CHAPTER 2

LITERATURE REVIEW

2.1 B in plant

2.1.1 Boron uptake and translocation

Active and passive uptake of B has been reported by many authors (Raven, 1980; Brown and Hu, 1994; Dannel *et al.*, 1998). Uptake is concluded to be most likely a passive, non-metabolic absorption of boric acid (Hu and Brown, 1997), however, the support for a passive uptake is not complete and there is need more scientific evidence. Bingham *et al.* (1970) found some evidence that B is taken up by passive absorption by investigating the absorption of B in excised *Hordeum vulgare* (barley) roots. The authors postulate that the entire plant is a free space for B. A passive absorption of B has been reported in cultured *Nicotiana tabaccum* (tobacco) cells and in the roots of *Helianthus annuus* (sunflower) and *Cucurbita maxima* Duch. (squash) plants by Brown and Hu (1994). The observation of passive absorption of B was for solution B between 0-10 mM. However, there is insufficient evidence to conclude that passive uptake is the only mechanism of B uptake.

Bowen (1972) investigated B movement in xylem, and concluded that long distance translocation of B from root to shoot occurs with the accumulation of B into various shoot tissues influenced by the rate of its transpiration. The gradients of B concentration within the various tissues of the shoot generally correspond to the age of the plant organ and by implication to the total flux of xylem sap due to

transpiration. Boron mobility in the phloem can also be indicated by tissue concentration gradients. Brown and Shelp (1997) identified two groups of plant differing in their capacity to retranslocate B. In the *Isomens arborea* and *Ulmus parvifolia*, old leaf tissue always contain higher B concentrations than in equivalent leaves of *Apium graveolens* and *Osmanthus fragrans*.

Brown and Hu (1996) reported that B retranslocation in the genera Prunus, Pyrus and Malus was facilitated by sorbitol. Therefore, they hypothesised that B is freely mobile in all species where the polyol sorbitol is a major sugar and where other sugar alcohols such as mannitol and dulcitol are present.

2.1.2 Boron function in plants

a) cell wall

The primary role of B in the cell wall is likely to be in cell wall structure rather than cell wall synthesis. The function of B in cell wall structure might be in cell wall formation and structural integrity such as cell wall rigidity. There have been many reports on the effect of B deficiency in cell wall structure eg. cell wall thickness (Lee and Aronoff, 1966) and cell wall packing (Matoh *et al.*, 1992). Not all cells respond in the same was as B deficiency decreased the thickness of collenchyma cell walls but increased the thickness of the phloem parenchyma cell wall (Spurr, 1957). Those effects can be attributed to reduced structural intergrity of the cell wall. Up to 98% of cellular B was located in the cell wall (Matoh *et al.*, 1992) or 96-97% of cellular B was located in the cell wall (Hu and Brown, 1994). The B in cell walls

interacts with polysaccaride polymers to form boratepolymer cross-links associated with rhamnogalacturonan II (RG-II) in a 1:2 complex (Matoh *et al.*, 1996) and cell wall B was bound within the pectin fraction that is polysaccaride polymer having many B-binding sites (Hu *et al.*, 1996). The differential B requirements of different species was found to be associated with the concentration of cell wall pectin in plant tissues (Hu *et al.*, 1996) and helps to explain the differences in B requirements between monocots (low) and dicots (high). In wheat, the internal B requirement do not vary between species.

b) Cell membrane

It is still unclear whether B has a primary function in the cell membrane. Although there have been report that the role of B in membrane functioning was secondary or tertiary, some evidence suggests a specific requirement for B in maintaining membrane integrity, and its function, especially ion transport. The effects of B deficiency have been reported to reduce adenosine triphosphatase (ATPase) and increase H^+ efflux (Goldbach *et al.*, 1990), inducing decreased membrane potential (hyperpolarisation) leading to K^+ leakage (Cakmak *et al.*, 1995). Such changes have been postulated to reduced osmotic pressure; change a shape of protein reducing proton pump activities and impair ion transport, such as phosphate (Robertson and Loughman, 1974); and reduce the capacity for phosphate absorption (Pollard, 1977). Findeklee and Goldbach (1996) and Goldbach (1997) concluded that

the effect of B deficiency on plasmalemma bound reactions is a secondary event. Cakmak *et al.* (1995) suggested that B has a stabilising effect on the plasma membrane and that B may react with hydroxyl-rich compounds to give stability in the cell membranes (Goldbach *et al.*, 1993; Shelp, 1993; Brown, 2002). Parr and Loughman, (1983) postulate that B could interact with the membrane via glycoprotein or glycolipid components to maintain the most efficient conformation. Barr *et al.* (1993) reported that B was directly associated with cell growth through its effect on the plasma membrane NADH oxidase and H^+ secretion. The effect of B deficiency on enzymatic activities and proton activities (K^+, H^+) may also point to a role for B in maintaining the structural integrity of the membrane. A structural requirement for B in the plasma-membrane may be a primary function for B (Cakmak *et al*, 1995)

