Chapter 3

A survey of B mobility in woody and field crop species: controlled experiments

3.1 Introduction

In the previous study (Chapter 2), the survey of leaves from field-grown plants gave some indication of B mobility from differences in B concentration between leaves of different ages. There are, however, some limitations with this method. Although the B status of the plants could be estimated from the tissue B concentration, it was not possible to precisely determine the age of the field-grown plants, and leaf age had to be inferred from their position. There is also the influence of season on plant growth which could have affected B concentration through a dilution or other effect. Boron distribution in plants is influenced not only by leaf age. Foliar B concentrations might be reduced by rainfall or a short period of guttation (Oertli, 1994) or they may fluctuate due to seasonal effects (Fernández-Escobar *et al.,* 1999). It is therefore necessary to study experimentally of B mobility under more controlled conditions. Studies of B retranslocation have been made in different ways, including foliar application of B (Hanson *et al.,* 1985; Hanson, 1991; Lehto *et al.,* 2000), withdrawal of B from the growing medium (Oertli, 1993) or separating fruiting from rooting media for peanut and subterranean clover, species which bury their fruits (Campbell *et al.,* 1975).

In addition to tropical woody and fruit species (Chapter 2), an understanding of B retranslocation in other crop species will be useful for B fertilization in each crop. Therefore, this study is aimed to examine evidence for B retranslocation in tropical woody and fruit species, which indicated the possibility of phloem B mobility in the previous chapter, and also in some field crop species.

Due to the long life cycle of woody and fruit species, applied B to leaves will be monitored to determine the direction of any translocation from leaves to other plant parts. For field crop species which have shorter growing periods, B translocation will be monitored by withdrawing B from the rooting medium.

3.2 Materials and methods

3.2.1 Experiment 1: Mobility of B applied to specific leaves of horticultural woody plants

Three plant species, which showed the possibility of B retranslocation (guava) and were inconclusive (jackfruit, coffee) in Chapter 2, were studied in this experiment. The study was conducted during March to June 2006. Guava and jackfruit were grown from cuttings and coffee from seed. Roots of the planting materials were washed with tap water before they were transplanted into sand culture in earthenware pots (30 cm diameter, 30 cm deep), containing washed river quartz sand. B-free nutrient solution (Table 3.1) was applied to each pot (1 litre) twice a day. Foliar application was applied after the third new leaf had become the YFEL (youngest fully expanded leaf) (about 1 month after transplanting). The YFEL to YFEL+2 (mature leaves, ML) from three branches of each tree were painted with 50 mM B as boric acid, to cover the entire upper surface of the leaves once a day for three days. The 3 treated leaves (mature leaves) and new leaves (all leaves above the YFEL, young leaves, YL) were determined for B concentration by the azomethine-H method (Loshe, 1982) the B gradients compared before foliar application, at the end of 3 days of foliar application and after two new leaves became fully expanded (17 days after commencement of the foliar treatment). Additionally, leaves in the same position were collected from control plants which did not receive foliar B treatment. There were 4 replicate pots per treatment.

3.2.2 Experiment 2: Boron retranslocation during early vegetative growth in field crop species

This experiment examined B retranslocation in 9 field crop species from the legume (Leguminosae) and grass (Gramineae) families (Table 3.3). All species were grown in sand culture (pots and sand were the same as in Experiment 1) and supplied with nutrient solution with sufficient B (B+) for the first period of vegetative growth until harvest 1, which was V_4 for the legumes; emergence of the 4^{th} leaf for maize (collar visible); and tillering for the other Gramineae. All species, except maize, were given the same nutrient solution (Table 3.1) and 10 μM B for B+. The legumes were inoculated with a commercial peat inoculant, and the KNO_3 was withdrawn from their nutrient solution after 7 days. Maize received a different nutrient solution (Table 3.2) which contained 20 μM B for B+. After harvest 1, B was withdrawn from the nutrient solution. The second harvest was at the end of vegetative growth, and this was V_7 for the legumes, emergence of the 12^{th} leaf for maize and maximum tillering for the other Gramineae. The experiment was conducted with 4 replicate pots for each harvest. At both harvests, samples of leaf blades were collected in the first, third and fifth position from the base of the stem (L1, L3 and L5, respectively). Leaf samples were analysed for B concentration by dry-ashing followed by the azomethine-H method (Lohse, 1982).

3.2.3 Experiment 3: Boron retranslocation during the mid reproductive stage of peanut and green gram

Seeds of peanut (*Arachis hypogeae* L. cv. Thainan 9) and green gram (*Vigna radiata* (L.) Wilczek cv. Kamphaengsan 1) were planted in pots containing sand (same as 3.2.1). Seeds were inoculated with commercial peat inoculants at sowing, and the KNO_3 was withdrawn from their nutrient solution after 7 days. Each pot initially contained 8 plants, which were thinned to 4 plants at 10 days after emergence. After germination, nutrient solution (Table 3.1) with 10 μM B (BA: B-adequate), or without boron for peanut or with 0.5 μM B for green gram (BD: B-deficient) was applied to each pot for twenty days for peanut or 25 days for green gram. After that, the sand in all pots was washed by running water through the pots for 20 minutes, twice in one day, 6 hours apart. Boron treatments were applied to the pots as follows: BA for the first 20 days for peanut or 25 days for green gram followed by BD for the following 30 days (BA/BD), with the same BA (BA/BA) and BD (BD/BD) throughout the experiment. Plants were harvested at day 20 for peanut (or day 25 for green gram) and day 50 for peanut (or day 55 or green gram).

At both harvests the main stem of the plants were partitioned into the following parts for B analysis:

- all parts above the youngest fully expanded leaf (growing point)
- the youngest fully expanded leaflets (YFEL)
- the stems + petioles below the YFEL
- the rest of the leaflets of the main stem (old leaflets)
- the rest of the main stem
- roots

There was additionally the analysis of the seed at the last harvest. Plant parts were oven dried at 80 °C for 48 hours and ground to pass a 1-mm mesh. Samples were extracted by dry-ashing and B concentrations were determined by using the Azomethine-H method (Lohse, 1982).

There were three replications in each B treatment. Data were presented as values and standard errors.

Table 3.1 The composition of nutrient solution for all species (except maize) (modified from Broughton and Dilworth, 1971).

Chemical	Concentration in nutrient solution (μM)
KNO_3	5000 (Only first 7 days for legumes)
$CaCl_2.2H_2O$	1000
KH_2PO_4	500
$MgSO_4.7H_2O$	250
K_2SO_4	250
$C_6H_5Fe.H_2O$	10
$MnSO_4.H_2O$	1
$ZnSO_4.7H_2O$	0.5
$CuSO_4.5H_2O$	0.2
$CoSO_4.7H_2O$	0.1
$NaMoO_4.2H_2O$	0.1

Table 3.2 The composition of nutrient solution for maize (modified from Broughton and Dilworth, 1971 and Mozafar, 1989)

Chemical	Concentration in nutrient solution (μM)
KNO_3	15000
$CaCl_2.2H_2O$	1000
KH_2PO_4	1000
$MgSO_4.7H_2O$	2000
K_2SO_4	250
$C_6H_5Fe.H_2O$	100
$MnSO_4.H_2O$	9
$ZnSO_4.7H_2O$	0.76
$CuSO_4.5H_2O$	0.31
$CoSO_4.7H_2O$	0.1
$NaMoO_4.2H_2O$	0.1

Table 3.3 Field crop species which were verified for boron retranslocation.

