes as influenced by B

B added (μM)	Genotype	Day of full ear emergence	Tiller plant^{-1}	Spikelet plant^{-1}	Top dry weight	Straw
0	Bonza	81	5	18	9.3	7.9
0	CMU 88-9	59	4	17	7.5	4.4
0	SW41	64	6	17	8.6	5.1
0	Sonora	55	5	16	6.8	3.5
0	Fang60	58	4	21	7.7	3.7
0.1	Bonza	80	6	17	8.9	7.3
0.1	CMU 88-9	59	4	18	6.8	3.9
0.1	SW41	61	4	17	6.5	3.5
0.1	Sonora	55	4	16	6.7	2.9
0.1	Fang60	58	4	18	6.9	3.1
0.33	Bonza	80	6	19	9.8	7.7
0.33	CMU 88-9	58	4	18	7.3	3.3
0.33	SW41	61	4	19	7.3	3.9
0.33	Sonora	54	4	18	5.9	2.6
0.33	Fang60	56	4	17	7.3	3.2
10	Bonza	81	6	18	12.8	8.4
10	CMU 88-9	54	4	19	8.2	3.6
10	SW41	62	5	20	9.2	5.0
10	Sonora	55	4	17	5.3	2.5
10	Fang60	57	4	17	8.4	3.5
F test:						
G (Genotype)		** (1.5)	** (0.5)	* (1.4)	** (0.9)	** (0.6)
B (Boron)		ns	ns	ns	** (0.8)	* (0.6)
G×B		ns	ns	ns	ns	ns

*significant at $p< 0.05$, **highly significant at $p< 0.01$ and ^{ns}not significant.

Values in the parentheses are respective LSD ($p<.05$)

4.3.2 B concentration in plant parts

Over the range of lower B supply from 0 to 0.33 μM B, shoot B concentration for each cultivar were relatively similar (Figure 4.3). However, among the cultivars, Fang 60 generally had the highest B concentration (5.7-6.3 mg kg^{-1}) and Bonza had the lowest (3.2-3.9 mg kg^{-1}). Boron concentration in shoots increased strongly with increasing B, to 8.5-12.7 mg kg^{-1} in 10 μM B, in all cultivars except Sonora 64 which only increased to 7.1 mg kg^{-1}. Boron concentration in roots was generally higher than shoots and not as strongly responsive to increased B supply. Indeed in CMU 88-9, the highest B concentration of 22 mg kg^{-1} was found in root at 0 μM B and the concentration at 10 μM B was only 18 mg kg^{-1}. Apart from the result in CMU 88-9, root B concentration was generally highest in Fang 60 (16-18 mg kg^{-1}) and lowest in Bonza (10-14 mg kg^{-1}).

Boron concentration in the spike responded differently to B supply among the cultivars (Figure 4.4). Fang 60 maintained significantly higher B concentration in the spike than other cultivars especially at 0 to 0.33 μM B. The lowest B concentration in the spike of Fang 60 was 4.7 mg kg^{-1} at 0 μM B with values increasing to 5.9 mg kg^{-1} at 0.33 μM B. By contrast B concentration in the spike of Bonza at 0 μM B was only 1.8 mg kg^{-1} and only increased to 3.2 mg kg^{-1} at 0.33 μM B. In the other cultivars, B concentrations were intermediate between those Fang 60 and Bonza and increased progressively with increased B supply. At 10 μM B, B concentrations in spikes of all cultivars were similar (6.3-7.3 mg kg^{-1}).

In the flag leaf, penultimate leaf and remainder of shoot (Figure 4.5), B concentration at particular B levels and their response to increasing B supply were relatively similar to the result for the whole shoot. That is there was not much difference in B concentration between 0 and 0.33 μM B and Fang 60 was highest and Bonza was lowest in B concentration. In the stem segment between flag leaf and penultimate leaf node (Figure 4.5), highest B concentration (7-9 mg kg^{-1}) at all levels of B supply were found in CMU 88-9. At 0 μM B, Bonza also maintained high concentration of B in the stem segment (6.7 mg kg^{-1}), but in Bonza stem segment B concentration decreased at higher levels of B supply (3.5-5.2 mg kg^{-1}).

In other plant parts i.e stem above flag leaf node, flag leaf sheath, penultimate leaf sheath and stem below penultimate leaf node, effects of B supply on B concentration did not vary significant among cultivars (Table 4.3).