c) Phenol metabolism

Although the primary function of B is still unclear, many reports have suggested that the major functions of B in growth and development of plants is based on its ability to form complexes with compounds having *cis*-diol configurations, such as the constituents of cell walls and the plasma membrane as well as with phenolic compounds. Under B deficiency, the impairment of physiological functions by B and associated morphological changes may be related to the formation of these B complexes. In this regard, the possible function of boron on phenol metabolism will be discussed.

Impairments in phenol metabolism and increases in levels of phenolics and polyphenoloxidase activity are a typical features of B deficiency. The formation of borate complexes with some phenolics, such as caffeic acid, is probably concerned with the regulation of the level of free phenols and the rate of synthesis of phenol alcohols as precursors of lignin biosynthesis. In B deficient tissue, the stimulation of the pentose phosphate pathway or restriction in biosynthesis of phenolic alcohols (Pilbeam and Kirkby, 1983) canthe result in an increase in free phenolic compounds.

Accumulation of phenolics in B-deficient tissues can also activate enzymes that use phenolics as substrates, the so called polyphenoloxidases (PPO). Oxidation of phenolics by PPO may lead to highly reactive intermediates such as caffeic quinone in the cell walls. These quiones are known to be highly toxic and very effective in producing toxic oxygen-free radicals such as superoxide species (Cakmak and Romheld, 1997). Accumulation of quinones are a major cause of damage to cell membranes by lipid peroxidation and cessation of growth under B deficient conditions. Moreover, the quinones produced by PPO are polymerised to brown pigments resulting in enhanced browning of leaf tissues and also in fruit during maturation.

Quinones formed by PPO can be reduced back to phenols by ascorbic acid and SH-compounds (e.g. glutathione) that are the antioxidants of cells and are involved in detoxification of toxic oxygen species. Ascorbic acid and SH-compounds are able to

block both phenol oxidation to quinones and polymerisation of quinones to brown pigments.

2.1.3 Boron in reproductive growth

An effect of B on pollen germination and pollen tube growth was first to demonstrated by Schmucker, (1933, 1934). Without B, pollen tubes swelled and burst, and germination of pollen in *Numphaea* was improved with the addition of stigmatic extract, containing a high concentration of B (Schmucker, 1934). Other authors also reported a direct relationship between the length of pollen tubes and the concentration of boric acid (Visser, 1955). A direct effect of B was also observed on germinating pollen grains by Cheng and Rerkasem, (1993).

The male reproductive tissue in cereals was affected by B deficiency leading to atrophy of anthers, while B deficiency did not affect the embryo sac or the ovary (Whittington, 1957). Some authors have observed an interaction between B and phytohormones such as indoleacetic acid (IAA) and gibberellic acid (GA) on unfertilised ovules of cotton grown *in vitro* (Birnbaum *et al.*, 1974).

2.2 Boron deficiency symptom

2.2.1Visible symptoms

The symptoms of B deficiency in wheat has been observed during anthesis (1) The wheat florets usually remain open ("gaping glumes") for several days at anthesis

(Figure 2.1), and the spike appears transparent against the sunlight when viewed with the sun behind them (Sthapit and Subedi, 1990 and Rerkasem *et al.*, 1997). Sthapit and Subedi (1990) has observed that the sterile spike may appear black from the distance at maturity.

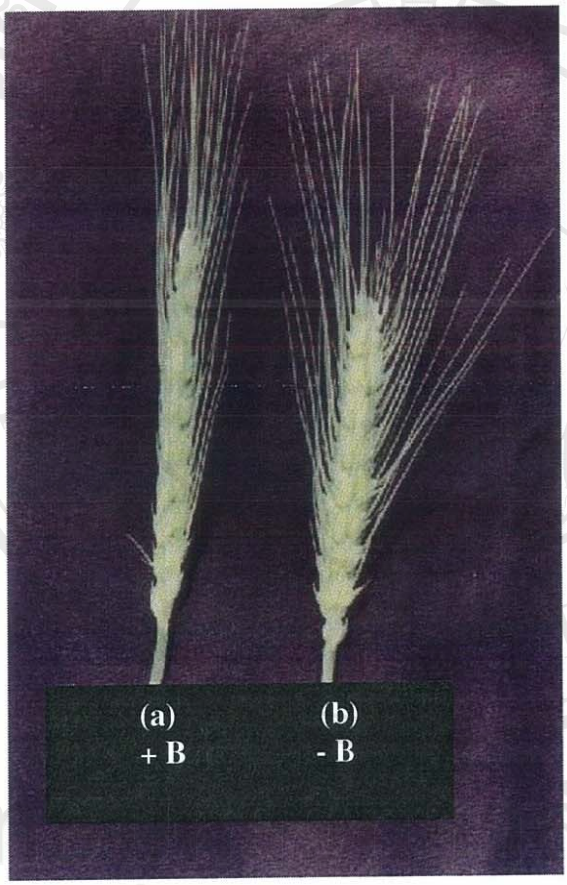

Figure 2.1 Spike at anthesis. (a) Normal spike from +B plant. (b) Sterile spike with B deficiency symptom (Gaping glumes) from –B plant.