Scientific name	Common name	Cultivar
Family: Leguminosae (Grain legumes)		
Dolichos lablab L.	Hyacinth bean (Lab lab)	-
Glycine max (L.) Merr.	Soybean	CM60
Pachyrizus tuberosus (Lam.) Spreng	Yam bean	-
Pisum sativum L.	Garden pea	-
Vigna mungo (L.) Hepper	Black gram	Regur
Family: Gramineae		
Oriza sativa L.	Rice	KDML105
Triticum aestivum L.	Wheat	Fang 60/ Bonza
Hordeum vulgare L.	Barley	SMGBL91002/ BRB9604
Zea mays L.	Maize	NW72

3.3 Results

3.3.1 Experiment 1: Mobility of B applied to a specific leaf

Plants which were grown without B supply showed B deficiency symptoms in younger leaves (Figure 3.1). Leaf veins continued to develop while the expansion of the interveinal area was restricted. Consequently, leaves were crinkled and curled. Moreover, coffee leaves were also malformed. These symptoms remained after application of foliar B.

Leaf dry weight of all plants increased with their age during the experimental period (Figure 3.2). At 17 days after the start of foliar B treatment, the effect of foliar B application became evident by a significant increase in dry weight of mature leaves (ML) in coffee and young leaves (YL) in guava. Foliar B application did not affect leaf dry weight of both leaf positions in jackfruit, YL of coffee, and ML of guava.

Boron concentrations in the mature leaf (ML) of all species increased dramatically at the end of the foliar treatment (day 3). After that, they decreased about 35-51% within 14 days. By contrast, leaf B concentrations in the young leaf (YL) of coffee and jackfruit were raised by 4% and 30%, respectively, while it dropped to 10% in guava. In non-treated plants, the B concentration in the ML of all plants and in YL of jackfruit was not significantly different among harvest whereas in YL of coffee and guava it was reduced (Figure 3.3).

Leaf B contents of the 3 species were affected differently by the foliar B treatment (Figure 3.4). Before treatment, B content in the ML of coffee, guava and jackfruit were 14.9, 11.0 and 15.2 μg plant^{-1}, respectively. The foliar B treatment increased the B content in ML about 5-9 times, while the B content in untreated trees remained unchanged. After 14 days, the B content in the ML of foliar treated coffee, guava and jackfruit were depressed by 25%, 18% and 22%, respectively. By harvest 3, the B contents in the YL and ML of non-foliar treated coffee and jackfruit continued to increase after harvest 2 while they changed very little in guava. In contrast, B contents in the YL in all 3 species increased too a much greater extent in the B-treated trees.

Figure 3.1 Boron deficiency symptoms in coffee, guava and jackfruit.

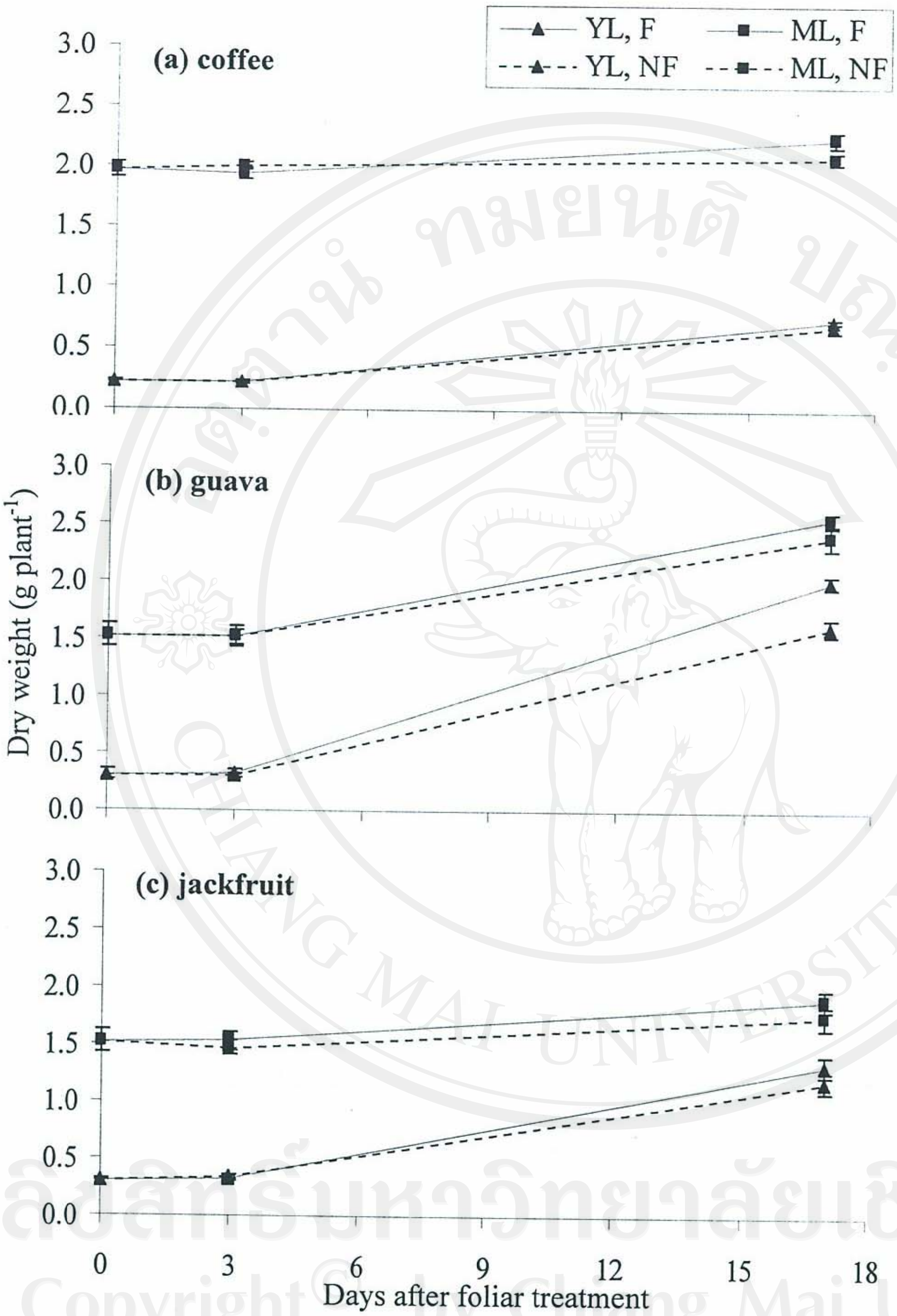

Figure 3.2 Leaf dry weight (g plant^{-1}) of coffee, guava and jackfruit in foliar application experiment. Means of four replicates are shown and vertical bars represent standard errors (SE) for corresponding mean values. YL - young leaves (all leaves above the YFEL); ML – mature leaves (the YFEL to YFEL+2); F – foliar B treatment; NF – without foliar B treatment.