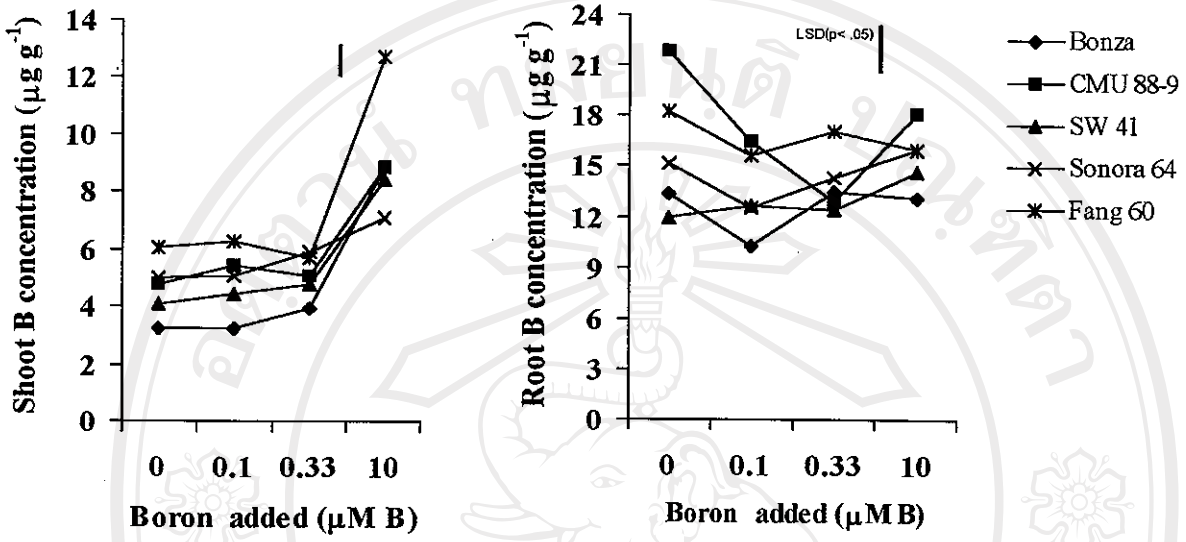

Figure 4.3 The effect of B on B concentration in the whole shoot and the root in five wheat genotypes.

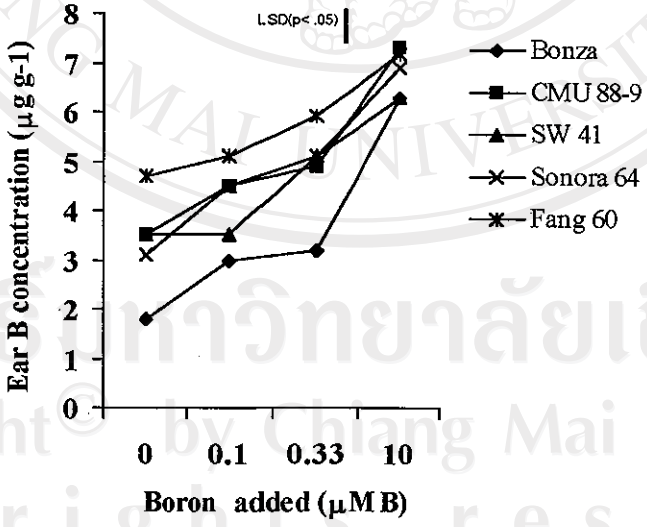

Figure 4.4 The effect of B on B concentration in the spike in five wheat genotypes

