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Chapter 12

Boron toxicity

Ross O. Nable[1], Gary S. Bañuelos[2] and Jeffrey G. Paull[3]
[1]*CSIRO Land and Water, P.M.B., P.O. Aitkenvale, QLD 4814, Australia*[*], [2]*Water Management Research Laboratory, USDA-ARS, 2021 S. Peach Av., CA 93727, USA and* [3]*Department of Plant Science, Waite Campus, University of Adelaide, Glen Osmond, SA 5064, Australia*

Abstract

Whilst of lesser prevalence than B deficient soils, B-rich soils are important, causing B toxicity in the field and decreased crop yields in different regions of the world. The highest naturally occurring concentrations of soil B are in soils derived from marine evaporites and marine argillaceous sediment. In addition, various anthropogenic sources of excess B may increase soil B to levels toxic for plants. The most important source is irrigation water, but others include wastes from surface mining, fly ash, and industrial chemicals. Ameliorating high-B soils is extremely difficult. A commonly used method of reclaiming high B soils is to extensively leach with low B water. Though used successfully, leaching may not be a permanent solution and causes difficulties with the disposal of the leachates. Other amelioration methods include the use of soil amendments (e.g. lime, gypsum) and the planting of plant genotypes that are tolerant of high external B concentrations. Although there are various methods available to determine the levels of B in soils, soil analysis can provide little more than a general risk assessment for B toxicity. Similarly, diagnosing B toxicity in plants, either by visible symptoms or tissue analysis has limited applicability. Thus at present, neither soil nor plant analysis can be recommended to precisely predict the growth of plants on high soil B. Recent physiological and genetic studies have provided some understanding of genetic variation in the response of plants to high concentrations of B. Moreover, these studies have facilitated the breeding of tolerant genotypes for cultivation on high B soils. Considerable genetic variation in response to high B has been identified in a wide range of plant species, most of which share a similar tolerance mechanism – reduced uptake of B in both shoots and roots. The tolerance mechanism appears to be under the control of several major additive genes, and specific chromosomal locations have been identified for the genes in some species. Considerable success has been achieved in breeding for tolerance to B toxicity, a process that is greatly aided by the ease with which genotypic variation for this characteristic can be assessed and the range of methods available to screen breeding populations.

Introduction

Boron toxicity is an important disorder that can limit plant growth on soils of arid and semi arid environments throughout the world. High concentrations of B may occur naturally in the soil or in groundwater, or be added to the soil from mining, fertilisers, or irrigation water. Although of considerable agronomic importance, our understanding of B toxicity is rather fragmented and limited. The present paper attempts to review the available literature on a broad range of topics, from the occurrence and detection of B toxic soils, to the effects of high B on plants, through to the management of B toxicity. It differs from earlier reviews on B toxicity (e.g. Gupta et al. 1985; Leyshon and Jame, 1993) by exploring in detail the physiology and genetypic variation for tolerance to B toxicity and how this variation can be utilised to maximise plant growth on high B soils.

Formation and distribution of boron laden soils

Sources of boron

Boron, the only non-metal among the elements of Group III in the periodic table, is not uniformly distributed in the earth's crust. The primary sources of

* E-mail: Ross.Nable@tvl.clw.csiro.au

B in most soils are tourmaline and the volatile emanations of volcanoes (Chesworth, 1991). Tourmaline from high temperature rocks is very resistant to chemical breakdown in the weathering zone and thus accumulates in the clastic fraction of sediments and sedimentary rocks. In igneous, metamorphic, sedimentary rocks, B occurs as borosilicates, which are resistant to weathering and not readily available to plants. Mobilisation of immobile forms of rock B occurs by weathering in the pedosphere, which includes soil reactions of acid-base, oxidation-reduction, and dissolution-precipitation. The dominant species in the soil when B from primary silicates goes into solution is $B(OH)_3$ (boric acid). This form of B is mobile and easily lost by leaching. In soils, this form of B can be taken up by vegetation, held by organic matter, or temporarily adsorbed on fine mineral fractions.

Distribution of naturally occurring high B soils

Soil is generally the primary source of trace elements for plants. However, there are exceptions in which toxic concentrations of trace elements in plants, e.g. B, can be traced directly to water from certain wells, or indirectly to land application of drainage water, and in soils with high B availability (Kubata, 1980). However, the adsorbed and solution phases of B in the soil influence potential B toxicity effects observed in the field (Cartwright et al., 1984; Shani and Hanks, 1993); and sometimes lead to decreases in crop yields grown in different regions of the world (Cartwright et al., 1986). There are few B rich soils compared to B deficient soils. Areas where high soil B are found include dry lands of South Australia (Cartwright et al., 1984, 1986), the Middle East (Ravikovitch et al., 1961), the west coast of Malaysia (Shorrocks, 1964), valleys along the southern coast of Peru (Masson, 1967), the Andes foothills in northern Chile (Caceres et al., 1992), solonchaks and solonetz soils of USSR (Zyrin and Zborishchuk, 1975), ferralsols of India (Takkar, 1982), rendzinas in Israel (Ravikovitch et al., 1961), and major $B_2O_2^{-7}$ deposits at Searles, Lake California (Chesworth, 1991). The highest concentrations of soil B are often concentrated in marine evaporites and in marine argillaceous sediment (Erd, 1980).

Activities contributing to boron laden soils

Irrigation water

Of all the potential sources, irrigation water is the most important contributor to high levels of soil B (Chauhan and Power, 1978; Table 1). Boron is often found in high concentrations in association with saline soils and saline well water (Dhankhar and Dahiya, 1980). In assessing the potential toxicity of B laden irrigation water, the physical and chemical characteristics of the soil must be considered (Goldberg, 1993). Sorption capacity of a given soil is crucial in determining the amount of B in solution. A soil that has high adsorption capacity would be expected to maintain lower soil solution B over a longer period of time than a soil with low adsorption capacity when both soils are irrigated with the same B laden water.

Soil adsorption sites may act as a pool from which B is supplied to solution or where B is adsorbed, depending on the changes in solution B concentrations and the affinity of soil for B. Thus, adsorbed B may buffer B concentration in soil solution (Keren and Bingham, 1985). The complex B sorption characteristics of a soil explain frequent observations that plant injury occurs more quickly on coarse textured soils than on fine textured soils when B laden water is used for irrigation. As the key to the assessment of B toxicity is the plant response to B in soil, it is the B concentration of the soil solution under field conditions that must be evaluated in relating soil B to plant response (Ryan et al., 1977). Moreover, water with high B levels can be used to irrigate B sensitive crops on soils that show a high affinity for B adsorption because large amounts of B in irrigation water will be adsorbed by the soil. Referring to Keren and Bingham (1985), safe concentrations of B in irrigation water range from 0.3 mg B L^{-1} for sensitive plants [i.e. avocado (*Persea americana*), apple (*Malus domestica*) and bean **(***Phaseolus vulgaris***)**], 1–2 mg B L^{-1} for semi tolerant plants [oat (*Avena sativa*), maize (*Zea mays*), potato (*Solanum tuberosum*)], and 2–4 mg B L^{-1} for tolerant plants [i.e. carrot (*Daucus carota*), alfalfa (*Medicago sativum*) and sugar beet (*Beta vulgaris*)]. Eventually, continued irrigation with B laden water will exceed the adsorption capacity of the soil and cause a possible reduction in crop yield (Jame et al., 1982). The level of B in solution that can be tolerated by the crop is the key information in determining criteria for allowable B concentration in irrigation water. The B concentration determined in a soil saturation extract (Bingham, 1973) is still used for

