Growth of some range plant species in response to boron concentration in a sand culture
by Roseann Therese Wallander

A thesis submitted in partial fulfillment of the requirements for the degree of Masters of Science in Land Rehabilitation
Montana State University

Abstract:
Under Montana coal mine reclamation guidelines, soil and overburden material that contains more than 5 ug of hot water soluble (HWS) boron (B) per gram is not acceptable material for the plant growth zone. These guidelines are based on the toxicity of boron to crop plants. In the arid and semi-arid western United States native plant species are used for mined land reclamation. Boron toxicity of native species has not been well researched. The objective of this study was to assess the effects of excessive boron on plant species used for mined land reclamation.

Atriplex canescens, Elymus cinereus, E. 1anceolatus, Medicago sativa, Melilotus officinalis, Oryzopsis hymenoides, Pascopyrum smithii and Pseudoroegneria spicata were seeded into pots in a greenhouse study. Each species was irrigated with six different boron concentrations (0.25, 1, 5, 10, 20, and 40 ug B mL^-1) in a diluted nutrient solution. Elymus lanceolatus was also seeded in a soil to which boron had been added. Emergence, plant height, aboveground yield, and plant boron concentrations were measured for each species for each boron treatment. Plants were observed for boron toxicity symptoms during the 96 day growing period.

Whereas aboveground yield of alfalfa was stimulated by the addition of 1 ug B mL^-1, overall the relative yield of all but one species decreased as boron concentration in the nutrient solution increased. Yield of fourwing saltbush was not significantly reduced by any level of boron concentration. Bluebunch wheatgrass yield was significantly ($p<0.05$) reduced by 20 ug B mL^-1 in the nutrient solution. Yields of basin wildrye, thickspike wheatgrass, yellow sweetclover, Indian ricegrass, and western wheatgrass were significantly reduced by 10 ug B mL^-1 . Alfalfa yield was significantly reduced by 5 ug B mL^-1. Except for alfalfa, average boron concentrations of plants that correspond with significant yield reduction were higher than boron concentrations reported to cause yield reduction in crop species.

Saturated paste extractable and HWS boron concentrations of the soil ranged from 0.6 to 16.0 ug B g^-1. Yield of thickspike wheatgrass grown in soil with 16 ug B g^-1 was not reduced.

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A thesis submitted in partial fulfillment
of the requirements for the degree

of

Masters of Science

in

Land Rehabilitation

MONTANA STATE UNIVERSITY
Bozeman, Montana

May 1993

APPROVAL

of a thesis submitted by

Roseann Therese Wallander

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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ACKNOWLEDGMENT

The Reclamation Research Unit at Montana State University supplied the materials and laboratory space for this research project. I thank my committee Frank Munshower, Dennis Neuman, Bill Inskeep, and Doug Dollhopf for their guidance with this project.

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ABSTRACT

Under Montana coal mine reclamation guidelines, soil and overburden material that contains more than 5 ug of hot water soluble (HWS) boron (B) per gram is not acceptable material for the plant growth zone. These guidelines are based on the toxicity of boron to crop plants. In the arid and semi-arid western United States native plant species are used for mined land reclamation. Boron toxicity of native species has not been well researched. The objective of this study was to assess the effects of excessive boron on plant species used for mined land reclamation.

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INTRODUCTION

Regulations which govern the Montana strip and underground mine siting act state that "a mine operator shall bury all toxic materials under adequate fill (Montana Department of State Lands 1980)." In Montana material is toxic if hot water soluble boron concentrations (HWS) are greater than 5 ug g^{-1} (Montana Department of State Lands 1983). The Montana guideline is based on toxicity of boron to crop plants (Becic 1983). In Montana, native plant species are used to reclaim coal mined land. Many of the native species may have evolved under conditions of high boron in the soil. Knowledge of boron toxicity to native perennial plants is limited (Becic 1983).

