

TABLE OF CONTENTS

Acknowledgements	iii
Abstract (English)	v
Abstract (Thai)	ix
List of Tables	xvii
List of Figures	xx
Introduction	1
Chapter 1 Literature review	4
1.1 Absorption of mineral nutrients by plant roots	4
1.2 Nutrient transport within plants	5
1.2.1 Xylem transport	5
1.2.2 Phloem transport	6
1.2.3 Retranslocation of mineral nutrients	8
1.3 Boron	9
1.3.1 Role of boron in plants	9
1.3.2 Boron deficiency symptoms in plants	10
1.4 Boron mobility in plants	12
1.4.1 Boron absorption	12
1.4.2 Xylem and phloem transport	13
1.4.3 Retranslocation of boron	13
1.4.4 Mechanism of boron mobility in plants	14

1.5 Methods for studying nutrient mobility	16
1.6 Concluding remarks	19
Chapter 2 A survey of boron mobility in tropical species: a field study	20
2.1 Introduction	20
2.2 Materials and methods	21
2.2.1 Boron mobility in mangosteen	21
2.2.2 Boron mobility in durian	22
2.2.3 Survey of tropical woody and fruit species for B retranslocation	22
2.3 Results	25
2.3.1 Boron mobility in mangosteen	25
2.3.2 Boron mobility in durian	25
2.3.3 Survey of tropical woody and fruit species for B retranslocation	26
2.4 Discussion	32
Chapter 3 A survey of B mobility in woody and field crop species: controlled experiments	34
3.1 Introduction	34
3.2 Materials and methods	36
3.2.1 Experiment 1: Mobility of B applied to specific leaves of horticultural woody plants	36
3.2.2 Experiment 2: Boron retranslocation during early vegetative growth in field crop species	37

3.2.3 Experiment 3: Boron retranslocation during the mid reproductive stage of peanut and green gram	38
3.3 Results	42
3.3.1 Experiment 1: Mobility of B applied to a specific leaf	42
3.3.2 Experiment 2: Boron retranslocation during early vegetative growth in field crop species	48
3.3.3 Experiment 3: Boron retranslocation during the mid reproductive stage of peanut and green gram	54
3.4 Discussion	62
Chapter 4 Boron mobility in peanut (<i>Arachis hypogaea</i> L.)	65
4.1 Introduction	65
4.2 Materials and methods	66
4.2.1 Experiment 1: Boron distribution and redistribution in peanut	66
4.2.2 Experiment 2: Confirming B remobilization using tracer B (^{10}B)	67
4.2.2.1 Experiment 2.1: ^{10}B – foliar application	67
4.2.2.2 Experiment 2.2: ^{10}B applied to the roots	69
4.2.3 Experiment 3: Boron mobility in two cultivars of peanut	71
4.3. Results	73

4.3.1 Experiment 1: Boron distribution and redistribution in peanut	73
4.3.2 Experiment 2: Confirming B remobilization using tracer B (^{10}B)	90
4.3.2.1 Experiment 2.1: ^{10}B -foliar application	90
4.3.2.2 Experiment 2.2: ^{10}B applied to the roots	94
4.3.3 Experiment 3: Boron mobility in two peanut cultivars	104
4.4. Discussion	113
Chapter 5 General Discussion	116
5.1 Criteria for determining B mobility	116
5.2 Variation of B mobility among plant species	118
5.3 Implications of B mobility for diagnosis of the B status of plants and for fertilizer management	125
5.4 General conclusions	127
5.5 Implications for further research	127
References	129
Curriculum vitae	142

LIST OF TABLES

Table	Page
1.1 Characteristic differences in mobility of mineral nutrients in the phloem	8
2.1 Tropical species sampled for foliar boron	24
2.2 Potassium (K) concentration (% DW) in young, mature and old leaves of 17 tropical plant species	29
2.3 Calcium (Ca) concentration (% DW) in young, mature and old leaves of 17 tropical plant species	30
2.4 Boron (B) concentration (mg B kg DW ⁻¹) in young, mature and old leaves of 17 tropical plant species	31
3.1 The composition of nutrient solution for all species (except maize)	39
3.2 The composition of nutrient solution for maize	40
3.3 Field crop species which were verified for boron retranslocation	41
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)	58
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)	59