Table 1. Mean levels of tissue boron in different plant species irrigated with B laden water or grown in high B soil under field conditions

Species	B concentration in irrigation water (mg L^{-1})	Soil total extract (mg kg^{-1})	B concentration in shoots (mg B kg^{-1} dry wt)	References
Fourwing saltbush (*Atriplex canescens*)	5–10	N/A	126[1]	Watson et al. (1994)
Wavy leaf saltbush (*Atriplex undulata*)	5–10	N/A	131[1]	Watson et al. (1994)
Desert saltbush (*Atriplex deserticola*)	5–10	N/A	121[1]	Watson et al. (1994)
Old man saltbush (*Atriplex nummularia*)	5–10	N/A	142[1]	Watson et al. (1994)
Cattle saltbush (*Atriplex polycarpa*)	5–10	N/A	135[1]	Watson et al. (1994)
Alfalfa (*Medicago sativa*)	N/A	14	158	Nicholaichuk et al. (1988)
Tall fescue (*Festuca arundinacea*)	N/A	405	120[1]	Bañuelos et al. (1995)
Indian mustard (*Brassica juncea*)	N/A	535	224[2]	Bañuelos et al. (1993a)
Hibiscus cannibinus (*Hibiscus cannibinus*)	N/A	465	685	Bañuelos et al. (1993a)
Cotton (*Gossypium hirsutum*)	5	N/A	1110[3]	Ayars et al. (1990, 1994)
Wheat (*Triticum aestivum*)	5	N/A	701[3]	Ayars et al. (1990, 1994)
Silver beet (*Beta vulgaris*)	5	N/A	1043[3]	Ayars et al. (1990, 1994)
Tomato (*Lycopersicon esculentum*)	8	N/A	277[4]	Shennan et al. (1995)

[1]Mean value from multiple harvests in three years.
[2]Mean value from two plantings in two years.
[3]Mean leaf values from multiple years.
[4]Mean leaf values from two years of application.
N/A – not applicable.

defining B guidelines for plants exposed to B. If the leaching fraction or B adsorption capacity of the soil is not taking into consideration, there is doubt over the use of soil extractable B as the sole parameter to evaluate B concentrations in irrigation water.

Generally, plant uptake of B from irrigation water containing B is relatively small. Thus B will accumulate in soil irrigated with B laden water, as seen in the following example. Fifty kilograms of B would be deposited to soil after applying 100 cm of B laden water with a concentration of 5 mg B L^{-1}. Assuming a dry matter yield of 10,000 kg ha^{-1} (i.e. alfalfa) that had a tissue B concentration of 200 mg B kg^{-1} dry wt, a total of 2 kg B would be removed by plant accumulation. Irrigation water containing this level of B may not be immediately toxic to plants, but after prolonged irrigation with such water, soluble soil B levels will equal or exceed those of the irrigation water, especially in regions of low rainfall or where water used for leaching is unavailable. When such accumulation has occurred, plants sensitive to B (Francois and Clark, 1979; Maas, 1987;) will perish or plants more tolerant to B will have to be grown, or the soil must be reclaimed (Jame et al., 1982).

Surface mining

Surface mining often produces waste carbonaceous materials that can be a B source. Carbonaceous shales,

coal lenses, leonardite, and coal stack are dominated by inert organic matter that often contains high B (Barth et al., 1987). Oxidation of these materials through mining processes can result in gradual release of substantial quantities of water soluble B. Total B concentrations are reported to be as high as 96 mg kg^{-1} soil in topsoil of western cool regions (Severson and Tidball, 1979), while hot water soluble B concentrations are as high as 26 mg L^{-1} in western mine soil spoil (Severson and Gough, 1983). Proposed maximum permissible levels of hot water soluble B is 8 mg kg^{-1} in mine soils in Montana, USA (Severson and Gough, 1983). Levels greater than 5 mg kg^{-1} may be considered toxic for plants (Ponnamperuma et al., 1979).

Fly ash

Fly ash is generated by electric power plants in increasing quantities because of increased use of coal for electricity production. Its use as an ameliorant on agricultural land to improve physical and chemical properties as well as its potential toxic effects have been studied (Carlson and Adriano, 1993; Pichtel et al., 1994). Contamination of land by residues of fossil fuel combustion (i.e. fly ash) can lead to high soil B concentrations (Adriano, 1986), especially if the B in fly ash is soluble and applied at a high rate to increase soil pH, i.e. 5–10% by wt (Eary et al., 1990; Kukier and Sumner, 1996). In one field study, fly ash was applied at a dry wt rate of 10% on a typical site in northern Britain with dry bulk density of 1.66 g cm^{-3} and a pH of 3.5 (Perkins, 1996). The concentrations of B in fly ash is of concern because large fractions of B in fly ash may be readily available to plants and may prevent the establishment of vegetation on soils containing fly ash (Elseewi et al., 1980b; James et al., 1982; Kukier et al., 1994; Piha et al., 1995), especially in the first growing season (Wong et al., 1996). Any general conclusions, however, have to be made with caution due to the enormous variability in fly ash chemical composition and differences in the physicochemical properties of amended soils (Eary et al., 1990; Mattigod et al., 1990). Boron concentrations of 700 mg $kg^{-1}$are often reported (James et al., 1982). The predominant forms of B in fly ash are probably soluble borates and less soluble borosilicates (James et al., 1982). Alkaline conditions decrease B solubility in fly ash, while neutral and acid reactions promote its solubility and release into solution (Elseewi et al., 1980a).

Industrial application

Boric acid and borate minerals are widely utilised in a number of industrial applications such as glass and porcelain manufacture, leather production, carpets, photographic chemicals, and fertilisers. The main application of B is, however, the use of sodium perborate as an oxidation bleaching agent in domestic and industrial cleaning products. The discharge of sodium perborate into the environment during production and end use of detergents has resulted in the accumulation of B in waste effluent and consequently in groundwater and natural aquatic systems (Vengosh et al., 1994).