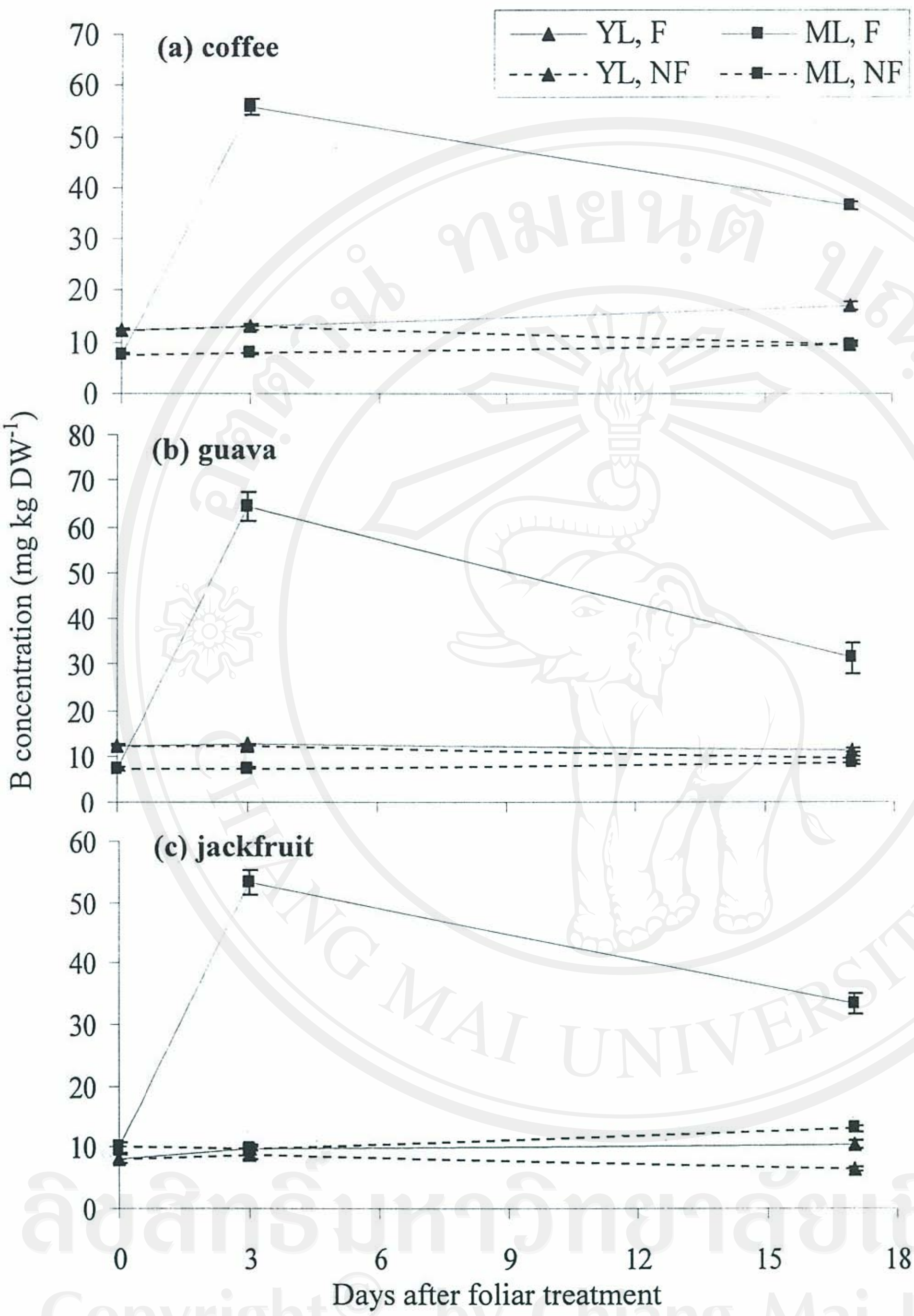

Figure 3.3 Leaf B concentration (mg kg DW^{-1}) of coffee, guava and jackfruit in foliar application experiment. Means of four replicates are shown and vertical bars represent standard errors (SE) for corresponding mean values. YL - young leaves (all leaves above the YFEL); ML – mature leaves (the YFEL to YFEL+2); F – foliar B treatment; NF – without foliar B treatment.

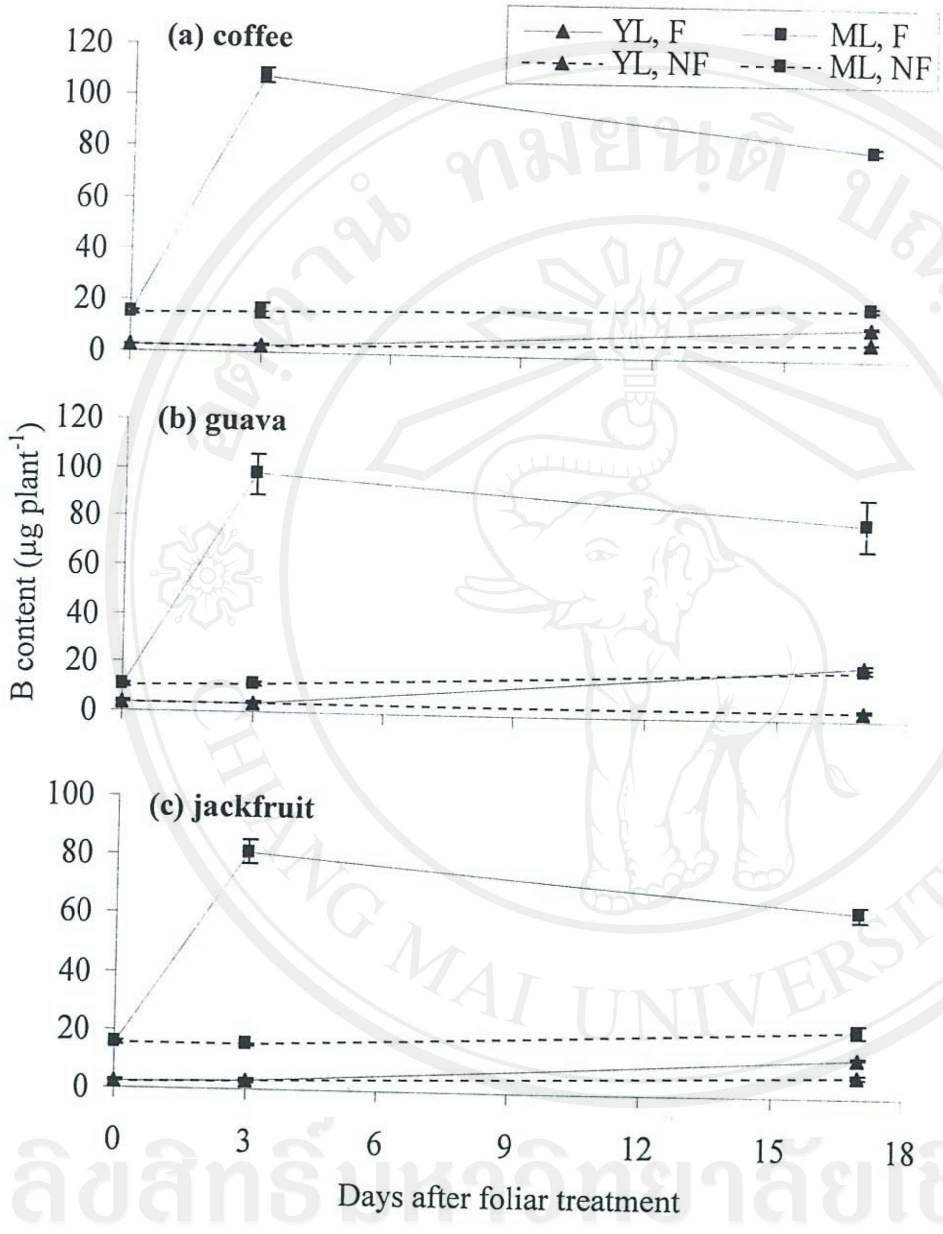

Figure 3.4 Boron content (µg plant^{-1}) of coffee, guava and jackfruit in foliar application experiment. Means of four replicates are shown and vertical bars represent standard errors (SE) for corresponding mean values. YL - young leaves (all leaves above the YFEL); ML – mature leaves (the YFEL to YFEL+2); F – foliar B treatment; NF – without foliar B treatment.

3.3.2 Experiment 2: Boron retranslocation during early vegetative growth in field crop species

At harvest 1, L1 and L3 of all the Gramineae had already emerged and had become fully expanded in all the legumes. By harvest 2, the dry weight of these leaves remained unchanged in maize and wheat cv. Bonza, whereas in rice, barley cv. BRB9604, lablab and soybean they continued to increase (Figure 3.5). In the case of yam bean and black gram, the dry weight was increased in L3 but not in L1. In contrast, L5 which was still not emerged or fully expanded at harvest 1 had grown much more by harvest 2 in all species and cultivars, in spite of the B withdrawal following harvest 1.