2.2.2 Pollen sterility

Although sterile florets appear to be complete with fully developed palea and lemma, anthers are absent or small, misshapen and shrunken producing malformed pollen grains with empty containing no starch (Figure 2.2). The effect was observed in association with visible abnormalities in the anthers and pollen, but without apparent effect on vegetative growth (Li *et al.*, 1978).

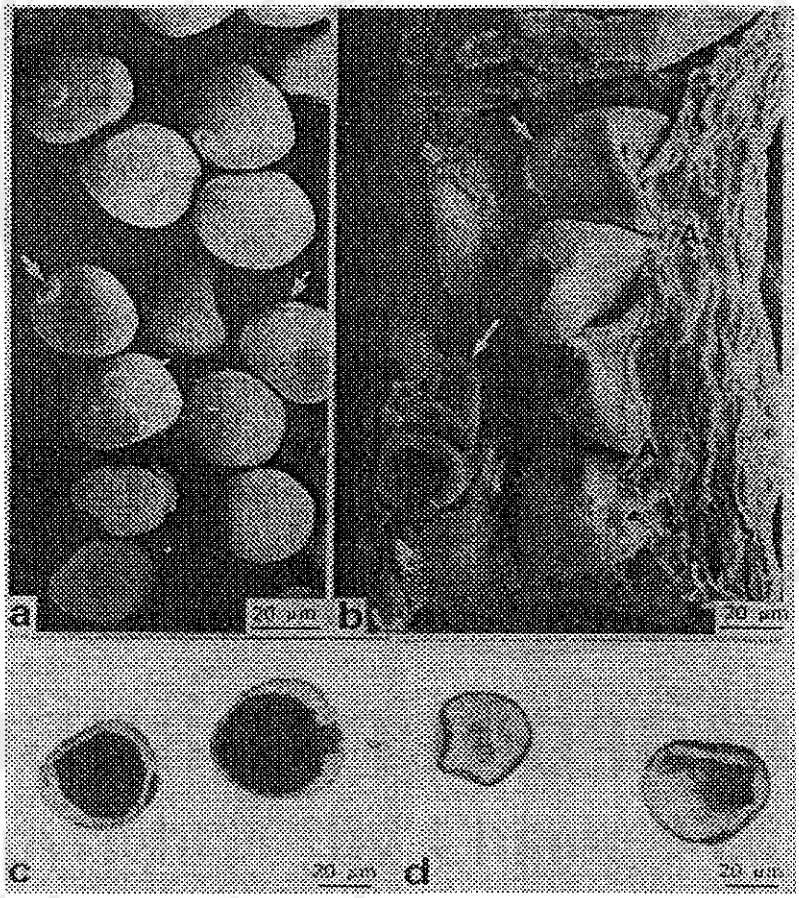

Figure 2.2 Scanning electron micrographs (a,b) and light micrographs (c,d) of wheat pollen towards anthesis. a)Normal turgid grains with prominent germ pores (arrows) from B+ plant. B) Shrivelled grains (arrows) inside anther tissue (A) from B0 plant. c) Pollen grains from B+ plant mounted in iodine solution. The cytoplansm contains numerous small starch grains. d) Pollen grains from B0 plant showing distorted shape and reduced cytoplasm. (Based on Rerkasem, 1989)

For anatomical investigation, at low soil B supply anther development proceeded normally at least until the vacuolated young microspore stage of microspore but by anthesis had become defomed and empty containing no starch (that is, do not stain with iodine) (Rerkasem *et al.*, 1997). Pollen that appears to have developed normally can still have been affected by boron deficiency (Cheng and Rerkasem, 1993). In addition, the adverse effect of B deficiency was observed in association with the limitation of B during the phase of anther development surrounding meiosis (Bennett *et al.*, 1973; Rawson, 1996; Huang *et al.*, 2000). Furthermore, the period from premeiotic interphase through meiosis to the young microspore stages (white to early green anther stages) during the spike length increases from 17 to about 160 mm (Figure 2.3) has been suggested to be the most sensitive stage of microsporogenesis to B deficiency in wheat (Huang *et al.*, 2000). Although the direct roles of B in pollen development are yet to be confirmed (Dell and Huang, 1997), it has been suggested that boron is required continuously for the development of cell wall function (Matoh *et al.*, 1992) that it is required in highest concentrations in developing pollen (Rerkasem, 1995).