Amelioration of boron laden soils

Leaching

When the amount of B added to the soil in irrigation water is greater than the amount of B removed by plant uptake and leaching, there will be a build up of B in the root zone (Ayars et al., 1994). Before soils containing high levels of B can be successfully used for agriculture, either their soluble B contents must be reduced to non-phytotoxic levels for the proposed crop or a tolerant genotype used. A commonly used method of reclaiming high B soils is to extensively leach with water (Prather, 1977; Leyshon and Jame, 1993). Applying water in excess of a plants water requirement is generally referred to as the leaching fraction (Hoffman, 1990). For efficient and continued crop production, the leaching fraction must be high enough to remove excess B but low enough to prevent loss of essential plant nutrients from the soil, especially from sandy acidic soils. The quantity of water necessary to leach B to a particular depth varies widely. If a low leaching fraction is used, the resultant soil B concentration near the soil surface will be close to those of the irrigation water and those near the bottom of the root zone will presumably be much higher. Much depends upon the original soil B concentration, the desired final B concentration, and the physical and chemical characteristics of the soil. Applying excessive water to leach B under field conditions is an old practice that is still suggested for reclaiming high B soils to satisfactory levels (Shennan et al., 1995; U.S. Salinity Lab. Staff, 1954). Recent field studies with irrigation water high in B have concluded that longer intervals of good quality water and/or intermittent ponding are necessary to remove B from the root

zone (Ayars et al., 1994; Shennan et al., 1995). If an attempt is made to reduce the B level in the soil solution by leaching with low B water, a portion of the absorbed B will go into solution. Therefore, it is expected that the rate of removal by leaching will be much slower for B than for other non-absorbed elements in the soil. In this regard, studies on the kinetics of B release would be valuable in elucidating mechanisms for B desorption from soil surfaces. It is important to note that native soil B may be less soluble and more difficult to leach than B accumulated from previous irrigations (Peryea et al., 1985). However, the reduction in soluble B following leaching may not be permanent. Boron can be regenerated through the mineralisation of B from the soil organic matter, or through weathering processes of soil minerals (Peryea et al., 1985). The ability of the soil to regenerate B diminishes with each leaching, indicating a finite concentration of reclaimable B.

Soil amendments

Besides leaching with water, amendments have been used to detoxify B laden soils. As B adsorption by soils is pH dependent (Keren and Bingham, 1985), liming some soils to increase the pH and thus promote adsorption of B from soil solution may provide a short term solution (Bartlett and Picarelli, 1973). In sodic soils, the B hazard can be ameliorated by the addition of gypsum, which improves water infiltration and converts readily soluble Na-metaborate to less soluble Ca-metaborate (Bhumbla and Ckhabra, 1982). Heavy applications of $Ca(H_2PO_4)_2$ also lower plant available B, especially in acid soils. Prather (1977) reported that sulphuric acid may effectively aid in reclaiming B laden soils. Although decreasing soil pH by the addition of sulphuric acid increases the concentration of water soluble B in the soils, readsorption of B occurs with time.

The placement of soil containing low concentrations of B with materials containing excessive B, such as carbonaceous spoil, may limit both upward and downward migration of B. Such placement depends upon the use of the site, depth of water penetration, patterns of ground water movement, topography, physical, and chemical traits of surrounding soil, and organic materials. Cover depths with soil low in B for material containing soluble and mobile B have yet to be established with any precision. Some field research has indicated that 50–70 cm of soil over most spoil types is probably adequate (Barth, 1984; Barth et al., 1987). Unpublished results by Ajwa and Bañuelos have provided some insight with the planting of B tolerant plant species, e.g. saltbush (*Atriplex*), and covering high B containing soil ($>$ 400 mg B kg^{-1} soil) with 47 cm of soil containing low B. They observed that B migrates towards the soil surface with water evaporation. Overburden only delayed B toxicity symptoms from appearing in the planted saltbush.

Under some circumstances it may be possible to alleviate B toxicity in plants by applying Zn to soils or as a foliar spray to affected plants. Graham et al. (1986) and Swietlik (1995) showed in controlled solution culture experiments with barley (*Hordeum vulgare*) and orange (*Citrus aurantium*), respectively, under conditions of Zn deficiency, excess B can be accumulated by plants and B toxicity develop, even though the levels of B in the medium do not result in B toxicity when ample Zn is supplied. To what extent this interaction occurs under field conditions remains to be shown. But as soils with low Zn and high B are encountered in some alkaline soils of semiarid regions, the possibility that B toxicity results from underlying Zn deficiency should be borne in mind.

Vegetation management

The planting of B tolerant species may be a means to revegetate soils containing elevated levels of soluble B and manage the movement of soluble B by plant uptake. However, limited information exists on how to utilise the ability of plants to take up and accumulate B as part of the revegetation strategy. Using both vegetation and water management as critical components for managing soil B has been suggested as an alternative to physically taking high B soils out of crop production (Bañuelos et al., 1993b). In a multiple year field study, Bañuelos et al. (1995) revegetated high B soil in central California and maintained the level of soluble soil B to a non-toxic level for the planted species. Some potential plant species that can be grown on high B soils are: saltbush (Watson et al., 1994), milkvetch (*Astragalus*) (Parker et al., 1991), barley (Nable, 1990a), wheat (Paull et al., 1988a), Indian mustard (*Brassica juncea*) (Bañuelos et al., 1993a), tall fescue (*Festuca arundinacea*) (Bañuelos et al., 1995), and some tree species (El-Motaium et al., 1994; Francois and Clark, 1979). Recent advances in genetic engineering are increasing the potential for breeding B tolerant plant species. Until more information is available, however, selection of B tolerant species will be dominated by trial and error experimentation. An alternative approach may be to

Table 2. Extraction methods used to assess available boron in soils

Method	Comments of referenced authors	Reference
Reflux 1:2 soil–water	Good for assessing plant available B.	Berger and Truog (1940)
Hot water soluble	Widely used; good prediction of deficient levels; site specific and no indication of B released from soil.	Bingham (1982)
Saturation extract	Comparable with solution B; B tolerance for plants based on this test, only a portion of absorbed B goes into solution; must be related to field moisture conditions.	U.S. Salinity Lab. Staff (1954), Gupta et al. (1985)
$CaCl_2$	Good for non-specifically absorbed B on soil surface at a variety of pH; indicates plant available B; similar to hot water extraction; estimates quantity factor, but not B released from soil.	Aitken and McCallum (1988); Iyenger et al. (1981); Spouncer et al. (1992)
Mannitol exchangeable B	Estimates leachable B, includes non-specifically and specifically absorbed forms; assesses regenerative power of soil for B.	Rhoades et al. (1970)
Acidified NH_2 HCl	Good for separating Mn minerals from Fe minerals; poor correlation with plant levels for calcareous soils.	Chao (1972); Cox and Kamprath (1977)
NH_4oxalate (pH 3.75)	Solubilises both crystalline and non-crystalline oxyhydroxides from soils; poor correlation to plant uptake of B.	DeEndredy (1963); Schwertmann (1964)
NH_4/DPTA	Used to determine availability of many nutrient elements in one extract.	Handreck (1990)

identify plants naturally occurring in soils high in B and utilise these for managing other high B soils.