Boron concentration gradients among leaf position at the first harvest varied from species to species (Figure 3.6). Some species (maize, rice, wheat cv. Fang 60 and black gram) had higher B concentrations in older leaves (L1 and L3) and lower B concentrations in younger leaves (L5). However, there were species with the B concentration gradient in the other direction, i.e. higher B concentrations in younger leaves and lower in older leaves, namely barley (cv. SMGBL91002, BRB9604), yam bean and lab lab. For the others, their B concentration gradients were not in either of these directions. Wheat cv. Bonza had higher B concentrations in L5 and L1 than in L3. Garden pea had the highest B concentration in L1, followed by L5 and then L3. The L3 of soybean had the highest B concentration, followed by L5 and L1. At harvest 2, following B withdrawal, the B concentration gradients from old to young leaves were changed in some plants, while in others they remained the same as before B withdrawal. From the gradient of lower B concentration in younger leaves before the withdrawal, at harvest 2 wheat cv. Fang 60 and rice had the highest B concentration in L3, followed by L5 and L1. For yam bean and barley (cv. BRB9604), which had the gradient of lower B concentration in older leaves before the withdrawal, the B concentration in L5 and L1 became higher than in L3 at harvest 2. In lab lab, which also had the gradient of lower B concentration in older leaves before the withdrawal, the B concentration in L1, L3 and L5 was indistinguishable after the withdrawal. When compared between the 2 harvests, the change in B concentration depended on the leaf position and plant. Following the withdrawal of B, the B concentration fell in L5 in wheat cv. Bonza, barley cv. SMGBL91002, garden pea, lablab, yam bean, soybean and black gram; increased in rice and wheat cv. Fang 60; and was unchanged in maize and barley cv. BRB9604. For L1, the B concentration declined after the withdrawal of B in maize, wheat cv. Fang 60, soybean and black gram; increased in wheat cv. Bonza; and was unchanged in rice, lablab and garden pea. Variation in the change in leaf B concentration following B withdrawal was also seen in L3.

Much more B accumulated in older leaves than in younger leaves at harvest 1 of almost all species, except maize and garden pea. On the other hand, the B content in younger leaves was higher than in older ones of most species at harvest 2. However, it was found that B remained high in older leaves of lab lab and yam bean and it did not differ among leaf positions in wheat cv. Bonza. Boron content in barley cv. BRB9604 was higher in L1 and L5 than in L3. On comparing the B content in individual leaf positions between harvests, in all species higher amounts of B accumulated in L5 following B withdrawal (harvest 2). Boron also increased in L3 of almost all plants, except for no difference or a small decrease in wheat cv. Fang 60, barley cv. SMGBL9604 and maize. For L1 (old leaves), the B content increased in most species, except there was no difference in wheat cv. Bonza, soybean barley cv. SMGBL91002 and garden pea, and a small depression in maize, wheat cv. Fang 60, and black gram (Figure 3.7).

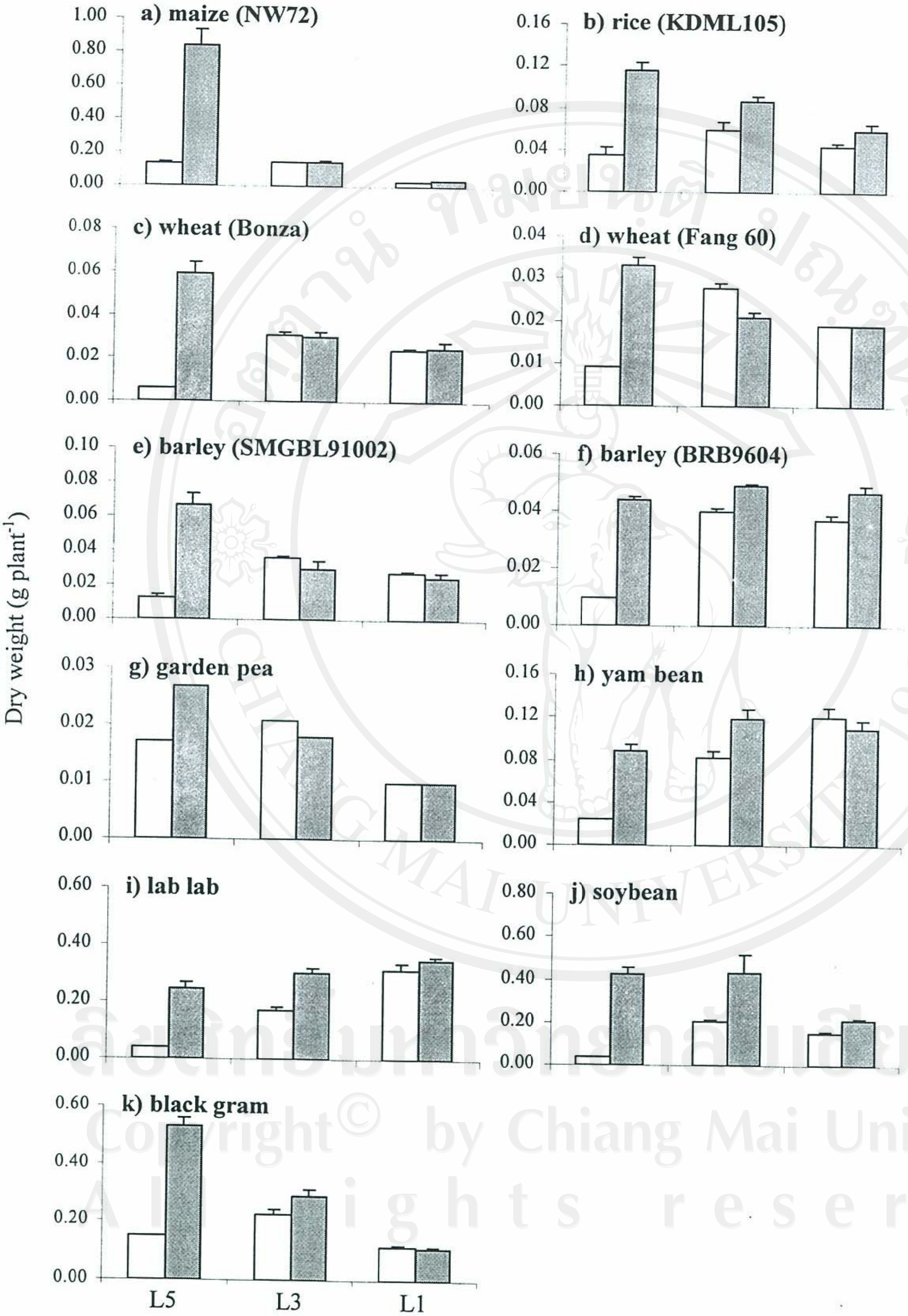

Figure 3.5 Leaf dry weight (g plant^{-1}) of 9 crop species. Bars are means of four replicates and vertical bars are standard errors (SE). ☐ Harvest 1 B+, ▩ Harvest 2 B+/B0