Boron toxicity is a concern for more areas than the reclamation of coal mined lands. Excessive boron in soil and water has resulted from several human practices. Agricultural drainage waters from farmlands in the San Joaquin Valley in California contain 15 ug B mL^{-1}. This drainage has contaminated groundwater at the Kesterson Reservoir (Benson et al. 1991). Dreesen and Wangen (1981) found elevated levels of boron in saltcedar (*Tamarix chinensis*) that was growing near effluent channels of a coal-fired power plant. Boron toxicity is one of several properties of the ash which affect the establishment of vegetation on pulverized fuel ash deposits (Hodgson and Townsend 1973).

High levels of boron also are created in nature. Young and Evans (1986) found that a substantial amount of boron was deposited by erosion and subaerial deposition from playas in the Great Basin of North America. In Nevada, Rollins et al. (1968) found higher levels of boron in soils of areas where wind deposited fine materials compared with areas where wind eroded fine particles.

Because of the agricultural importance of this element, numerous determinations of boron concentrations in agricultural crop plants are available (Berger 1949, Bradford 1966, Gupta 1979, Maas 1987). Knowledge of the boron nutrition of native plants is needed to successfully reclaim western mining disturbances. The objective of this study was to determine the effects of excessive boron on plant species used for mined land reclamation.

REVIEW OF LITERATURE

Boron in plants

Boron is a micronutrient that plants require for normal growth and reproduction. Plant analyses reveal very low concentrations (less than 100 ug g^{-1} dry weight) of this element (Salisbury and Ross 1985). The amount of boron required for plant growth differs for each plant species. When plants take up more boron than necessary, plant growth and reproduction may be injured or reduced. This range between the concentration required to the concentration at which boron is toxic is narrow and varies for each plant species (Eaton 1944).

While a specific role for boron in plant growth has not been identified, research indicates that boron may be involved in several plant physiological processes. Reviews by Dugger (1983), Shkolnik (1984) and Marschner (1986) summarized research to determine the physiological role of boron in plants. They separated this research into six general categories within which boron may play several roles.

1. Boron complexes with organic structures.
2. Cell elongation and division and nucleic acid metabolism.
3. Carbohydrate and protein metabolism.
4. Tissue differentiation, auxin and phenol metabolism.
5. Membrane permeability.
6. Pollen germination and pollen tube growth.

Plant uptake of boron from the soil solution into the root and subsequent transport from the root through the xylem is not strictly a passive process (Raven 1980). Bowen (1972) showed that the ratio of boron uptake to water uptake can be higher or lower than the ratio of boron to water in the solution surrounding plant roots. Boron transfer from the root to the shoot may be by mass flow in the transpiration stream. This would suggest that boron concentration in the roots and transpiration stream are similar. However, a study with two genetic strains of tomato (*Lycopersicon esculentum*) plants has shown that boron transport from the root to the shoot differed between the two strains. While both contained the same amount of boron in the roots, transpiration of boron was much greater in one strain than in the other (Brown and Jones 1971). Once in the leaf of the plant boron is not relocated to other parts of the plant (Wolf 1940).

Boron toxicity symptoms usually appear in the leaves of plants. These symptoms appear on the leaf as tip burn, tip and marginal burn, marginal burn, irregular areas, or yellow and dead areas between veins (Marschner 1986). According to Bradford (1966) moderate to acute boron toxicity appears as a necrosis on the leaf. This necrosis begins as a yellowing at the tip and or margins of the leaf and spreads to the interveinal tissue eventually reaching the midrib. Symptoms of boron toxicity do not always appear on leaves. Effects of excess boron in apricots (*Prunus armeniaca*) appear as enlarged nodes and shortened internodes of branches (Eaton 1944, Bradford 1966). Oertli and Kohl (1961) determined that within leaves with symptoms of boron toxicity necrotic areas contained the highest amount of boron, while chlorotic areas contained less boron than necrotic areas and green areas of leaves contained the least amount of boron. Those researchers found that boron toxicity was confined to areas in which boron was most concentrated. They noted that tissue, or in some cases, whole leaves containing excess boron may die and fall off the plant. By that process the boron concentration in the plant was reduced in some species.