Diagnosis of boron toxicity in soils and plants

Soil analysis

Soil sampling and analysis should identify soil horizons with excessive B. For a number of years, researchers believed that soils containing more than 5 mg L^{-1} of hot water soluble B were unsuitable for growing crops based on the response of agronomic crops to B. However, this value is not an accurate reflection of the plant species and growing conditions in arid and semi arid reclamation situations. Many native species are well adapted to B levels in excess of 5 mg L^{-1}. The plant available fraction is the best indicator for evaluating a soil's potential for inducing B toxicity in plant species. However, the form of B in soils will greatly affect its availability to plants (Fleming, 1980; Keren and Bingham, 1985; Leyshon and Jame, 1993). Generally, total B concentration is a poor indicator of plant available B. Plant available B in a specific soil is controlled by the soil's physical and chemical properties, such as pH, soil texture, clay mineralogy, organic matter, etc. (Goldberg, 1993). As these properties vary between soils, specific extraction techniques are not always reliable in predicting plant available B (Parker and Gardner, 1981; Su et al., 1994). Certain extraction reagents can specifically attack specific soil components and release different fractions of B (Table 2). In one study, 7 to 10 mg L^{-1} of B extracted with ammonium acetate reduced yields in pines (*Pinus*) by only 10% (Smidt and Whitton, 1975), while 35 mg B L^{-1} in a saturated paste extract did not significantly reduce yields (Schuman, 1969). Basin wild rye (*Leymus cinereus*) tolerates 37 mg B L^{-1} extracted from a water saturated fraction before yields are reduced by 50% (Roundy, 1985). While present knowledge is insufficient to define precisely the acceptable B levels in a growth medium, soil containing more than 5 to 8 mg B L^{-1} of hot water soluble B may require special revegetation considerations. Extraction methods that evaluate plant available B at one point in time will be different from methods that evaluate the capacity

of a soil to supply B. It is also difficult to predict the B concentration of the soil solution within the root zone before a complete equilibrium is attained due to the complex B adsorption/desorption and precipitation/dissolution reactions in soil (Goldberg, 1993). Equilibrium is especially important in potentially B toxic soils that have been created by the use of high B water for irrigation. In this regard, Maas (1987) has provided a comprehensive summary of B tolerance based on plant response to B in soil solution. Although there are various methods available to determine the levels of B in soils, it seems that soil analysis can provide little more than a general risk assessment for B toxicity. It is very difficult to utilise soil analysis to precisely predict the growth of plants on high B soils.

Visible symptoms of boron toxicity in plants

Amongst a wide variety of plant species, the typical visible symptom of B toxicity is leaf burn – chlorotic and/or necrotic patches, often at the margins and tips of older leaves (Bennett, 1993; Bergmann, 1992; Eaton, 1944). These symptoms reflect the distribution of B in most species, with B accumulating at the end of the transpiration stream (Chapter 7). The chlorotic/necrotic patches have greatly elevated B concentrations compared with the surrounding leaf tissues (Oertli and Roth, 1969) and some species (e.g. barley) show characteristic patterns for different genotypes.

Contrary to the general perception, leaf burn is not the visible symptom of B toxicity in all species. In species in which B is phloem mobile (e.g. *Prunus, Malus, Pyrus*), in which B accumulates in developing sinks rather than at the end of the transpiration stream (Chapter 7), the symptoms of toxicity are fruit disorders (gummy nuts, internal necrosis), bark necrosis which appears to be due to death of the cambial tissues, and stem die back (Brown and Hu, 1996).

Visible symptoms of B toxicity do not appear to develop in roots. As B concentrations in the roots remain relatively low compared to those in leaves, even at very high levels of B supply (Nable, 1988; Oertli and Roth, 1969), perhaps toxic concentrations do not occur in root tissues. In young squash plants (*Cucurbita pepo*), an early effect of developing B toxicity is decreased chlorophyll concentrations, followed by reduced growth, loss of leaf area and decreased CO_2 fixation; all of these effects occurring well before the development of visible toxicity symptoms (Lovatt and Bates, 1984). There may also be an inhibition of ureide metabolism in the leaves of nodulated soybean (*Glycine max*) (Lukaszewski et al., 1992), and complexing of ribonucleotides which causes metabolic disturbances (Loomis and Durst, 1992). Leaf cupping, a specific visible symptom of B toxicity in some species, has been suggested to result from inhibition of cell wall expansion, through disturbance of cell wall crosslinks (Loomis and Durst, 1992).

Plant analysis

Whilst critical values for B toxicity have been established in many crop and tree species (Gupta, 1993; Table 1), there are serious problems with the use of foliar analysis for diagnosing B toxicity. In species that accumulate B in their leaves, these tissues normally contain about 40 mg to 100 mg of B kg^{-1} dry wt. However, the leaves can contain 250 mg kg^{-1} dry wt when B in the soil approaches toxic levels. Leaf concentrations of B may exceed 700 to 1000 mg kg^{-1} dry wt in extreme conditions of B toxicity. What is of particular concern is that there is an unacceptably wide range of critical values for B toxicity, sometimes even for the same species. In wheat and barley, for example, critical values range from 10 to 130 mg B kg^{-1} dry wt (Gupta, 1977; Gupta et al., 1976; Kluge and Podlesak, 1985; Paull et al., 1988a; Riley et al., 1994). The cause of the problem stems from the steep gradient of B within leaf blades, with B accumulating in tips and margins (Nable et al., 1990c; Oertli, 1994), and how this gradient is affected by environmental conditions. Depending upon the levels of transpiration, for example, leaf blades have been shown to accumulate vastly different amounts of B in their leaves, though mostly concentrated at the tips and in the margins, with the majority of the leaf blades having similar concentrations. Under these different transpiration conditions, the overall leaf B concentrations are very different, though the effect on growth can be the same (Nable et al., 1990c). Accordingly, experimental conditions lead to different critical levels for B toxicity being established, with those derived from glasshouse experiments being considerably higher, in general, than those from field experiments. Furthermore, as B is readily leached from leaves by rain (Nable and Moody, 1992), there is another reason why foliar analysis of field grown plants should be interpreted with caution.

As suggested by Shorrocks (1995), "it is perhaps preferable to think of B analysis as a relatively crude tool, and accept its limitations", rather than trying to use leaf analysis as a tool for the precise prediction of B

toxicity. There seems considerable merit in his proposal to compare B concentrations in healthy regions of leaves with those in necrotic/chlorotic regions. If there is a large gradient between these regions then it is very likely that B toxicity is the causal agent, not other factors such as climate or pathogens. Such an approach could be very informative in species that accumulate B in their leaves.

As it has only recently been demonstrated that B is phloem mobile in some species (Chapter 7), and that B does not accumulate in leaves under conditions of B toxicity, there is not much information available yet on diagnosing B toxicity in these species. From what is available it appears that in species such as peach (*Prunus persica*), *Prunus*, pear, and almond, that fruit, buds, hulls and young stems are much better indicators of B toxicity than leaves (P H Brown, pers. comm.). Boron concentrations greater than 300 mg kg^{-1} dry wt indicate that B toxicity may be present.