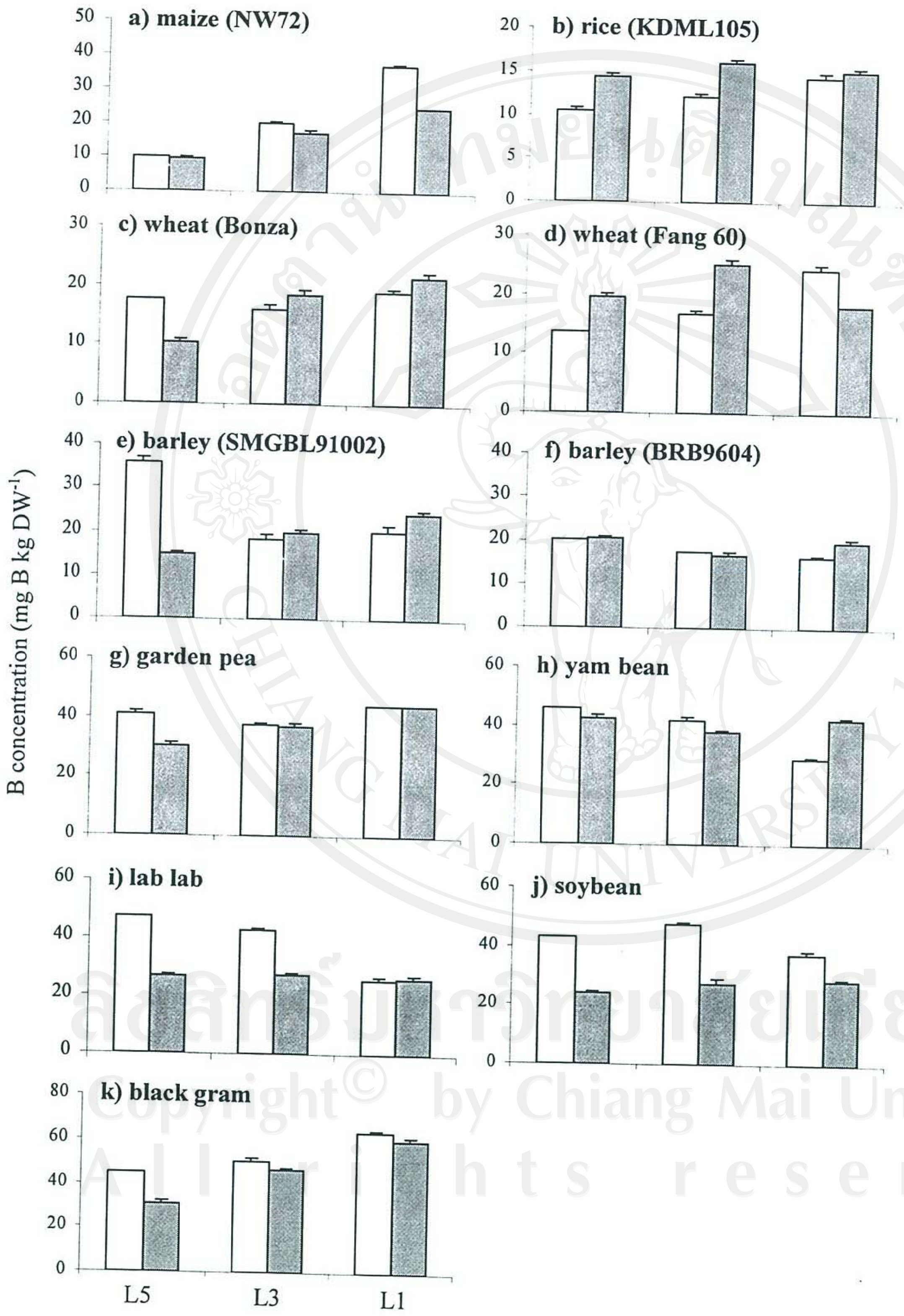

Figure 3.6 Leaf B concentration (mg B kg DW^{-1}) of 9 crop species. Bars are means of four replicates and vertical bars are standard errors (SE). □ Harvest 1 B+, ▩ Harvest 2 B+/B0

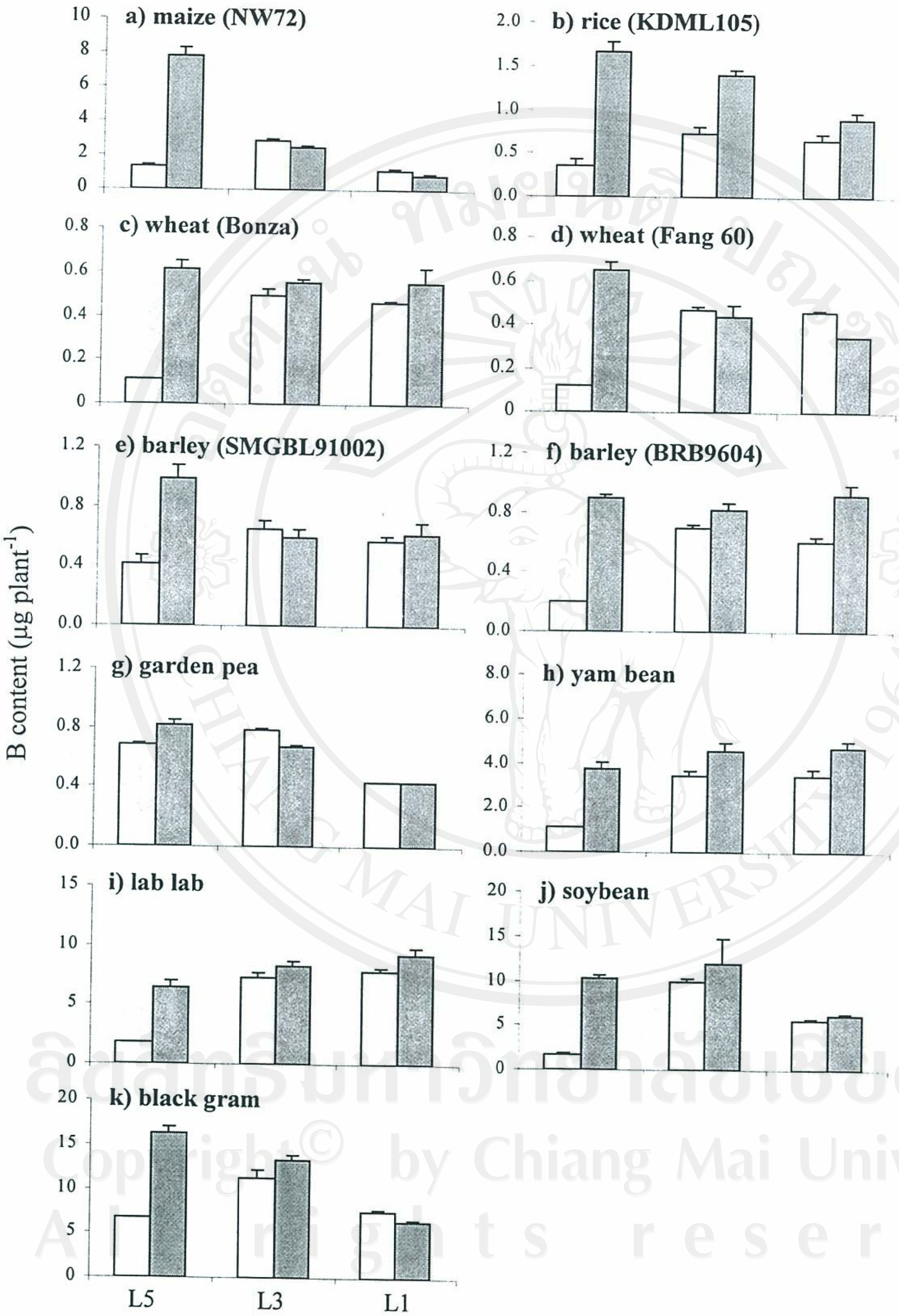

Figure 3.7 Leaf B content (µg B plant^{-1}) of 9 crop species. Bars are means of four replicates and vertical bars are standard errors (SE). ☐ Harvest 1 B+, ▩ Harvest 2 B+/B0

3.3.3 Experiment 3: Boron retranslocation during the mid reproductive stage of peanut and green gram

At harvest 1 (day 20 for peanut and day 25 for green gram), dry weights in each part and total dry weight of peanut and green gram were not significantly affected by B supply (Table 3.4). After the plants grew for a further 30 days, biomass of both plants increased in almost parts except leaflets of peanut with continuous BD. Moreover, it was found that seed dry weight of green gram and pod dry weight of peanut which received BD for 30 days (BA/BD and BD/BD) was reduced when compared with plants grown in adequate B continuously throughout the experiment (BA/BA). However, BA/BD plants produced more seed or pod yield than in BD/BD plants, being 1.8 and 3.5 times in peanut and green gram, respectively.