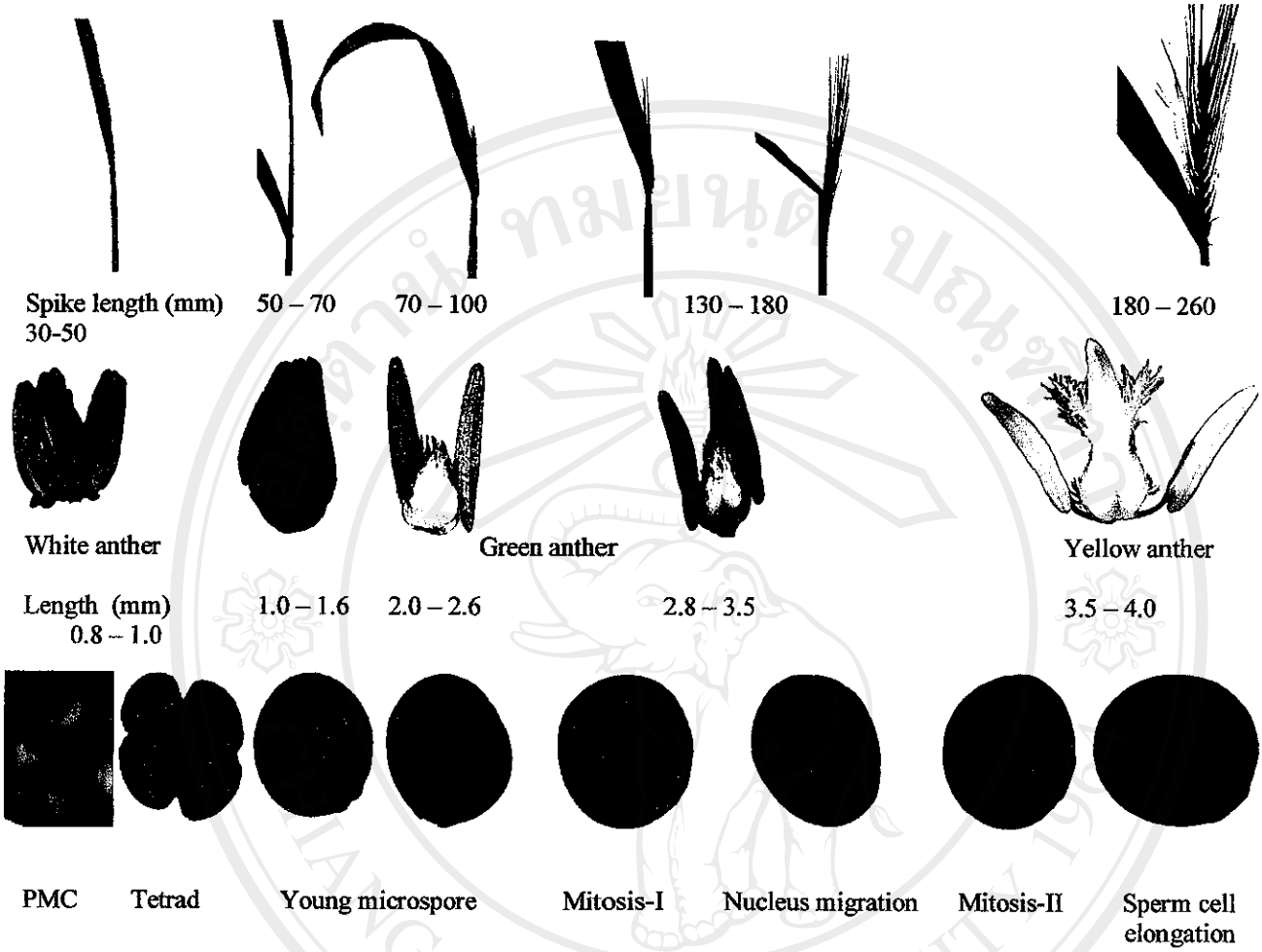

Figure 2.3 Stages in development of spring wheat ears, anthers and microspores referred to in the text. (Based on Dell *et al.*, 2002)