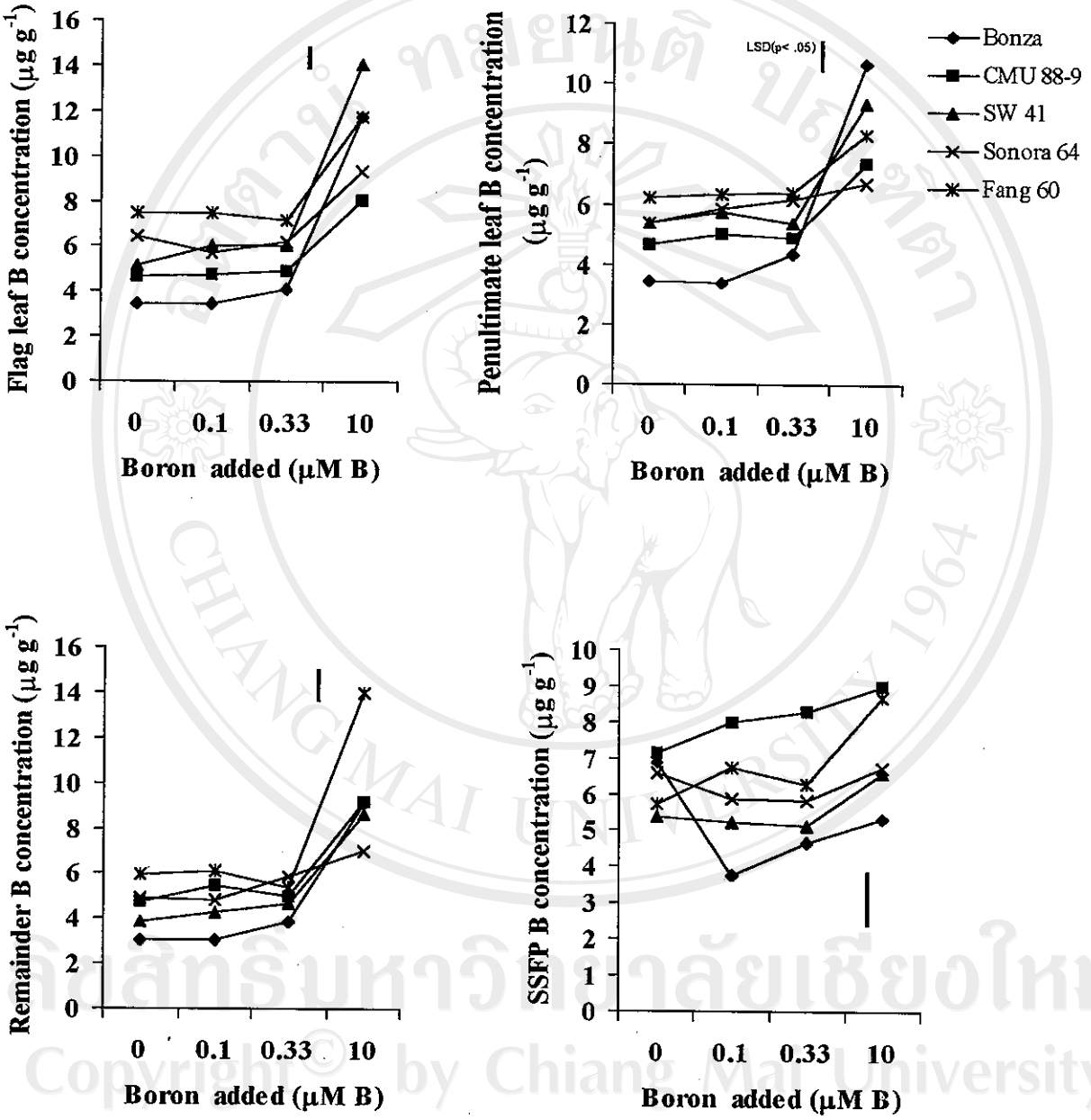

Figure 4.5 The effect of B on B concentration in the flag leaf, the penultimate leaf, the remainder of the whole shoot and the stem segment between flag leaf and penultimate leaf node (SSFP) in five wheat genotypes.

Table 4.3 Tissue B concentration (μg g^{-1}) of the flag leaf sheath (a), the penultimate leaf sheath (b), stem below penultimate leaf node (c) and stem above flag leaf node (d) at full boot as influenced by B.