Plant tolerance to boron toxicity

Genetic variation in response to high levels of boron

Genetic variation in response to high concentrations of B occurs at both the inter- and intra-specific levels. There have been many investigations on interspecific variation in response to B, with each species or genus represented by a single variety, for example, Eaton (1935, 1944), Francois and Clark (1979), Haas (1929), Oertli and Kohl (1961) and Purvis and Hanna (1938). All of these investigations identified a wide range in response to B, either on the basis of plant growth, the development of symptoms of B toxicity, or both. The range in variation was often such that the most tolerant entries were unaffected at treatments that killed the most sensitive entries.

More recent investigations have demonstrated a wide range of intra specific variation in response to B occurs in a number of crops, including bread wheat (*Triticum aestivum*) (Chatterjee et al., 1980; Mehrotra et al., 1980; Paull et al., 1988a), durum wheat (*Triticum turgidum* var. *durum*) (Brooks, 1991; Jamjod, 1996; Yau et al., 1995), barley (Christensen, 1934; Nable, 1988), rice (*Oryza sativa*) (Cayton, 1985, Paliwal and Mehta, 1973; Ponnamperuma et al., 1979), peas (*Pisum sativum*) (Bagheri et al., 1992; Materne, 1989), annual medics (Paull et al., 1992b), citrus (*Citrus* spp.) (Chapman and Vanselow, 1955; Haas, 1945), pecan (*Carya illinoensis*) (Picchioni and Miyamoto, 1991) and strawberry (*Fragaria ananassa*) (Blatt, 1976). Thus, the classification of each species in many of the earlier studies will be dependent on the variety tested.

Tolerance to B toxicity not only operates at the level of whole plants, it also operates at the organ and cellular level. Differences amongst wheat genotypes in susceptibility to B toxicity, expressed in whole plants, is also expressed at the organ and cellular level (Huang and Graham, 1990). In root cultures, genotypes classified as susceptible from field and glasshouse experiments produce shorter root axes and less lateral roots than tolerant genotypes in media with high B concentrations. Similarly, susceptible genotypes produce less callus than tolerant genotypes.

Following the identification of B toxicity in southern Australia (Cartwright et al., 1984, 1986), several germplasm collections were screened for response to B under a single B treatment, following the method of Moody et al. (1988), to determine the extent of variation within Australian varieties and to identify accessions that could be used in breeding more tolerant varieties (Table 3). In all cases a large variation in symptom expression and plant vigour was identified, including accessions more tolerant than all Australian varieties. Further studies, including a range of B treatments, confirmed the variation for all crops to be due to differential response to B (Bagheri et al., 1992; Jamjod et al., 1997; Nable, 1988; Paull et al., 1988a, 1992a, 1992b).

Tolerant genotypes of a number of crops originated from similar regions. In general, these correspond to where high concentrations have been reported in the soil or ground water, or symptoms of B toxicity have been observed on crops. This indicates that B has exerted a selective pressure on the crops and it is probable that tolerance of B would occur in other crops with centres of diversity in these regions. A high frequency of B tolerant bread wheat (Moody et al., 1988) and durum wheat (Jamjod, 1996) originate from the eastern Mediterranean, western Asia/north Africa (WANA), the Indian subcontinent, China, Japan and South America. While B tolerant medics (Paull et al., 1992a) and peas (Bagheri et al., 1994) originate from the eastern Mediterranean, WANA and the Indian subcontinent.

Genetics of differential tolerance to boron toxicity

The genetic control of tolerance to high concentrations of B has been investigated for several species to enable efficient strategies for breeding of B tolerant varieties

Table 3. Crops in which germplasm collections have been screened for response to B. The% tolerant accessions refers to the frequency of lines more tolerant than all Australian varieties of that crop

Crop	Species	Genotypes tested	% tolerant	References
Wheat	*Triticum aestivum*	1576	6	Moody et al. (1988)
Durum wheat	*Triticum turgidum* var. *durum*	300	2	Jamjod (1996)
Barley	*Hordeum vulgare*	>1500		Boyd, pers. comm.
		350		Jenkin (1993)
Pea	*Pisum sativum*	135	2	Paull et al. (1992b)
		617	4	Bagheri et al. (1994)
Medics	*Medicago* spp.	681	2	Paull et al. (1992b)

to be adopted. Boron tolerance of bread wheat (Paull et al., 1991a), durum wheat (Jamjod, 1996), barley (Jenkin, 1993) and field pea (*Pisum sativum*) (Bagheri et al., 1996) is controlled by partially dominant nuclear genes. However, the degree of dominance expressed by an F1 hybrid varies according to the B treatment. At low B treatments (i.e. near the threshold treatment for the tolerant parent) F1 hybrids respond in a similar manner to the tolerant parent, while at high B treatments they tend towards the sensitive parent (Jamjod, 1996; Jenkin, 1993; Paull et al., 1991a). Thus the most appropriate boron treatment for screening segregating populations will depend on the genetic composition of the test population. For example, a higher treatment would be appropriate for identifying homozygous tolerant plants in an F2 population than for identifying heterozygous plants during backcrossing where an excessively high treatment would result in the heterozygous plants being phenotypically similar to the more sensitive parent.

Studies of F2 and F3 populations of bread (Paull et al., 1991a) and durum (Jamjod, 1996) wheat, barley (Jenkin, 1993) and peas (Bagheri et al., 1996) have all identified major genes conferring tolerance to B. Several independent but additive genes occur in each species. Despite being similar phenotypically, tolerant lines of both bread and durum wheat might differ genetically with respect to tolerance to B (Chantachume, 1995; Jamjod, 1996; Paull et al., 1991a). Transgressive segregation occurred among the progeny derived from crosses between these tolerant genotypes and included lines more tolerant and more sensitive than both parents. Thus, by understanding the genetic relationships among moderately tolerant and tolerant accessions it is possible to develop lines with a greater level of B tolerance than that available in a germplasm collection.

Genes conferring tolerance to B have been located to chromosomes of cereals by several methods, including intervarietal substitution lines, interspecific substitution and addition lines and monosomic analysis, and linkage has been established between some genes conferring tolerance to B and other loci. In particular, chromosome 4A and chromosomes of homologous group 7 have been implicated in response to B. Chromosome 4A of the Chinese Spring/Kenya Farmer and Chinese Spring/Sapporo intervarietal substitution line series has a major effect on response to B, with both substitution lines being more sensitive than Chinese Spring (Paull et al., 1988b, 1995). Evaluation of the progeny of CS×CS(KF4A) indicated that the bo3 gene is linked to the stem rust resistance gene Sr7a of Kenya Farmer, located on the long arm of chromosome 4A (Paull et al., 1995). Further evidence of the significant effect of chromosome 4A on response to B was provided by backcross reciprocal monosomic analysis (Snape and Law, 1980), with the tolerant lines G61450 (from Greece), Benventuto Inca (Argentina) and India 126 (India) crossed to the Condor (moderately sensitive) monosomic series (Chantachume, 1995; Chantachume et al., 1994). Progeny containing chromosome 4A derived from the tolerant lines were significantly more tolerant than progeny with chromosome 4A of Condor. In addition, an RFLP marker, XksuG10 (Gill et al., 1991) located on chromosome 4A, was identified as linked to a B response gene by QTL analysis of F7 lines of G61450×Kenya Farmer (very sensitive) (Paull et al., 1995). Monosomic analysis has demonstrated the Bo1 gene of bread wheat (Chantachume, 1995; Chantachume et al., 1994) and BoT1 and BoT2 genes of durum wheat (Jamjod, 1996) are located on chromosome 7B.