3.6	Boron contents ($\mu\text{g plant}^{-1}$) 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)	60
4.1	Summary of experiments for detailed study for B mobility in peanut	72
4.2	The effect of B withdrawal on the number of lateral branches of peanut	81
4.3	The effect of B withdrawal on the number of pegs and pods of peanut at harvest 2 and harvest 3	82
4.4	The effect of B withdrawal on the number of pods and % hollow heart seed of peanut at harvest 4	83
4.5	The effect of withdrawal B on dry weight (g plant^{-1}) of reproductive parts of peanut	84
4.6	Boron concentration (mg B kg DW^{-1}) in various parts of peanut	86
4.7	Boron content ($\mu\text{g plant}^{-1}$) in various parts of peanut.	88
4.8	Dry weight (g plant^{-1}) of peanut (cv. TAG 24)	99
4.9	Reproductive growth of peanut (cv. TAG 24) with adequate or deficient ^{10}B and then transferred into ^{11}B	100
4.10	^{10}B content ($\mu\text{g plant}^{-1}$) of peanut cv. TAG 24	103
4.11	Vegetative and reproductive growth of 2 peanut cultivars before foliar B application (H1: 60 days after germination)	106
4.12	The effect of foliar B application on vegetative and reproductive growth of 2 peanut cultivars at the end of foliar B application (H2: 67 days after germination)	107

4.13	The effect of foliar B application on vegetative and reproductive growth of 2 peanut cultivars at the 83 days after germination (H3: grain maturity)	108
4.14	Boron concentration (mg B kg DW^{-1}) in various parts of two peanut cultivars with and without foliar B	109
5.1	Variation of B mobility among plant species base on results of this thesis	120
5.2	Variation of B mobility among plant species from the literatures	122

LIST OF FIGURES

Figure		Page
2.1	Position of mangosteen leaf sample collection	21
2.2	Position of durian leaf sample collection	22
2.3	Trends in nutrient concentration of mangosteen with leaf age at two positions in the canopy	27
2.4	Concentration of K, Ca and B in durian leaves	28
3.1	Boron deficiency symptoms in coffee, guava and jackfruit	44
3.2	Leaf dry weight (g plant ⁻¹) of coffee, guava and jackfruit in foliar application experiment	45
3.3	Leaf B concentration (mg kg DW ⁻¹) of coffee, guava and jackfruit in foliar application experiment	46
3.4	Boron content (µg plant ⁻¹) of coffee, guava and jackfruit in foliar application experiment	47
3.5	Leaf dry weight (g plant ⁻¹) of 9 crop species	51
3.6	Leaf B concentration (mg B kg DW ⁻¹) of 9 crop species	52
3.7	Leaf B content (µg B plant ⁻¹) of 9 crop species	53
3.8	Boron partitioning within plant parts of peanut (upper) and green gram (lower)	61
4.1	Diagram of peanut plants	68

4.2	Diagram showing parts of peanut (cv. TAG 24) sampled at three harvests	70
4.3	The effect of B withdrawal on dry weight (g plant^{-1}) of peanut	78
4.4	The effect of B withdrawal on dry weight (g plant^{-1}) of various parts of peanut (cv. Tainan 9) main stem	79
4.5	Normal peanut plants (cv. Tainan 9) at harvest 1 (day 25)	80
4.6	Boron deficiency symptom (water soaked young leaves) in peanut cv. Tainan 9	80
4.7	The effect of B withdrawal on reproductive parts of peanut cv. Tainan 9 at harvest 4 (day 103)	85
4.8	The effect of foliar B on dry weight of peanut cv. Tainan 9	92
4.9	^{10}B isotope abundance in parts of peanut plants cv. Tainan 9	93
4.10	Boron deficiency symptoms in peanut cv. TAG 24	97
4.11	Plant height (cm), root length (cm), number of lateral branches/plant and number of new leaves/plant of peanut (cv. TAG 24) which were grown in different B status	98
4.12	Effects of changing B status on peanut cv. TAG 24	101
4.13	^{10}B isotope abundance in parts of peanut plants cv. TAG 24 (Experiment 2.2)	102
4.14	Boron content ($\mu\text{g plant}^{-1}$) of older plant parts developed before foliar treatment of 2 peanut cultivars	111
4.15	Boron content ($\mu\text{g plant}^{-1}$) of plant organ formed after foliar treatment of 2 peanut cultivars	112