Genotype	B added in sand culture (μM)				
	0	0.1	0.33	10	mean
(a) Flag leaf sheath					
Bonza	4.6	4.0	4.2	5.8	4.6 d
CMU 88-9	4.8	4.7	5.5	7.2	5.6 c
SW41	5.6	6.0	5.7	7.1	6.1 c
Sonora	7.0	7.9	7.7	7.6	7.5 b
Fang60	7.8	8.3	8.3	9.4	8.4 a
mean	5.9 b	6.2 b	6.3 b	7.4 a	
F test G**, B**, G×B^{ns}					
(b) Penultimate leaf sheath					
Bonza	4.9	6.3	6.1	7.5	6.2 c
CMU 88-9	6.5	7.2	7.4	9.6	7.7 b
SW41	7.6	7.2	7.2	8.3	7.6 b
Sonora	8.3	9.6	9.8	9.7	9.3 a
Fang60	8.9	9.5	9.8	10.4	9.6 a
mean	7.2 c	7.9 b	8.0 b	9.1 a	
F test G**, B**, G×B^{ns}					
(c) Stem below penultimate leaf node					
Bonza	4.3	4.5	4.5	5.5	4.7 b
CMU 88-9	5.0	4.1	4.4	6.2	4.9 b
SW41	4.7	4.4	4.4	5.1	4.7 b
Sonora	4.2	4.8	4.2	5.9	4.8 b
Fang60	5.4	6.1	5.6	6.4	5.9 a
mean	4.7 b	4.8 b	4.6 b	5.8 a	
F test G**, B**, G×B^{ns}					
(d) Stem above flag leaf node					
Bonza	7.5	7.6	8.2	11.1	8.6 c
CMU 88-9	12.4	13.8	13.8	19.9	15.0 a
SW41	10.5	11.5	10.6	14.5	11.8 c
Sonora	13.0	13.2	12.3	15.6	13.5 b
Fang60	13.7	13.1	13.5	15.0	13.8 ab
mean	11.4 b	11.8 b	11.7 b	15.2 a	
F test G**, B**, G×B^{ns}					

**highly significant at $p < 0.01$, ^{ns}not significant

4.3.3 B content in plant parts

At 0, 0.1 and 0.33 μM B, B contents in shoots of each cultivar were similar, but generally increased at 10 μM B (Figure 4.6). Sonora 64 differed from all other cultivars in having lower B content in shoot and no increase in B content at 10 μM B. There was no correlation between B content in the shoot and GSI at 0 to 0.33 μM B. In fact, Bonza contained as much or more B than Fang 60 in shoots despite much lower GSI. The higher B content of Bonza was even more evident for rest of shoot (Figure 4.6). In rest of shoot, Sonora 64 generally contained lower B than other cultivars. By contrast in the flag leaf, Bonza contained much lower B than other cultivars at 0 to 0.33 μM B (Figure 4.7). Among the other cultivars, B content in the flag leaf did not differ much from 0 to 0.33 μM B and did not differ among the cultivars. However, it may be significant that Fang and Sonora 64 maintained higher B content at 0 μM B compared to 0.1 μM B. The responses in penultimate leaves were similar to the flag leaf (Figure 4.7). In the spike, effects of B supply on B content did not vary among cultivars (Table 4.4). Likewise, in stem segment and leaf sheaths changes in B content with B supply did not differ significantly among cultivars (Table 4.4).

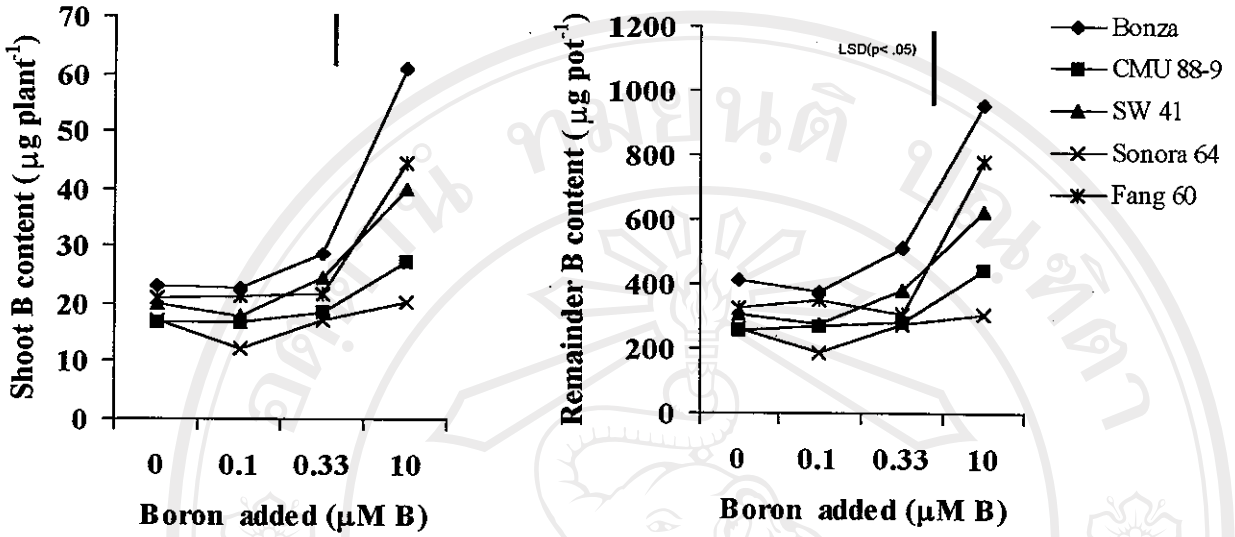

Figure 4.6 The effect of B on B content in the whole shoot and the remainder of the whole shoot in five wheat genotypes.