2.2.3 Boron concentration in plant tissues

The requirement of B in reproductive development is really higher than for the vegetative development. In wheat plant were found to concentrate more B into anthers than into the carpels, glumes, leaves (Lohnis, 1937; 1940). Boron was much more concentrated in the anthers and carpels than in the remainder of the ear or even the flag leaf. (Rerkasem *et al*, 1997). The B concentrated in the anthers and the flag leaf were two times (Rerkasem and Lordkaew, 1996) and five to six times (Rerkasem, 1996) that in the whole ear, respectively. In addition, success of grain set has been shown to be associated with higher functional B requirement in anther, more importantly than that in the carpel (Rerkasem *et al*, 1993). However, male sterility and grain set failure have been associated with 7-9 mg B / kg in the anther, 5-8 mg B/ kg in the carpel, 2-3 mg B/kg in the whole ear (Rerkasem and Lordkaew, 1996) and 3-7 mg B/kg in the flag leaf at booting stage (Rerkasem and Loneragan, 1994).

2.2.4 Assessment of grain set failure

Various methods have been used for the assessment of grain set failure or floret fertility in wheat. Some authors used the grain set index (GSI) to measure grain set in wheat (Rerkasem and Loneragan, 1994) and barley (Jamjod and Rerkasem, 1999). The GSI is defined as the percentage of grain bearing florets in the 2 basal florets of 10 central spikelets. Others measure grain set (fertility) (LAC method)

with the percentage of grain bearing florets in the total number of competent florets of the whole ear (Sthapit, 1988). These two measures are calculated as follows.

$$\text{a) GSI (\%)} = \frac{\text{Number of grains per F1+F2, of 10 central spikelets}}{20} \times 100$$

(Rerkasem and Loneragan, 1994)

where F1 and F2 are the first and second florets of a spikelet.

$$\text{b) Fertility (\%)} = \frac{\text{Number of grains per spike}}{\text{Number of competent florets per spike}} \times 100$$

(Sthapit, 1988)

In this study, the GSI (Rerkasem and Loneragan, 1994) is used. The author has proposed an indicator that should be sensitive to the specific failure of grain set and should therefore be responsive to boron deficiency, which induce wheat sterility. The GSI does not include basal those florets which may be infertile regardless of the B status, such as the terminal florets of each spikelet and those in the terminal and basal spikelets. By contrast, the LAC method always includes some of the naturally unproductive florets, and so gives higher estimates.

2.3 Boron efficiency

2.3.1 Definition

For every element examined, there are genotypic differences in nutrient efficiency arising from different adaptations to nutrient stress in plants. These have been exploited for increasing productivity in low nutrient soils (Dambroth and El Bassam, 1990). Differences in the yield or growth in low nutrient soils are usually described as genotypic differences in nutrient efficiency, and are the basis for selection of crop genotypes tolerant of low nutrient supply, or nutrient-efficient genotypes. Nutrient efficiency has been defined as the ability to produce a high plant yield in soils too deficient in one or more mineral nutrients for a standard cultivar, regardless of the underlying mechanism (Graham, 1984; Buso and Bliss, 1988). A standard cultivar is a sensitive traditional or commercial cultivar widely grown in a specific area. It is used as a benchmark for selecting a nutrient efficient cultivar imported from outside the area.

Nutrient efficiency can also be defined as the ability of plants to convert nutrient supply into desired output. In this definition, a "nutrient-efficient" genotype is one that better converts limited nutrient into high yield or relative growth than other genotypes, which by comparison are ' nutrient-inefficient' (Lynch, 1998). Nutrient efficiency can be further defined as the plant's ability to take up nutrients or acquire nutrients from the rhizosphere solution and/or utilize them in the production of total above and/or below ground plant biomass or utilizable plant material (seed, grain,

fruit, forage) (Blair, 1993). In the same way, B efficiency can be defined as the ability of plant genotypes to grow without any adverse effect in soil or other rooting media with a low level of B that is limiting to other genotypes (Rerkasem and Jamjod, 1997b) or the plant's ability for nutrient uptake and utilisation (Haneklaus and Schnug, 1993). In this study, the definition given by Rerkasem and Jamjod (1997b) is used.

2.3.2 Genotypic variation in B efficiency

Requirement for B and the degree of sensitivity to low B supply may explain much of the reported differences in response to B among plant species. Monocotyledons require less B than dicotyledons, and agricultural species of the Cruciferous and Umbelliferous familes in particular have high B requirements (Martens and Westermann, 1991). Plants that are commonly sensitive to low B soil include *Medicago sativa* (lucerne), *Brassica spp* (rape), *Beta vulgaris* (beet), celery *Apium graveolens* (celery), grape *Vitus vinifera* (grape), *Malus sylvestris* (apple), pear *Pyrus communis*(pear), *Gossypium hirsutum* (cotton) and sunflower (*Helianthus annuus*) (Jones, 1991). *Triticum aestivum* (wheat) (Rerkasem *et al.*, 1989; Li *et al.*, 1978) and *Hordeum vulgare* (barley) (Rerkasem and Jamjod, 1989) are cereals that have been reported to be adversely affected in low B soils, and among temperate pasture legumes, *Trifolium pratense* (red clover) is the most sensitive to low B, while the most tolerant is *Trifolium repens* (white clover) (Sherrell, 1983).