Studies of boron nutrition in crop plants revealed that on a dry weight basis mature, normal leaves contain an average of 20 to 100 ug B g^{-1} and deficient leaves contain less than 15 to 20 ug B g^{-1}. Toxicity occurs when leaf boron concentration exceed 200 to 250 ug B g^{-1} (Wilcox 1960, Gupta et al. 1985, Maas 1987). Gupta (1979) summarized the deficient, sufficient and toxic levels of boron (dry weight basis) for 24 species of crop plants. In general, for most of the species listed, plant boron concentrations corresponding to conditions of deficiency, sufficiency, and toxicity fall within the concentrations previously noted. Gupta cited a study which found that boron toxicity occurs in sugar beets (*Beta vulgaris*) when plant boron concentrations exceeded 800 ug B g^{-1}. Brenchley and Warington (1927) showed that barley (*Hordeum vulgare*) plants required less boron than legumes for normal growth. Cartwright et al. (1984) found that barley plants were severely affected if boron concentrations in the plants exceeded 62.4 ug B g^{-1}.

Fifty-two species of crop plants in Eaton's (1944) sand culture study of boron tolerance were classified into groups of boron sensitive, boron semi-tolerant and boron tolerant. Eaton calculated a tolerance value for each species. He determined the mean dry weight of each species of plants grown in sand that was irrigated with nutrient solutions containing trace, 1, 5, 10 and 15 ug B mL^{-1}. The average dry weight of plants irrigated with solutions containing 5, 10 and 15 ug B mL^{-1} was divided into the average dry weight of plants irrigated with nutrient solution containing a trace or 1 ug B mL^{-1} (Eaton used the larger). This quotient multiplied by 100 resulted in a tolerance value for each species. Tolerance values ranged from 50 (most sensitive) to 217 (least sensitive). Boron tolerant species included: asparagus (*Asparagus officinalis*), artichoke (*Cynara scolymus*), cotton (*Gossypium* *hirsutum*) and sweet clover (*Melilotus indica*). Blackberry (*Rubus* sp.), lemon (*Citrus limon*), elm (*Ulmus americana*), lupine (*Lupinus hartwegii*) and kidney bean (*Phaseolus vulgaris*) were classified as boron sensitive plants. The semi-tolerant class included Kentucky bluegrass (*Poa pratensis*), barley, corn (*Zea mays*), milo (*Sorghum vulgare*), oats (*Avena sativa*), alfalfa (*Medicago sativa*), and tomato.

Berger (1949) observed that the most tolerant plants in Eaton's study (1944) had the lowest boron concentrations (dry weight basis) while the least tolerant plants had highest boron concentrations in the plant tissue. Oertli et al. (1961) noted that sensitivity towards excessive boron supply is related more closely to uptake rates than to differences in tolerance of tissues. Nable (1988) found that a large range of resistance to boron toxicity in wheat and barley cultivars was governed by the ability of the cultivar to restrict boron accumulation in the plant.

Gupta (1984) measured plant boron concentrations in alfalfa in response to boron fertilization and liming in the field. Deficiency symptoms appeared on alfalfa plants when plant boron concentrations were less than 30 ug g^{-1}. There were no differences in plant boron concentrations due to boron by lime interaction. However, liming reduced plant tissue boron concentration in half of the alfalfa samples.

Maas (1987) used the work of Eaton (1944) along with that of other researchers to describe maximum ranges of boron concentration in soil water which agricultural crops can tolerate. These ranges of soil boron concentrations represent a threshold above which yield is reduced. While some crops exhibited toxicity symptoms at lower boron concentrations yield was not reduced. Maas established six categories of boron tolerance based on those threshold soil boron concentrations.