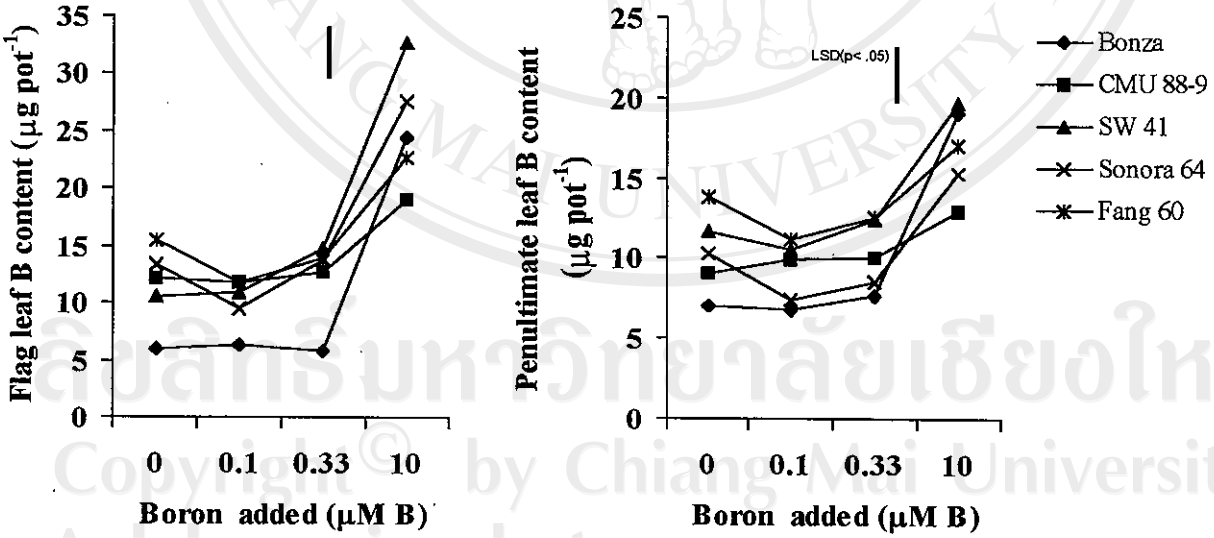

Figure 4.7 The effect of B on B content in the flag leaf and the penultimate leaf in five wheat genotypes.

Table 4.4 Boron content (μg pot^{-1}) of flag leaf sheath (FLS), penultimate leaf sheath (PLS), spike, stem above flag leaf node (SAFL) and stem segment between flag leaf and penultimate leaf node (SSFP) at full boot as influenced by B.

B added (μM)	Genotype	FLS	PLS	Spike	SAFL	SSFP
0	Bonza	7.9	6.2	3.6	1.7	7.0
0	CMU 88-9	9.6	6.7	7.5	1.9	9.1
0	SW41	11.3	9.1	6.8	2.8	7.8
0	Sonora	13.2	9.3	6.4	2.5	6.6
0	Fang60	14.9	10.5	10.2	2.1	7.5
0.1	Bonza	7.2	7.9	5.9	1.7	4.5
0.1	CMU 88-9	9.7	7.8	10.1	1.6	8.8
0.1	SW41	11.2	10.3	6.5	3.2	6.6
0.1	Sonora	11.7	7.2	7.9	1.7	4.3
0.1	Fang60	12.3	9.5	8.4	1.5	5.8
0.33	Bonza	6.7	6.5	5.8	1.6	4.5
0.33	CMU 88-9	11.4	8.0	12.8	1.9	9.6
0.33	SW41	14.1	9.9	12.5	2.7	7.6
0.33	Sonora	12.2	11.7	10.8	2.2	4.5
0.33	Fang60	15.1	11.3	12.6	1.7	7.0
10	Bonza	9.0	7.8	9.0	2.1	7.3
10	CMU 88-9	12.6	8.6	13.3	2.2	9.6
10	SW41	15.1	9.8	12.9	3.1	8.8
10	Sonora	17.1	11.6	16.6	3.6	8.1
10	Fang60	16.9	12.0	14.5	2.0	9.8
F test:						
G (Genotype)		** (1.9)	** (1.5)	** (1.7)	** (0.4)	** (1.2)
B (Boron)		** (1.7)	ns	** (1.5)	** (0.3)	** (1.0)
G×B		ns	ns	ns	ns	ns