In peanut, B concentrations in various parts of BD plants at H1 were similar, whereas in BA plants, which generally had much higher B concentration than BD, the highest concentrations were in old leaflets (Table 3.5). Boron concentration in roots and stems + petioles was less than in leaflets in BA plants. Interrupting the B supply at day 20 affected B concentrations at H2. In BA/BD plants, B concentrations in each part were dramatically less than in BA/BA plants. Although B concentrations in BA/BA plant where depressed from H1, the concentrations of B remained high in all plant parts (Table 3.5).

The B content in BA peanut plants at day 20 was 21.9 μg in old leaflets and 5.3 μg in the rest of the main stem. When they were grown for 30 more days with B withdrawn from the nutrient solution (BA/BD), the B content decreased to 9.0 μg in old leaflets and increased to 24.8 μg in the rest of the main stem. At H2, the B content increased in stems + petioles and roots but was depressed in leaflets except the old leaflets of BA/BA plants. Moreover, the B content in the youngest fully expanded leaflets in BA/BD plants was significantly higher than in BD/BD plants (Table 3.6).

The partitioning of B in peanut plants was affected by the external B status (Figure 3.8). In BD plants, more than half of the B was accumulated in roots (about 59%) at H1. In the upper shoot, it was found that older parts (old LL and old S+P) had higher B accumulation than in the younger organs (growing point and YFEL) and the percentage of B in leaflets was higher than in stems + petioles. On the other hand, B-adequate peanut plants (BA) contained the highest B in old leaf blades which were similar to those in roots (37 and 33%, respectively) while there was little difference among the other parts. When plants grew until H2, the percentage of B in roots in BD/BD plants was slightly increased (62%). Boron in old stems + petioles in these plants was increased whereas in old leaflets and younger parts of shoot it was reduced. However, B allocated to peanut pods was about 9% of total plant B. The percentage of B in roots did not differ between harvests for BA/BA plants. The partitioning of B to old stems + petioles increased but it was depressed in old leaflets and leaflets of YFEL. It was found that B in the growing point and stems + petioles of YFEL was similar to H1 plants. Boron withdrawal altered B partitioning within peanut plants. Boron was partitioned in BA/BD plants in the same way as in BD/BD plants. About 14% of the plant B accumulated in BA/BA pods whereas about 9% of B was allocated to pods of BA/BD and BD/BD plants.

For green gram, at day 25 (H1) the B concentration in BD was slightly lower in the growing point than in the older tissues and roots. The B concentrations in all plant parts were higher in BA plants, the highest B concentration being in the growing point and the lowest in roots (Table 3.5). At H2 (55 days), the concentration of B in all parts decreased significantly in all treatments. The extent of the decline of B concentration from H1 to H2 was greatest in the growing point and the YFEL, leaflets and stems + petiole, in BA/BD. The decline in B concentration was smallest in the old leaflets and stems + petioles. There was little difference in B concentration among plant parts in BD/BD plants. It was also found that the B concentration in the youngest fully expanded leaflets and the stems + petioles of YFEL of BA/BD plants was greater than in corresponding parts of BD/BD plants. From the results of B content in plant parts of green gram (Table 3.6), 25-day-old BA green gram accumulated twice the total plant B of BD plants, and this was particularly evident in young tissues (growing point and YFEL). At 55 days (H2), BA/BA green gram still accumulated a greater amount of B in all parts than BA/BD and BD/BD plants. The greatest amount of B was observed in older parts (old leaflets and the rest of the main stem) of all treatments when compared with younger parts (growing point, the youngest fully expanded leaflets and the stems + petioles below the YFEL). Nevertheless, withdrawing B (BA/BD plants) led to a higher B content in the YFEL and seed than in plants supplied with 0.5 μM B throughout the experiment (BD/BD).

Boron was distributed to roots and old leaflets of BD green gram with greater amount at H1 (27% and 30%, respectively) while in the growing point, the YFEL and the old stems + petioles were similar, and the stems + petioles below the YFEL had the lowest B content. In BA plants, the highest B allocation was to old leaflets. The percentage of B in leaflets of the YFEL, growing point and roots were similar. The lowest amounts of B were partitioned to old stems + petioles and stems + petioles below the YFEL, which had 12% and 7% of total plant B, respectively. Additional B was directed into older parts (old leaflets and old stems + petioles) of BD/BD green gram by H2. By contrast the B content was quite low in seeds, the stems + petioles of YFEL, leaflets of YFEL and growing point at H2. It was found that B distribution of vegetative organs within BA/BD and BA/BA plants paralleled that in BD/BD plants. The percentage of total plant B in seeds was strongly affected by the B treatment, being highest (32%) in BA/BA plants, intermediate (12%) in BA/BD plants and lowest (6%) in BD/BD plants (Figure 3.8).

Table 3.4 Dry weight (g plant^{-1}) of peanut and green gram plants at H1 (day 20 in peanut; day 25 in green gram) and H2 (day 50 in peanut; day 55 in green gram). Values are means of three replicates (SE).

Plant part[a]	B supply				
	H1		H2		
	BD	BA	BD/BD[b]	BA/BD	BA/BA
Peanut					
Growing point	0.091 (0.022)	0.099 (0.025)	0.198 (0.050)	0.230 (0.032)	0.188 (0.026)
YFEL, LL	0.100 (0.007)	0.121 (0.010)	0.091 (0.017)	0.170 (0.041)	0.171 (0.022)
YFEL, S+P	0.041 (0.005)	0.051 (0.010)	0.075 (0.014)	0.097 (0.010)	0.104 (0.022)
Old LL	0.288 (0.029)	0.310 (0.054)	0.221 (0.026)	0.534 (0.040)	0.557 (0.022)
Old S+P	0.187 (0.035)	0.246 (0.043)	0.904 (0.096)	1.615 (0.134)	1.655 (0.029)
Pods			0.323 (0.047)	0.579 (0.067)	0.686 (0.099)
Roots	0.918 (0.136)	0.959 (0.097)	2.091 (0.135)	2.423 (0.137)	2.441 (0.169)
Total	**1.626 (0.225)**	**1.786 (0.190)**	**13.698 (0.551)**	**16.463 (1.267)**	**14.657 (2.852)**
Green gram					
Growing point	0.133 (0.013)	0.161 (0.020)	0.382 (0.053)	0.535 (0.105)	0.486 (0.079)
YFEL, LL	0.181 (0.024)	0.228 (0.004)	0.581 (0.020)	0.389 (0.201)	0.557 (0.017)
YFEL, S+P	0.071 (0.006)	0.079 (0.003)	0.525 (0.054)	0.372 (0.043)	0.382 (0.062)
Old LL	0.324 (0.057)	0.305 (0.017)	4.094 (0.193)	3.592 (0.420)	3.014 (0.090)
Old S+P	0.174 (0.019)	0.190 (0.003)	3.282 (0.229)	2.933 (0.321)	2.621 (0.089)
Seeds			1.056 (0.081)	3.532 (0.256)	5.537 (0.382)
Roots	0.429 (0.028)	0.414 (0.010)	2.382 (0.181)	2.122 (0.288)	2.127 (0.209)
Total	**1.312 (0.066)**	**1.376 (0.045)**	**12.302 (0.597)**	**13.474 (1.203)**	**14.722 (0.382)**

[a]Plant parts: Growing point - all parts above the youngest fully expanded leaf
YFEL, LL - the youngest fully expanded leaflets
YFEL, S+P – the stems + petioles below YFEL
OLD LL - the rest of the leaflets of the main stem (old leaflets)
OLD S+P - the rest of the main stem

[b]BD/BD - 0 μM B for peanut or 0.5 μM B for green gram (B-deficient) throughout the experiment,
BA/BD - 10 μM B for first 20 days for peanut (or first 25 days for green gram) followed by 0 μM B (for peanut) or 0.5 μM B (for green gram) for the following 30 days
BA/BA - 10 μM B (B-adequate) throughout the experiment

Table 3.5 Boron concentrations (mg B kg DW^{-1}) in various parts of peanut and green gram plants at H1 (day 20 in peanut; day 25 in green gram) and H2 (day 50 in peanut; day 55 in green gram). Values are means of three replicates (SE).