Introduction

Plants acquire nutrient elements from the soil via absorption by their roots. The nutrients are then transported in xylem sap by water movement in the transpiration stream to the shoot. However, they may be retranslocated, via the phloem, to other plant parts, including the shoot tip and reproductive tissues where transpiration is low (Smith and Loneragan, 1997). Transport in the phloem is important for long-distance transport in plants especially during seed germination, when external nutrient supply is lacking for vegetative stage, during reproductive growth and the period before leaf drop in perennials (Marschner, 1995). This is because phloem transport takes place in both upward and downward directions and does not depend on transpiration so it can transport mineral nutrients to the organs which transpire less or not at all (Shelp *et al.*, 1995). Nutrient retranslocation or phloem mobility can be determined by a number of criteria, including direct analysis of nutrient concentration in phloem sap, movement of isotopes, development of deficiency symptoms, measurement of the rate of influx of an element during fruit development, comparison of measured contents in different plant parts, and determination of concentration gradients in plants from older to younger leaves (Van Goor and Van Lune, 1980; Marschner, 1995).

While all nutrients move readily in the xylem, they vary widely in the extent of their mobility in the phloem. Boron may be classified as intermediate in phloem mobility, but it is different from other essential elements in that its phloem mobility

varies among plant species (Marschner, 1995; Brown and Shelp, 1997). In most species B mobility is confined to the transpiration stream. Hence, B accumulates in the tip and edge of leaves or older leaves at all times. For example, Brown and Hu (1998) demonstrated higher B concentrations in old or mature leaves in comparison to younger leaves of pecan, tomato, strawberry and walnut. They also reported that pistachio and walnut, grown under field conditions, contained the highest B concentration in mature leaves and the lowest B concentration in fruit and seed tissue (Brown *et al.*, 1994). Boron deficiency symptoms always appear on younger and immature tissues, such as in squash (Hu and Brown, 1994) and tomato, whereas B toxicity symptoms occur in the tip, margins and interveinal areas of leaves where concentrations are high (Oertli, 1994). Immobility of B was also found in the ^{10}B tracer experiment of Brown and Hu (1996). Foliar ^{10}B , applied to mature leaves of pistachio and walnut, did not move out of treated leaves and there were the lowest B concentration in younger leaves and fruit tissues remained low.

By contrast, other observations indicate that B is phloem mobile in some plants. Hanson (1991) reported that the B content in leaves of apple (*Malus domestica*), pear (*Pyrus communis*), plum (*Prunus domestica*) and cherry (*Prunus ceasus*) which were treated with foliar B (500 mg L^{-1}) decreased to levels similar to non-treated leaves and the highest B concentration was found in untreated buds. Applying B to leaves of olive at anthesis also increased B concentrations in leaf blades, petioles, and bark of bearing shoots, flowers and fruits (Delgado *et al.*, 1994). In addition, phloem B mobility has been demonstrated in species which produce sugar alcohols as the primary photosynthates such as in apple, pear, plum, cherry (Brown and Hu, 1996), celery and peach (Hu *et al.*, 1997).

The retranslocation of B may be associated with B efficiency of plants as Shelp and Shattuck (1987b) found a relationship between the B retranslocation capacity and tolerance to B deficiency in two rutabaga cultivars. Moreover, management of B fertilization has been affected by patterns of B mobility, especially for foliar application. In species in which B is immobile, foliar-applied B was effective only for direct-applied tissues. On the other hand, in species where the B is phloem mobile, foliar-applied B was effective at any time and B could be supplied to organs developed after application (Brown and Hu, 1996).

As mentioned above, most reports on B mobility concern temperate plants and information for tropical species is very limited. Consequently, this study proposes to examine B mobility in tropical crop species. Information on B mobility in tropical species should be useful for improving the diagnosis of B deficiency by tissue sampling and analysis and by visual symptoms and also the management of B fertilization in crop production. Moreover, the variation of B retranslocation among plant species will influence the direction for the selection of breeding program of plants tolerant to B deficiency.