Large genotypic differences in B efficiency have been found within many crop species and Rerkasem and Jamjod (1997b) have highlighted the relevant literature in their recent review. Genotypic variation among cultivars has also been found in *Lycopersicon esculentum* (tomato) (Brown and Jones, 1971), *Beta vulgaris* (garden beet) (Walker *et al.*, 1945), cotton and sunflower (Agarwala *et al.*, 1984), in Sesame indicum (sesame) and *Brassica jundea* (mustard) (Sakal *et al.*, 1991), *Brassica napus* (oil seed rape) (Stangoulis *et al.*, 2000; Xue *et al.*, 1998) and *Lens culinaris* (lentil) (Srivastava *et al.*, 2000). Moreover, the range of B efficiency assigned to a particular crop species can differ according to the genotypes compared. For example, wheat (cv. Fang 60) is more efficient than green gram (cv. CMU 55) and barley (cv. BRB 2). In contrast, by changing the wheat to SW 41 cultivar, wheat becomes the most sensitive to B among a range of crop species (Rerkasem and Jamjod, 1997b).

Within a species, a wide range of genotypic variation in B efficiency has been demonstrated by screening large numbers of genotypes on low B soil. The range of sensitivity in relation to performance in B sufficiency varies with species, such as 9-41% for *Vigna mungo* (black gram), 34-100% for *Vigna radiata* (green gram) (Rerkasem, 1990), 11-71% for *Arachis hypogaea* (peanut) (Keerati- Kasikorn *et al.*, 1993), and 64-100% for wheat (Rerkasem and Jamjod, 1997b).

For wheat, the range of sensitivity in terms of grain set index (%) without added B can be as large as 0-100%. In addition, Rerkasem and Jamjod (1997b) have

found responses of genotypes to range from complete male sterility through those partially affected to no deficiency symptom. They classified the genotypes by the Grain Set Index (GSI) in sand culture without added B into five classes of efficiency namely very inefficient (0-20%), inefficient (21-50%), moderately inefficient (57-70 %), moderately efficient (71-85%) and efficient (> 85%).

2.3.3 Boron efficiency mechanism

Two primary mechanisms have been suggested for the genotypic differences in nutrient efficiency, (a) acquisition of the nutrient by the roots, and (b) utilization of the nutrient by the plant (Marschner, 1995).

Increase in B uptake is thought to be one mechanism underlying B efficiency. For example, Brown and Jones (1971) found that the B efficient Rutgers tomato was 15 times more efficient in absorbing B from the medium than a B inefficient genotype, T3238. At toxic B levels, genotypes of barley, wheat (Nable, 1988; Nable *et al.*, 1990), annual medics and pea (Nable, 1991; Paull *et al.*, 1992) have been found to differ in their ability to take up B. Nable (1988) and Nable *et al.* (1990) showed that barley and wheat genotypes that were more tolerant to B toxicity were also able to restrict B transport to the shoot. In oil seed rape, B efficient 92-13 took up more B than the B-inefficient 51 under low B supply (Yang *et al.*, 1993). Likewise, Sakal *et al.* (1991) screened six varieties of sesame and mustard under low B and suggested that efficiency in yield response was associated with increased B uptake. Rerkasem and Jamjod (1997b) have suggested that root geometry and rhizosphere effects are

two possible ways through which B uptake may contribute towards B efficiency. However, the topic has not yet been researched in any detail. Further, a greater uptake ability may explain the higher B concentration in certain species when growing in the same low B soil. For example, the higher tissue concentrations in dicotyledons (>20 mg B/kg) compared to monocotyledons (5-10 mg B kg^{-1}) has been associated with assumed greater uptake ability in dicotyledons (Gupta, 1979), and similarly among different genotypes in sunflower (Blamey *et al.*, 1979), oilseed rape (Yang *et al.*, 1993) and tomato (Brown and Jones, 1971).

Utilization efficiency is also related to the plant's B requirement, in particular the very large differences in internal B requirement between monocots and dicots (Bergmann, 1992). The lower B requirement for monocots was found to be associated with the low B concentrations in cell walls (Hu and Brown, 1994). Matoh *et al.* (1996) have shown that the internal B requirement is closely related to the pectin content in the cell wall, as mentioned earlier. It has been suggested that the differences in the internal B requirement among species or genotype may be predicted by the pectin content (Hu *et al.*, 1996). However, the relative B requirement between cultivars of celery, wheat and tomato was not related to the amount of B in cell wall pectin (Bellaloui and Brown, 1998). Chapman *et al.* (1997) have reported that the low B requirement for monocots such as wheat was associated with a low B absorption rate per unit root weight when compared to dicots such as pea.