Plant part[a]	B supply				
	H1		H2		
	BD	BA	BD/BD[b]	BA/BD	BA/BA
Peanut					
Growing point	14 (1)	39 (2)	9 (2)	7 (1)	36 (5)
YFEL, LL	14 (1)	62 (3)	9 (2)	9 (2)	43 (2)
YFEL, S+P	12 (2)	29 (1)	7 (1)	6 (1)	27 (1)
Old LL	10 (0)	71 (1)	10 (3)	17 (1)	49 (2)
Old S+P	11 (0)	22 (0)	7 (2)	15 (1)	20 (1)
Pods			11 (1)	11 (0)	31 (1)
Roots	13 (0)	20 (0)	12 (1)	15 (0)	20 (2)
Green gram					
Growing point	16 (1)	45 (1)	7 (0)	5 (0)	32 (1)
YFEL, LL	14 (1)	40 (1)	5 (0)	7 (1)	33 (2)
YFEL, S+P	18 (0)	38 (1)	6 (1)	7 (0)	27 (1)
Old LL	19 (1)	38 (1)	7 (0)	15 (2)	39 (1)
Old S+P	17 (0)	26 (1)	7 (0)	11 (1)	21 (0)
Seeds			4 (0)	5 (1)	21 (0)
Roots	18 (0)	24 (0)	11 (0)	15 (0)	20 (1)

[a]Plant parts: Growing point - all parts above the youngest fully expanded leaf
YFEL, LL - the youngest fully expanded leaflets
YFEL, S+P – the stems + petioles below YFEL
OLD LL - the rest of the leaf lets of the main stem (old leaflets)
OLD S+P - the rest of the main stem

[b]BD/BD - 0 μM B for peanut or 0.5 μM B for green gram (B-deficient) throughout the experiment,
BA/BD - 10 μM B for first 20 days for peanut (or first 25 days for green gram) followed by 0 μM B (for peanut) or 0.5 μM B (for green gram) for the following 30 days
BA/BA - 10 μM B (B-adequate) throughout the experiment

Table 3.6 Boron contents (µg plant^{-1}) of peanut plants and green gram at H1 (day 20 in peanut; day 25 in green gram) and H2 (day 50 in peanut; day 55 in green gram). Values are means of three replicates (SE).

Plant part[a]	B supply				
	H1		H2		
	BD	BA	BD/BD	BA/BD	BA/BA
Peanut					
Growing point	1.28 (0.35)	3.85 (1.19)	1.76 (0.76)	1.68 (0.21)	5.60 (0.68)
YFEL, LL	1.39 (0.02)	7.55 (0.90)	0.85 (0.38)	1.58 (0.39)	7.44 (1.33)
YFEL, S+P	0.50 (0.02)	1.50 (0.34)	0.55 (0.21)	0.55 (0.13)	2.84 (0.66)
Old LL	2.86 (0.25)	21.93 (3.66)	2.35 (0.75)	9.05 (0.83)	27.37 (1.09)
Old S+P	1.98 (0.36)	5.31 (0.95)	6.50 (0.93)	24.82 (1.43)	33.15 (1.10)
Pods			3.56 (1.25)	6.20 (0.55)	20.85 (8.64)
Roots	11.53 (1.75)	19.68 (2.17)	25.78 (3.03)	36.96 (2.17)	47.97 (7.26)
Total	**19.55 (2.58)**	**59.82 (7.88)**	**44.37 (4.95)**	**81.54 (2.21)**	**148.08 (14.01)**
Green gram					
Growing point	2.16 (0.17)	7.31 (0.81)	2.02 (0.50)	2.77 (0.48)	15.55 (1.86)
YFEL, LL	2.49 (0.28)	9.14 (0.30)	2.86 (0.04)	4.20 (0.60)	18.34 (1.44)
YFEL, S+P	1.27 (0.11)	2.99 (0.07)	2.98 (0.18)	2.65 (0.13)	10.12 (1.19)
Old LL	6.07 (0.98)	11.52 (0.76)	27.88 (1.40)	52.04 (0.83)	117.76 (2.25)
Old S+P	2.96 (0.37)	4.96 (0.09)	21.37 (1.40)	31.74 (1.78)	56.24 (0.85)
Seeds			4.44 (0.71)	15.80 (1.50)	118.26 (7.36)
Roots	5.52 (0.26)	7.11 (0.28)	19.16 (0.83)	24.26 (1.90)	33.55 (2.32)
Total	**20.47 (1.20)**	**43.03 (1.82)**	**80.71 (2.76)**	**133.47 (2.56)**	**369.83 (9.93)**

[a]Plant parts: Growing point - all parts above the youngest fully expanded leaf
YFEL, LL - the youngest fully expanded leaflets
YFEL, S+P – the stems + petioles below YFEL
OLD LL - the rest of the leaflets of the main stem (old leaflets)
OLD S+P - the rest of the main stem

[b]BD/BD - 0 µM B for peanut or 0.5 µM B for green gram (B-deficient) throughout the experiment,
BA/BD - 10 µM B for first 20 days for peanut (or first 25 days for green gram) followed by 0 µM B (for peanut) or 0.5 µM B (for green gram) for the following 30 days
BA/BA - 10 µM B (B-adequate) throughout the experiment