Wild species are a potential source of genes for related cultivated crops, and a number of members of

Triticeae and aneuploid stocks of wheat including chromosomes of these related species have been evaluated for response to B. Tall wheatgrass (*Agropyron elongatum*) is tolerant to B (Schuman, 1969) and its tolerance is expressed in the amphiploid with bread wheat. However, the amphiploid is not significantly more tolerant than the most tolerant bread wheats (Paull et al., 1991b, 1992b). The chromosome 7E addition line is more tolerant than Chinese Spring (Paull et al., 1992a) and this is further evidence of the significance of the chromosomes of homologous group 7 in controlling response to B. Chromosomes of homologous group 5 have also been shown to have a significant effect on response of cereals to B (Manyowa and Miller, 1991). The Chinese Spring/"alien" addition lines including chromosomes 5R of Imperial rye and 5S1 of Aegilops sharonensis were significantly more tolerant then Chinese Spring.

Physiology of tolerance to boron toxicity

Exclusion mechanisms

An examination of tolerance to B toxicity amongst diverse plants species reveals that the B concentration in leaves and shoots are usually not closely related to B tolerance. However, in more closely related species, genotypes susceptible to B toxicity generally have higher concentrations of B in leaves and shoots than do tolerant genotypes (Eaton, 1944; Francois and Clark, 1979). For example: *Helianthus tuberosus* (Jerusalem artichoke) has higher concentrations of B in its leaves than the more B tolerant *Helianthus annuus* (sunflower); *Citrus limonin* (lemon), accumulates more B in its leaves than its B tolerant relative *Severina buxifolia* (Chinese box orange) (Eaton and Blair, 1935); *Lycopersicon esculentum* (cultivated tomato) is more susceptible to B toxicity and accumulates more B in its shoots than its wild relative *L. cheesmanii* (Toledo and Spurr, 1984); and in several cereal and legume species, genotypes susceptibility to B toxicity have shoot B concentrations much higher than in those of tolerant genotypes (Bagheri et al., 1992; Chhipa and Lal, 1990; Paull et al., 1988a, 1992a, 1992b). Similarly, stem B concentrations are closely related to the development of B toxicity in *Prunus* and can be used to rank rootstocks for B tolerance (El-Motaium et al., 1994).

Thus, many B tolerant genotypes are able to maintain lower B concentrations in their shoots than related, susceptible genotypes. Whether or not these B tolerant genotypes operate exclusion mechanisms that result in decreased B accumulation in the entire plant, cannot for the most part be determined, for there is little data on B concentrations in roots. However, where both roots and shoots have been examined in solution culture experiments, exclusion mechanisms have been shown to operate in a wide range of species. For example, B tolerant genotypes of wheat (Figure 1) and barley (Nable, 1988) and peas and medics (Paull et al., 1992b) maintain lower concentrations of B in both root and shoots than do susceptible genotypes. That the ranking of these genotypes for B tolerance (and leaf B concentrations) is the same for plants grown at high B concentrations in solution culture or in soil in pots and the field, indicates that the exclusion mechanism operates under all conditions. To understand how

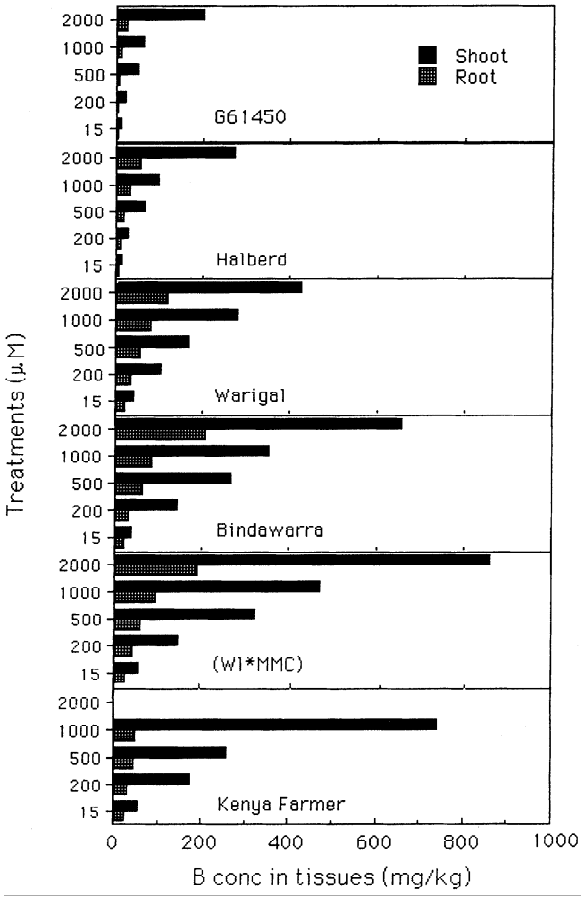

Figure 1. Boron concentration in the roots and shoots of six wheat (*Triticum aestivum*) genotypes grown in solution culture at five levels of B. The relative responses of the genotypes to B toxicity were: G61450 – tolerant; Halberd – moderately tolerant; Warigal – moderately sensitive; Bindawarra – moderately sensitive; and (W1∗MMC) – sensitive. Adapted from Nable (1988).

B accumulation may be regulated under conditions of potential B toxicity, it is necessary to re-examine some aspects of B absorption.

It was noted in Chapter 4 that B is absorbed from solutions as the small, neutral molecule, $B(OH)_3$, and the transmembrane movement of boric acid is primarily determined by its ability to partition into the lipid bilayer. For most molecules of MW $>$ 50, there is a direct relationship between the transmembrane permeability and a measure of its ability to partition into the lipid bilayer, such as an oil/water partition coefficient. Using a partition coefficient for $B(OH)_3$ in water/ether of 0.035 (Bachelet et al., 1947), and based upon the relationship between partition coefficient and membrane permeability (Walter and Gutknecht, 1986), $B(OH)_3$ is predicted to have a very high transmembrane permeability of approximately 4.6×10^{-4} cm s^{-1}. Based upon this value, assuming an external $B(OH)_3$ concentration of 1m*M* (i.e. 1 mol m^{-3}; which is in the range to induce B toxicity) and an (initial) internal concentration of zero, the flux per unit area of membrane would be 4.6×10^{-6} mol m^{-2} s^{-1}. Such a flux is several orders of magnitude greater than the observed protein mediated transmembrane flux of most solutes across membranes (e.g. see Tables 6.1 and 6.2 in Hope and Walker, 1975), suggesting that most of the flux is not protein mediated. Similarly, the structure of the boric acid molecule indicates high membrane permeability that would effectively short circuit any active regulatory mechanism for B absorption at high external concentrations (Raven, 1980). Thus, under conditions of potential B toxicity, B absorption into roots appears to be governed by passive transport processes.