Boron-efficient cultivars have often been found with higher B concentrations in their leaves, such as in the uppermost mature leaves of sunflower (Blamey *et al.*, 1979). Similarly, genotypes of black gram and green gram which were less sensitive to B deficiency had higher B concentrations in their youngest fully expanded leaves (Rerkasem., 1990). In oilseed rape, Yang *et al.*, (1993) also found that a B-efficient cultivar contained higher B concentration in the youngest open leaf under low B supply, as did others (Xue *et al.*, 1998; Luo, 1998). There are several possible mechanistic explanations for this. A genotype may be better at taking up B from the soil, as discussed earlier, or it may be better at utilising B within the plant.

An increased translocation of B from the root to the shoot may be associated with B efficiency. Under B deficiency, the B–efficient Rutgers tomato transported greater amounts of B from the root to the shoot than the B-inefficient T3238 cultivar (Brown and Jones, 1971). In celery, Pope and Munger (1953) reported differences between the B-efficient Summer Pascal and the B-inefficient S48-54-1, but did not suggest a mechanism for the difference. Under the same low external B condition, Summer Pascal produced significantly more dry matter than S48-54-1. This difference was shown to be due to a restriction in B translocation from the root to the shoot in the B-inefficient cultivar (Bellaloui and Brown, 1998).

Boron efficiency may be associated with an increased ability to recycle accumulated B into the growing point. Brown and Hu (1996) and Brown and Shelp, (1997) showed that B retranslocation was important to B efficiency in some species.

In cauliflower, an increase in B remobilisation in two cultivars was associated with their tolerance to B deficiency (Shelp and Shattuck, 1987). In broccoli, greater remobilization of B into the inflorescence was responsible for the avoidance of anatomical disorders in the inflorescence due to B deficiency in some cultivars (Shelp *et al.*, 1992). Moreover, Stangoulis et al. (2001) recently reported that greater B efficiency in oilseed rape cultivar Huashuang 2 was associated with the retranslocation of ^{10}B from old leaves whereas B-inefficient cultivars lacked this capacity.

For many species, the response to low B is associated with adverse effects of B deficiency on reproductive development. It is well known that B deficiency depresses grain set in cereals through male sterility, i.e. poorly developed anthers and pollen in cereals such as barley (Ambak and Tadano, 1991), *Zea mays* (maize) (Agrawala *et al.*, 1981) and wheat (Li *et al.*, 1978). This has been shown to be with a consequence of specific roles of B in reproduction, such as pollen germination in maize (Agrawala *et al.*, 1981) and pollen *development* in wheat (Rerkasem *et al.*, 1993; Dell and Huang, 1997; Dell *et al.*, 2002).

For wheat, B efficiency has been shown to be associated with the effect of B deficiency on male fertility. In low B soil, a B-efficient wheat genotype (Fang 60) had normal anthers and pollen and set grain normally, whereas a B-inefficient genotype (SW41) had poorly developed anthers and pollen and set only a few grains (Rerkasem *et al.*, 1997). In contrast, in the early vegetative response to B, measured

as the rate of elongation of the youngest emerged blade, in Fang 60 was more adversely affected by B deficiency than SW41 (Rerkasem *et al.*, 1993). This suggests that the mechanism of B efficiency in vegetative growth may be different than that for reproductive growth. It further suggests that the difference between reproductive responses in Fang 60 and SW41 may lie in the B supply, or the B demand or both, for the reproductive process.

Wheat anthers contain a high B concentration compared to other plant parts at flowering, and there is a close correlation between B concentration in the anthers to grain set failure and male sterility (Rerkasem *et al.*, 1997). The B requirement during the premeiotic interphase to the late tetrad stage is very sensitive to B deficiency (Huang *et al.*, 2000). On the other hand, Cheng and Rerkasem (1993) found no difference in pollen germination *in vitro* between the B-efficient Sonora 64 and the B-inefficient SW 41 under low B. The authors suggested that B efficiency may not be associated with the role of B in pollen germination and that the difference may be in the genotypes' capacity to produce viable pollen, and to supply B to the germinating pollen in the stigma and style. Thus, genotypic variation in B efficiency in wheat may primarily be associated with the effect of B deficiency on male gamete development.