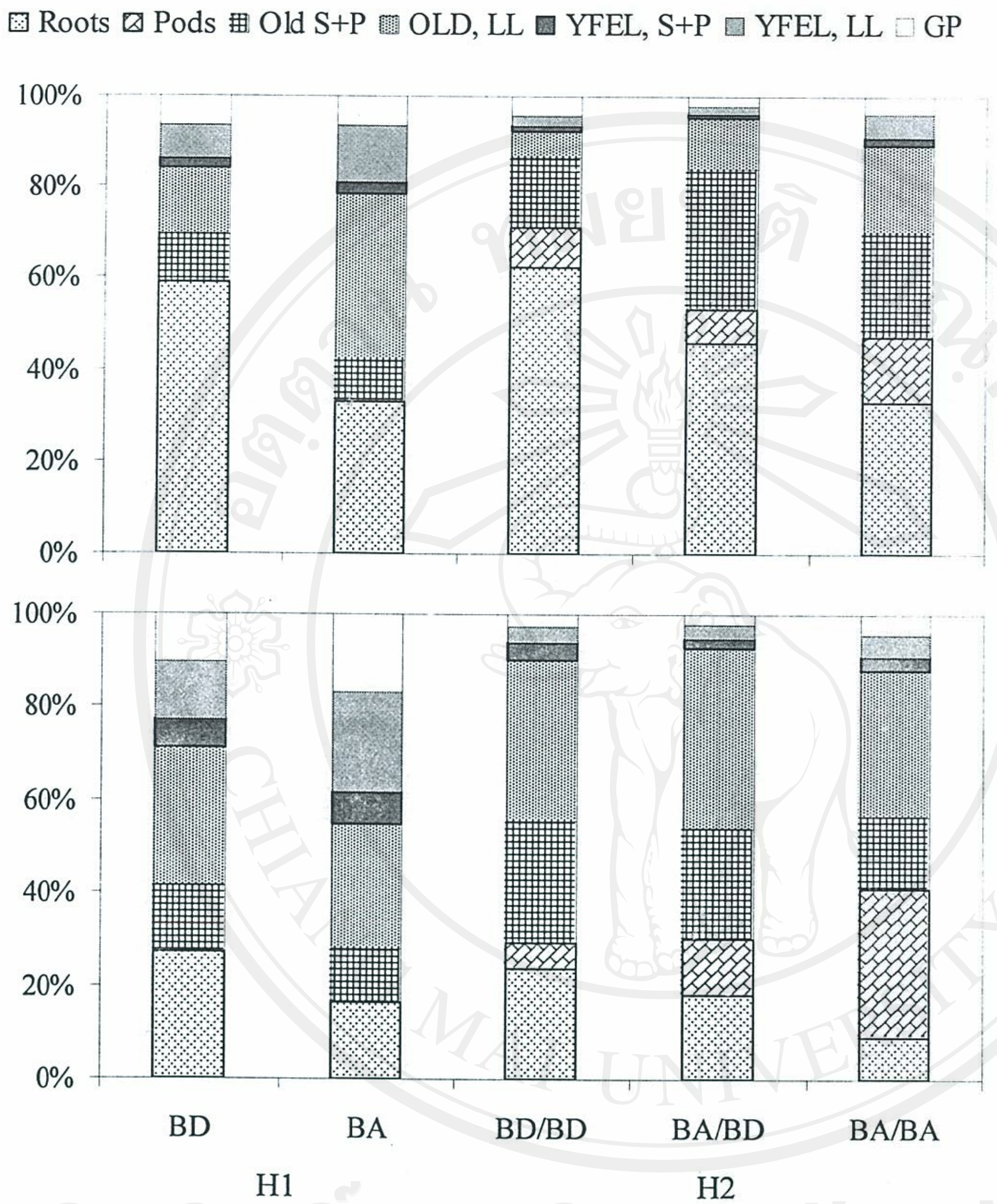

Figure 3.8 Boron partitioning within plant parts of peanut (upper) and green gram (lower).

Plant parts: Growing point - all parts above the youngest fully expanded leaf
YFEL, LL - the youngest fully expanded leaflets
YFEL, S+P – the stems + petioles below YFEL
OLD LL - the rest of the leaflets of the main stem (old leaflets)
OLD S+P - the rest of the main stem

BD/BD - 0 μM B for peanut or 0.5 μM B for green gram (B-deficient) throughout the experiment,
BA/BD - 10 μM B for first 20 days for peanut (or first 25 days for green gram) followed by 0 μM B (for peanut) or 0.5 μM B (for green gram) for the following 30 days
BA/BA - 10 μM B (B-adequate) throughout the experiment

3.4 Discussion

The results of Experiment 3.1 confirmed the observation in Chapter 2. The data on leaf B content before and after foliar B application was used for indicating B mobility in plant species. Young leaves (YL) of all species (coffee, jackfruit and guava) had increasing B contents compared to non-treated trees whereas the B content of old leaves (ML) of treated trees declined over time. This indicated the movement of B out of treated leaves (Hanson, 1991). The data on B concentration could not be used for indicating B mobility because of the dilution effect. For instance, although the B concentration of treated-leaves (ML) fell, it increased in YL of coffee and jackfruit but decreased in guava. The latter may be a consequence of an increase in the dry matter of the YL over time. Additionally, due to the short duration of the experiment or the low concentration of foliar B applied, foliar application of B did not correct B deficiency symptoms which occurred in the first period of the experiment even though the B concentration in leaves was increased. Coffee requires more than 25 mg B kg DW^{-1} in the third or fourth pair of leaves from the tip of active growing for maintaining normal growth (Winston, 1996 cited by Reuter and Robinson, 1997), but the maximum increase in boron concentration in young coffee leaves in the current study was only 17.1 mg B kg DW^{-1}. For guava, treated plants had 11.1 mg B kg DW^{-1} in young leaves, which is a little higher than the 7 mg B kg DW^{-1} reported in the third leaf pair of deficient guava by Salvador *et al.* (1999).

Withdrawal of B from the nutrient supply during vegetative growth (Experiment 2) did not affect leaf dry weight and B deficiency symptoms. As for Experiment 2, the amount of B in leaves in each position was a useful indication of B remobilization in plant species. A comparison of B content between the two harvests was used to show variation in nutrient distribution of each species. Although the B content increased in younger leaves (L5) of all species over time, the amount of B in older leaves (L1 and L3) differed among plant species. The reduction of B in older leaves, especially in L1, suggested that B in these leaves may be exported in the phloem to other parts of the plant as discussed by Smith and Loneragan (1997). Thus, overall, the results suggested that B may be remobilized in maize, wheat (cv. Fang 60), and black gram.

The study of B mobility during the mid reproductive stage of peanut and green gram suggested that the majority of the B that was supplied to these plants in the first period (BA/BD) accumulated in old leaves. However, in these plants, a small amount of B may have been retranslocated to the YFEL and reproductive parts due to an observed increase in the B content of these parts compared with BD/BD plants. The source of this increase could not be identified. Two possibilities are accumulation from export from old leaves or from B remaining in vascular tissues. To determine the source of B, experiments using $^{10}B/^{11}B$ isotopes are necessary as described in Chapter 4.

Withdrawal of B had no effect on vegetative growth of peanut or green gram in the following 30 days. The normal development of vegetative parts after interrupting the B supply suggests that B applied during the first 20 days for peanut and 25 days for green gram was enough for vegetative development. Boron concentrations in leaflets of H1 plants were higher than in other parts and remained high in old leaflets of B-sufficient plants continuously supplied with external B. This probably is because leaves transpire more vigorously than other parts of the shoot and it is well known that B is transported long-distance in the xylem to sites of water loss

(Tanner and Beevers, 2001). Campbell *et al.* (1975) reported that during development of fruits of peanut and subterranean clover in a B-deficient medium, B could be transported to fruits of peanut and burrs of subterranean clover. This is consistent with the current work that indicates that B could be exported out of leaflets to other vegetative parts. It was shown that B concentrations and contents in leaflets formed during a period of adequate external B supply decreased strongly after the B was withdrawn whereas they increased in newly-formed parts of peanut and also in green gram.

This is the first time of the reports on B mobility in some tropical species. Boron immobility was found in lab lab, soybean, garden pea, yam bean, rice, wheat (cv. Bonza) and barley while B retranslocation has been indicated in guava, jackfruit, maize, wheat (cv. Fang 60), black gram, green gram and peanut. This thesis was also confirmed B retranslocation in coffee as reported in the paper of Leite *et al.* (2007). However, indication of B retranslocation in wheat cv. Fang 60 was contradicted previous reports (Huang *et al.*, 2001; Subedi *et al.*, 2001; Nachiangmai *et al.*, 2004). Nachaingmai *et al.* (2004) showed that B retranslocation from previously taken up to the ear of Fang 60 was not exist. This thesis was studied during vegetative stage hence the contradiction could be occurred.

Thus, from the results of three experiments it can be concluded that in some species of tropical plants B may be remobilized from parts of the shoot that accumulate B such as old leaves or from foliar-treated leaves to other parts of the shoot such as reproductive organs. It was also found that B remobilization varies among tropical crop species. However, in order to identify more detailed study is needed using more precise methodology (Chapter 4).