Experimental evidence supporting passive transport processes for B absorption (at least at normal to high external B concentrations) can be found in several uptake studies. In barley (Nable et al., 1990b), sunflower, squash and cultured tobacco (*Nicotiana tobaccum*) cells (Brown and Hu, 1994), B accumulation increases linearly with increasing external B concentrations, shows no multiphasic kinetics, and is not saturable over a wide range of external B concentrations (Figure 2). Furthermore, the inclusion of metabolic inhibitors in the uptake solution (Brown and Hu, 1994) or exposure of plants to temperatures from 2–42 °C (Brown and Hu, 1994; Nable et al., 1990b) does not inhibit B accumulation in any species.

Different abilities to passively transport B appears to be associated with differential tolerance to B toxicity. For in barley, the comparative tolerance of genotypes to B toxicity is reflected in the relative differences in passive B accumulation rates over a wide range of B supply (Nable et al., 1990b; Figure 2). Each genotype has a characteristically different ability to passively accumulate B, a difference that is apparently constitutive and not induced by high B. Furthermore, whilst root temperatures from 5–25 °C markedly affect the growth of barley genotypes, temperature has no effect on the relative susceptibilities of genotypes to B toxicity. Similar results from less detailed experiments with other species (medics, wheat, oats; Nable, unpublished data), indicate a general phenomenon in which the relative tolerance of genotypes to B toxicity is associated with genetic differences in passive B accumulation.

Interestingly, Si accumulation, which also differs greatly amongst barley genotypes, closely reflects B accumulation and the relative tolerance of barley genotypes to B toxicity (Nable et al., 1990b; Walker and Lance, 1991). Thus, the mechanism that governs differences in passive B accumulation also appears to govern Si accumulation in barley. A number of similar properties of $B(OH)_3$ and $Si(OH)_4$ may account for the observed association. Both molecules are weak acids in aqueous solutions, both are mainly undissociated at physiological pH values (pKa1 values of 9.25 and 9.82, respectively at 25 °C), indicating that both are absorbed as neutral molecules, both are thought to move passively across biological membranes and the accumulation of both by plants is greatly influenced by transpiration rates (Raven, 1980, 1983). Yet, addition of Si to plants does not reduce B accumulation, suggesting there is no competition for an active site on a transport protein, despite the apparent similarity of their absorption pathway. Moreover, there is no close relationship between B and Si accumulation in medics. Medic genotypes accumulate very little Si, irrespective of their vastly different levels of B accumulation (Jones and Handreck, 1969; Paull et al., 1992b). Thus, it appears that in the case of medics, and perhaps other dicotyledonous species, a different additional mechanism to that which regulates both B and Si absorption in cereals, controls Si absorption independently of B absorption.

Internal tolerance mechanisms

Except for certain halophytes in which solutes such as sorbitol might inactivate excess B (Rozema et al., 1992), we are unaware of data showing genotypic variation in the an ability of tissues to tolerate high B concentrations.

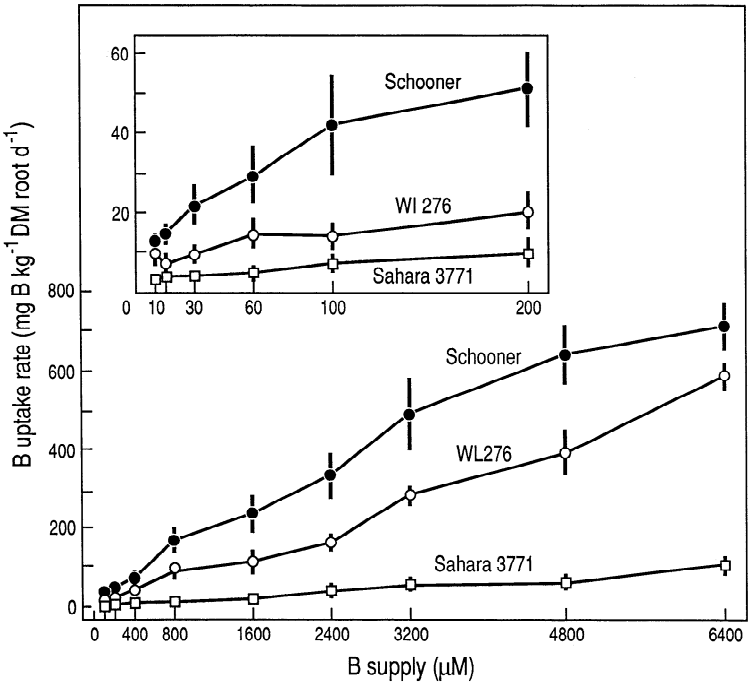

Figure 2. The relationship between external boron concentration and B accumulation by three barley (*Hordeum vulgare*) genotypes differing in response to B toxicity. The relative responses of the genotypes to B toxicity were: Sahara 3771 – tolerant; WI 276 – moderately tolerant; and Schooner – sensitive. From Nable et al. (1990b).

There is also the possibility that B tolerance is related to altered distribution of accumulated B. That is, preferential distribution at the cellular, tissue, or organ level. Again, in cereals, the pattern of B distribution amongst individual leaves and roots is similar in genotypes having greatly different levels of tolerance to B toxicity, despite great differences in total amounts of B accumulated and the actual B concentrations of individual parts (Nable, 1989).

It was noted earlier that there are differences in the phloem mobility of B amongst species which results in B being accumulated in either leaf margins (phloem immobile) or in fruits, cambial tissue, and stems (phloem mobile) (Brown and Hu, 1996). As most species that transport B in the phloem are susceptible to B toxicity, phloem immobility could be viewed as an internal tolerance mechanism. As such, phloem immobility keeps B away from key metabolic sites, retaining it instead in leaf margins, where despite suffering leaf burn, plants are still able to maintain considerable photosynthetic area.

It thus appears that in some species tolerance to B toxicity is governed by an exclusion mechanism – the ability of plants to restrict B accumulation. However, given that differences in B accumulation can be so large, and given that B absorption is not controlled by a protein mediated process, how might plants regulate B accumulation? Several possibilities exist, and these will be discussed briefly.