**highly significant at $p< 0.01$ and nsnot significant.

Values in the parentheses are respective LSD ($p<.05$)

4.3.4 Relative B distribution within the whole plant

Cultivars differed in their partitioning of B between roots and shoots (Table 4.5). CMU 88-9 generally retained more B in the root compared to others cultivars at all levels of B supply. By contrast, Bonza retained relatively high proportions of B in root at 0 μM B, and to a lesser extent at 0.33 μM B. In all cultivars, the proportion of B distributed to shoot increased substantially at 10 μM B.

In shoots, the distribution of B with increasing B varied among cultivars for the ear and the remainder of the shoot (Table 4.5). Bonza had the lowest proportion of plant B content in its ear at all levels of B supply and also had the lowest proportion of plant B in the stem above the penultimate leaf. In the remaining cultivars at 0 μM B, the relative B content in the ear was 3 times greater than for Bonza. At 0 μM B, Fang 60 appeared to have the greatest relative B content in the ear but the difference was not significant compared to Sonora, SW 41 and CMU 88-9. With increasing B supply, relative B content allocated to the ear increased in CMU 88-9 and Sonora but not in SW 41 and Fang 60. In blades, relative B content in Bonza was less than other cultivars at all levels of B supply.

In the remainder of shoot, CMU 88-9 tended to have less relative whole plant B than other cultivars, perhaps because of greater relative content in root (Table 4.5). Remainder of the shoot included all tillers in addition to older leaf and main stem of shoot.

Table 4.5 The effect of B on the relative distribution within the whole plant in wheat genotypes.

B level	Genotype	Relative B distribution (%)					
(μM B)		Ear	SAPL	Blade	SBPL	Remainder	Root
0	Bonza	0.40	0.94	2.95	3.23	44.87	47.61
0	CMU 88-9	1.10	1.62	5.48	2.96	37.56	51.27
0	SW 41	1.16	1.79	7.25	4.25	52.17	33.38
0	Sonora 64	1.15	1.65	8.33	3.81	47.67	37.38
0	Fang 60	1.51	1.43	8.09	4.04	48.23	36.70
0.1	Bonza	0.83	0.86	3.91	4.21	52.52	37.66
0.1	CMU 88-9	1.68	1.75	6.53	2.40	44.97	42.67
0.1	SW 41	1.17	1.75	7.68	4.14	48.67	36.58
0.1	Sonora 64	1.98	1.49	8.97	2.86	46.62	38.08
0.1	Fang 60	1.08	0.95	5.78	3.46	44.82	43.90
0.33	Bonza	0.58	0.61	2.67	2.79	51.56	41.80
0.33	CMU 88-9	2.18	1.97	7.19	2.90	47.71	38.06
0.33	SW 41	1.69	1.38	6.91	3.99	51.13	34.89
0.33	Sonora 64	2.03	1.25	8.67	2.72	51.48	33.86
0.33	Fang 60	1.77	1.22	7.44	3.42	42.97	43.17
10	Bonza	0.70	0.72	4.67	2.08	73.86	17.97
10	CMU 88-9	1.67	1.47	6.68	2.26	56.14	31.78
10	SW 41	1.29	1.19	7.73	2.52	62.49	24.77
10	Sonora 64	2.78	1.95	12.01	3.46	51.92	27.89
10	Fang 60	1.29	1.05	6.10	2.93	69.53	19.10
F-test							
G (Genotype)		**	**	**	**	**	**
B (Boron)		**	**	ns	ns	**	**
G×B		**(0.5)	ns	ns	ns	**(8.9)	**(9.2)

** highly singnificant at $p < .01$, ns not significant
SAPL=stem above penultimate leaf node, SBPL=stem below penultimate leaf node

4.3.5 Relative B distribution in the upper shoot of the main stem

In the upper shoot of the main stem, there was little consistent difference in B partitioning to the ear among cultivars or with increasing B supply (Figure 4.8). Similarly, there was no consistent difference among cultivars or with increasing B supply for the partitioning of B into stem above the flag leaf, penultimate leaf and sheath, and flag leaf sheath. At 10 μM B, flag leaves accumulated a higher percentage of B content in the upper shoot. At 0 μM B and to a lesser extent at other levels of B supply, the relative B content in stem between flag leaf and penultimate leaf decreased with increasing GSI of the cultivar. For example, Bonza contained 18 % of upper shoot B in this stem segment whereas Fang 60 contained only 10 %.