Boron-inefficient and efficient wheat genotypes are not differentiated by the B concentration in their flag leaf (Rerkasem and Loneragan, 1994) or whole ear (Rerkasem and Lordkaew, 1992; Rerkasem *et al.*, 1997). To date, it is still unclear if B-efficient genotypes require less B for their anther and pollen development or they

are better at supplying B into the nontranspiring anthers. Rerkasem and Lordkaew (1996) showed that B deficiency decreased the B content in the anthers in B-inefficient SW 41. It is also possible that the dry matter accumulation in the chaff (lemmas and glumes) of the ear may act as a strong competing sink for B, against the anthers and carpel.

In conclusion, I postulate that B efficiency in wheat may be associated with the demand for B by the anthers, or the supply of B into the non-transpiring ear when enclosed inside the leaf sheath before ear emergence (Figure 2.4). Furthermore, internal competition for B between the male gametophyte, with their high B demand, and other sinks in the ear, may also play a role.

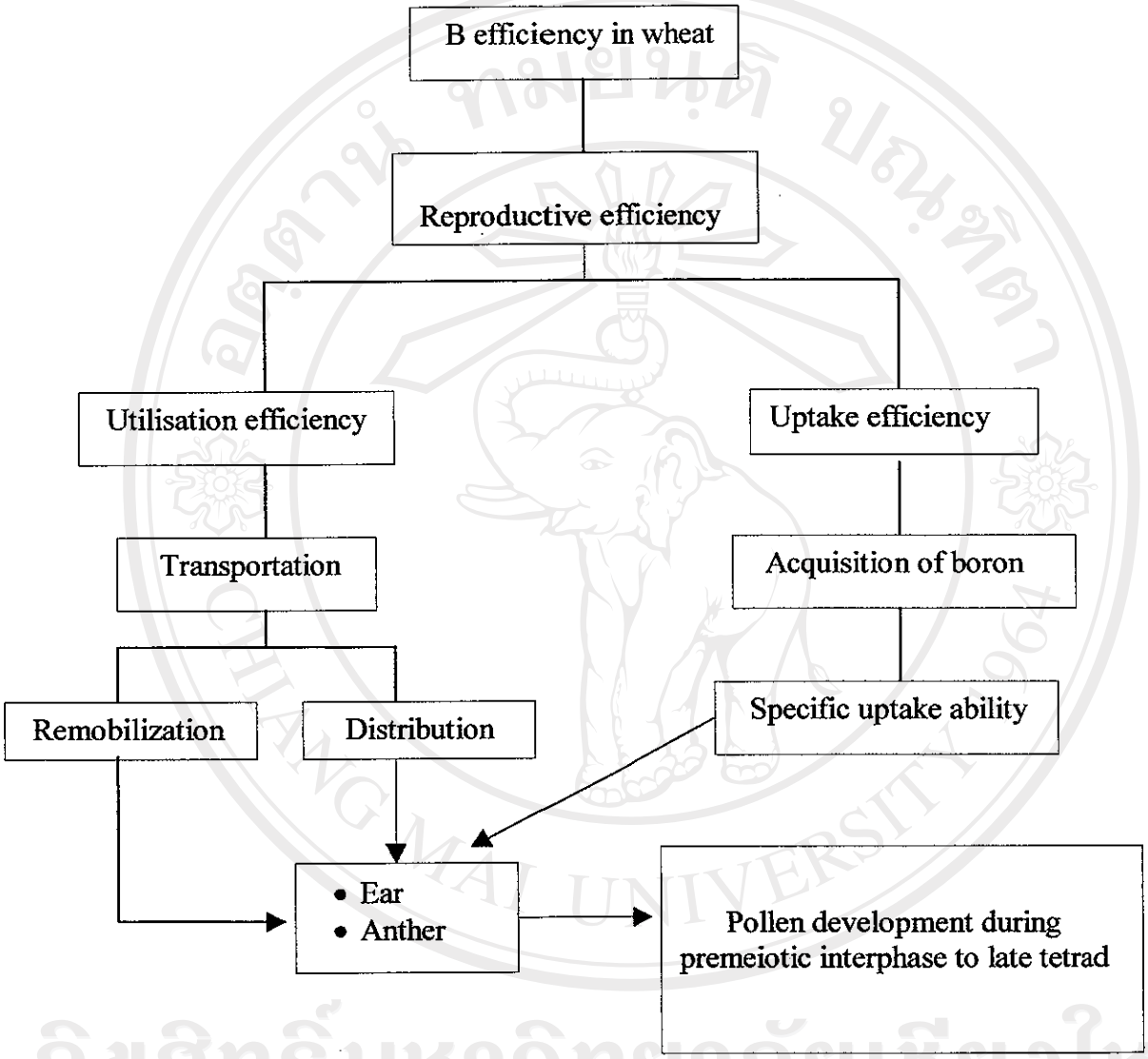

Figure 2.4 Possible mechanisms of genotypical differences in B efficiency in wheat.