Due to the readiness by which B binds to polysaccharides and organic acids of various kinds, particularly those with alcohol groups, the secretion of B chelating compounds into rhizosphere, perhaps associated with mucilage, would be likely to reduce the amount of free B around the root, and thus of B entering the plant. Yet, in numerous solution culture experiments with a wide range of species, usually with a mixture of genotypes in the same container, differential tolerance to B toxicity continues to be expressed (Nable, 1988; Nable et al., 1990a, 1990b). Whilst under such conditions, rhizosphere complexation seems unlikely to be the tolerance mechanism, there remains the possibility, particularly under non-sterile conditions, that exudates are important, as they may act immediately adjacent to the root surface, but be metabolised before they have diffused to the bulk solution. However, as seen with pollen tube and tobacco cell cultures, in the presence of high B concentrations very high sugar concentra-

tions are necessary to alleviate B toxicity (Yokota and Konishi, 1990). Furthermore, the exudate would be required over the entire surface of the root to bind the high amounts of $B(OH)_3$ which would be diffusing to the root surface under conditions of potential B toxicity.

Similarly, it seems unlikely that inactivation in the cell wall or cytoplasm of root cells could be the mechanism controlling B exclusion. For although such complexation has been shown to occur (Brown and Hu, 1994), the amounts of $B(OH)_3$ which would need to be bound are enormous, particularly for plants grown in solution culture, where there is a continuously replenished, well mixed supply of B. Also, some threshold pattern of accumulation might be expected, with plants being able to resist increasing B accumulation until a level is reached where the ability to complex is exceeded and B floods into the plant. No such threshold has been reported. If B is being complexed in root cell walls or cells, high B concentrations would be expected in roots, with tolerant genotypes having higher concentrations than susceptible genotypes. In fact, B concentrations in roots are generally quite low, with tolerant genotypes of several species having lower concentrations than susceptible genotypes (Nable, 1988; Nable et al., 1990b; Paull et al., 1992b).

As the transmembrane flux of $B(OH)_3$ is not mediated by proteins (at least at moderate to high external B concentrations), would it possible for an exclusion mechanism to operate through differences in the ability of $B(OH)_3$ to cross the lipid bilayer? That is, by changing the ability of the molecule to partition into the bilayer. For other molecules (including water, glucose and ions), it is known that both major lipid components of plant membranes, phospholipids and sterols, can affect the transport across the lipid bilayer. There is no theoretical reason why changes in the composition of the lipid bilayer could not have similar effects on the transport of $B(OH)_3$. Whether or not such changes form the basis of the observed exclusion mechanism is unknown.

Finally, as B is known to be greatly influenced by transpiration rates (Raven, 1980), there is the possibility that genotypic differences in B accumulation are governed by differences in transpiration rates and the transport of B in the xylem. However, to achieve the differences in B accumulation that have been observed, several fold differences in water use efficiency (WUE) are required (Nable, 1988). In fact, observed differences in WUE between B tolerant and susceptible barley genotypes are much lower, with a range from 2.5-4.0 g dry wt kg^{-1} water.

Breeding for tolerance to boron toxicity

High concentrations of B in the soil result in a significant yield reduction to barley crops (e.g. 17% reduction in yield, Cartwright et al., 1984), a problem that is widespread throughout the cereal growing districts of southern Australia (Cartwright et al., 1986). Additionally, two other lines of evidence indicate the full agronomic and economic significance of B toxicity, and the potential to overcome this problem through breeding. Namely: (1) the association between high levels of B and the cultivation of tolerant wheat varieties (Paull, 1990; Rathjen and Pederson, 1986); and (2) the performance of near isogenic lines under normal and high levels of B (Campbell et al., 1994, 1995; Moody et al., 1993).

There is a wide range in genetic variation in response to B among Australian wheat varieties released during the twentieth century ranging from very sensitive to moderately tolerant in comparison to the total range in variation in wheat (Moody et al., 1988). Distinct differences occur in the response of varieties selected in different regions and virtually all moderately tolerant varieties were selected in South Australia or Victoria, while varieties from New South Wales, Queensland and Western Australia are generally sensitive (Campbell et al., 1994; Paull et al., 1990). All moderately tolerant Australian varieties are related and can be traced to Federation and Currawa. Varieties in this family, especially Federation, Ghurka, Quadrat, Insignia, Heron, Olympic, Halberd and Spear, have been the most widely cultivated varieties in South Australia and Victoria throughout the twentieth century and have regularly accounted for greater than 50% of the total wheat production in South Australia, as was the case in Victoria prior to the introduction of stripe rust (*Puccinia graminis tritici*) in 1979. Furthermore, the regions of maximum cultivation of tolerant varieties correspond to those where high levels of soil B occur, such as the Eyre Peninsula of South Australia and the Mallee and Wimmera of Victoria, and tolerant varieties often account for 90 percent of wheat production in high B regions (Rathjen and Pederson, 1986). In recent years Halberd and Spear have been cultivated extensively on the sodic soils of Western Australia where high concentrations of B would be expected. High concentrations of B therefore appear to have had

a major effect on both selection during breeding and subsequent adoption of varieties by farmers.

The concentrated distribution of B tolerant wheat varieties in regions where high levels of soil B predominate might be considered circumstantial evidence of the impact of B status on Australian agriculture. More compelling data have been obtained from variety trials and the comparative yields of tolerant and sensitive near isogenic lines (NILs). The association between grain yield and the B response of wheat varieties and breeding lines, as measured by the concentration of B in plant tissues, was demonstrated soon after the recognition of B toxicity in South Australia. Cartwright et al. (1987) analysed the grain of 150 lines grown at a high B site and found the B concentration in grain of the high yielding lines (130% of site mean) was 5.9 mg kg^{-1}, compared with 8.5 mg kg^{-1} for the low yielding lines (69% of site mean). Similarly, Rathjen et al. (1987) demonstrated that three years of selection at five sites from a broadly based population of breeding lines resulted in disruptive selection that could be attributed to the B status of the site of selection. The highest yielding lines selected at high B sites yielded significantly more, and had lower concentrations of B in grain than the highest yielding lines selected at low B sites, when compared at a high B site.

As response to B is conferred by major additive genes, backcrossing is an appropriate breeding method to transfer tolerance into otherwise well adapted varieties. Several sets of NILs of wheat have been developed through backcrossing, mostly transferring the Bo1 allele from Halberd to moderately sensitive varieties. Evaluation of these NILs over a range of sites in southern Australia has consistently demonstrated a yield advantage in the order of 5–10% for the tolerant selections when grown at high B sites (Campbell et al., 1994; Moody et al., 1993).

Breeding for tolerance to B toxicity is greatly aided by the ease with which genotypic variation for this characteristic can be assessed and the resulting range of methods that can be utilised to screen breeding populations. For example, as tolerance to B toxicity is consistently related to B concentrations in various plant tissues (e.g. leaf, grain), whether plants are grown under controlled conditions in the glasshouse or in the field, the measurement of tissue B concentrations has been an approach that is successfully utilised as a screening method in several breeding programs (e.g. Bagheri et al., 1996; Jamjod, 1996; Paull et al., 1990). The effect of high B concentrations on the early plant growth, either shoot growth of plants grown in soil (e.g. Paull et al., 1990) or root growth of plants grown on filter paper (Chantachume et al., 1995), is an alternative approach that has also been successfully utilised as screening strategies. Both of these approaches give the same ranking of genotypes.

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