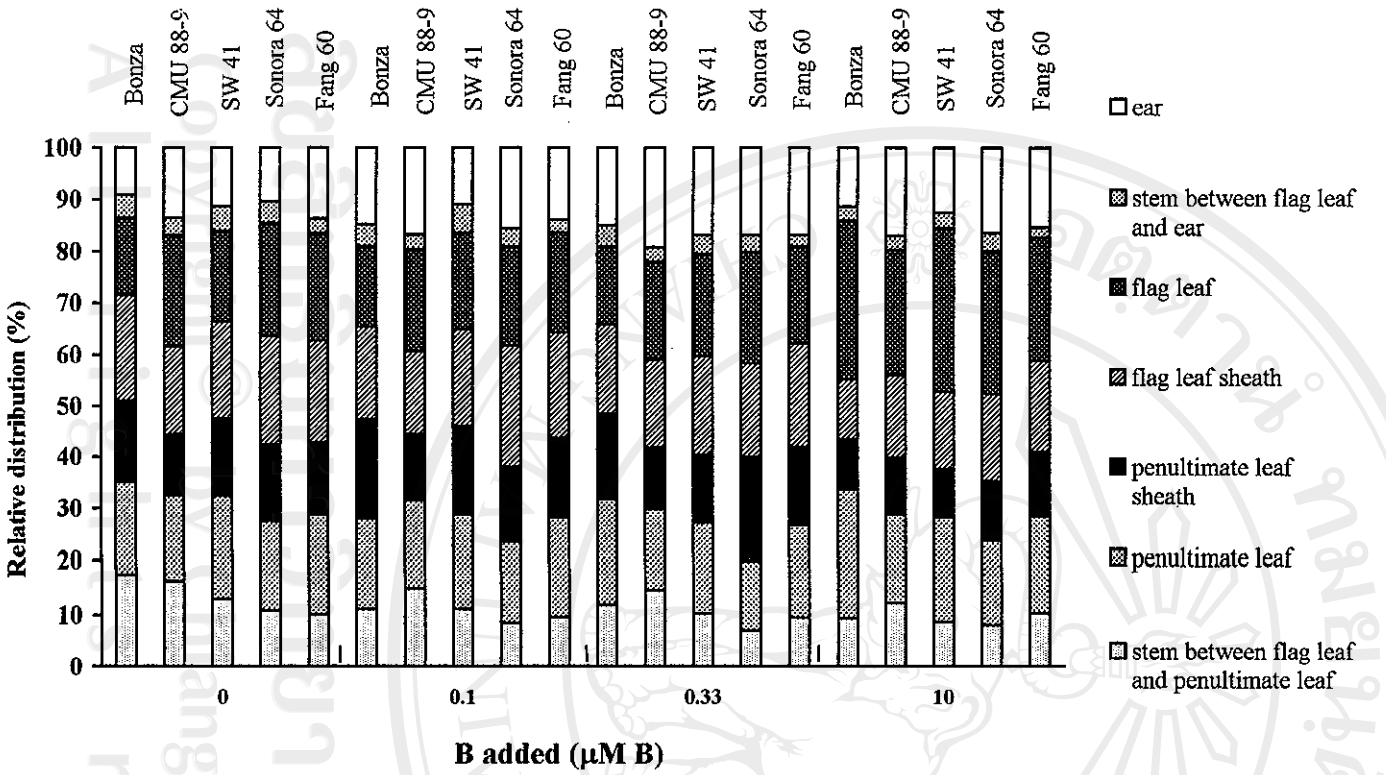

Figure 4.8 The effect of B on the relative distribution in the upper part of the shoot of the main stem in wheat genotypes

4.4 Discussion

The present results clearly showed differences in grain set among wheat cultivars in response to B supply consistent with previous reports (Rerkasem and Loneragan, 1994). The adverse effect on grain yields in the susceptible cultivars (Bonza, SW 41, CMU 88-9) were associated with the depression of grain set, i.e. the number of grains spike^{-1}, grains spikelet^{-1}, grain set index (GSI), without any apparent effect on dry weight of the straw and the average size of the spike as measured by the number of spikelets. The results confirm earlier suggestions of B deficiency depressing seed yield by depressing seed set (Li *et al*, 1978; Rerkasem *et al*, 1989; Rerkasem and Loneragan, 1994). In this study, the association of grains spike^{-1} and grains spikelet^{-1} with grain yields can be used to measure sterility in wheat as in the previous report (Rerkasem and Loneragan, 1994). Grain set failure and male sterility in wheat is known to be associated with the impairing of pollen development by B deficiency (Li *et al.*, 1978, Rerkasem *et al.*, 1997, Huang *et al.*, 2000). Although pollen development during meiosis is known to be a sensitive stage of reproductive development under low B supply, it is still unclear whether this is the reason of the difference in B efficiency among wheat genotypes. However, the transport of adequate amounts of B into the developing ear and the anthers at this critical stage of their development may be the key to the fertility of pollen and success of grain set.

Fang 60 stands out from the other cultivars by the significantly higher B concentration in the ear at booting stage at low B supply. This result alone could be

sufficient to explain the superior grain set of Fang 60 compared to others. Similarly, the consistently lower ear B concentration of Bonza could explain the very low grain set of this cultivar at low B supply. Boron concentration in the spike of Fang 60 was always greater than 4.5 mg kg^{-1} whereas in Bonza it was 3.2 mg kg or less: the other cultivars had intermediate B concentrations. This result seems to refine the critical B range for the spike at booting as suggested by Rerkasem and Loneragan (1994). The previous study gave the range of 3-7 mg kg^{-1} in the spike of affected wheat plants. In the present study, greater than 4.6 to 5 mg kg^{-1} appear to be sufficient B in the spike at booting for high grain set. At less than 3.6 mg kg^{-1} grain set was severely affected. Rerkasem and Loneragan (1994) suggested at critical range of 5-7 mg kg^{-1} in flag leaf at booting for predicting grain set. From the present results with a larger range of cultivars and B efficiencies, a relatively similar critical range of 5-7.5 mg kg^{-1} appeared to distinguish between low grain set and maximum grain set.

At low B supply B concentration in the shoot was correlated with GSI of the cultivars. With the exception of CMU 88-9, the root B concentration was also reasonably well correlated with GSI. CMU 88-9 accumulated higher B concentration in the root at low B supply even though its GSI was severely depressed.

Even though Fang 60 had highest B concentration in the shoot and generally in roots its B content in shoot and root did not exceed that of less efficient cultivars. Similarly, the low B concentration in shoot and root of Bonza was not reflected in lower B content. From the B content results, there is no indication that the more

efficient cultivar had higher B uptake. This suggests that differences in B utilisation may be the mechanism for B efficiency in wheat. Some evidence of this can be seen in CMU 88-9. The higher concentration in the root of CMU 88-9 at low B supply was consistent with the high retention of B in root of this cultivar at all levels of B supply. Thus, in CMU 88-9 reduced translocation of B into the shoot may be the main cause of low grain set or GSI. Bellaloui and Brown (1998) concluded that translocation of B from root to shoot was also a mechanism of B efficiency in celery. The present results suggest that poor root-to-shoot transfer of by is not a characteristic of B efficiency in a species, but rather one for particular cultivars.

In the other cultivars, differences in partitioning of B within the shoot can partly explain differences in grain set. For example there was an inverse correlation between relative B content in the stem below the flag leaf for a cultivar and its grain set index. This may suggest that the inefficient cultivars have restricted transfer of B in the stem from xylem to phloem. Huang *et al.* (2001) suggested that xylem to phloem transfer in the stem was necessary to explain the accumulation of B in the spike during the critical stages of microsporogenesis and proposed that variation in transfer efficiency might explain cultivar differences in GSI. Increased B retention in the stem below the flag leaf of inefficient cultivars such as Bonza was associated with lower B concentration in the spike of those cultivars. However, apart from the lower partitioning of B content into the spike of Bonza, GSI in other cultivars was not correlated with relative B content in the spike. The critical stage of

microsporogenesis occurred well before booting stage (Huang *et al.*, 2000), hence the B content and partitioning in the spike may not adequately reflect the supply of B to the ear during the critical stage. This is supported by the results reported in the next chapter.