Two species in the very sensitive category, lemon and blackberry can tolerate no more than 0.5 ug B g^{-1}. Grape (*Vitis vinifera*), lupine and strawberry (*Fragaria* sp.) are among 27 species in the sensitive category which can tolerate from 0.5 to 1.0 ug B g^{-1}. Moderately sensitive species can tolerate 1.0 to 2.0 ug B g^{-1} in the soil water. This category includes Kentucky bluegrass and sweetclover. The boron threshold of moderately tolerant category ranges from 2.0 to 4.0 ug B g^{-1}. Tolerant species have a threshold range from 4.0 to 6.0 ug B g^{-1}, this category includes alfalfa and beets. Only two species comprise the very tolerant category, cotton and asparagus have threshold ranges from 6.0 to 10.0, and 10.0 to 15.0 ug B g^{-1}, respectively.

Gestring and Soltanpour (1987) derived equations to describe yield reduction and toxicity symptoms of four alfalfa varieties in three different soils using different boron indices. The investigators determined that plant boron concentration was the best index to predict boron toxicity in alfalfa. They determined that alfalfa yield was significantly reduced when plant boron concentration exceeded 850 to 975 ug g^{-1}. Using only soil boron concentration the equation did not predict alfalfa yield reduction or boron toxicity symptoms ($r^2 < 0.56$). Better prediction resulted when other soil variables (pH, OM content and percent clay) were included in the equation ($r^2 > 0.83$).

Boron in soils

Boron in primary minerals

In general, rocks of marine origin contain more boron than rocks of volcanic origin (Christ and Harder 1969, Aubert and Pinta 1977, Norrish 1975, Ebens and Shacklette 1982). Total boron content of shale rocks (n = 216) from the Sauk sequence in the western United States ranges from less than 30 to 220 ug B g^{-1}, with a geometric mean of 43 ug B g^{-1}. Only sixteen of 392 limestone and dolomite samples from that same sequence contained measurable boron concentrations, these ranged from less than 46 to 130 ug B g^{-1} (Connor and Shacklette 1975).

Minerals containing boron slowly dissolve and release boron to soils. All of the boron in soils (total boron) can be separated into three phases: 1) dissolved in the soil solution, 2) adsorbed on a solid component (clay mineral, organic matter or metal oxide precipitate), or 3) part of a soil mineral. Plants remove boron that is dissolved in the soil solution (Miljkovic et al. 1966, Keren et al. 1985, Jin et al. 1987). Less than five percent of total soil boron is dissolved in the soil solution (Berger and Truog 1940, and Jin et al. 1987, 1988). Boron that is dissolved in the soil solution is in equilibrium with boron in the adsorbed and mineral phases. Boron is released from the adsorbed and mineral phases to replace that which was removed from the soil solution by plant uptake (Rhoades et al. 1970, Peryea et al. 1985).

Mattigod et al. (1985) showed that in neutral and acidic conditions dissolved boron is present in the form of boric acid (H_3BO_3). In basic conditions dissolved boron is present as the borate ion ($B(OH)_4^-$). Under conditions of changing pH the proportion of boron present as borate ion increases as the pH of the solution increases.

These investigators also found that formation of boron complexes may occur if other ions are dissolved in the solution.

In a 1942 survey of boron status of soils in the United States, Whetstone et al. (1942) found that total boron in 300 soil samples ranged from 4 to 88 ug B g^{-1} with water soluble boron approximately 1 ug g^{-1}. Connor et al. (1976) found that total boron in surface and subsurface soils in the Powder River Basin area of Montana and Wyoming ranged from less than 20 up to 70 ug B g^{-1}. Severson and Tidball (1979) reported that the geometric mean of total boron concentrations in the topsoil in the Northern Great Plains coal region was 41 ug g^{-1}. Boron concentration in the subsoil of this region ranged from 16 to 115 ug g^{-1}. The geometric mean of the subsoil boron was 43 ug g^{-1}.

Shacklette and Boerngen (1984) measured total boron concentration in surface materials across the United States. They found that total boron ranged from less than 20 to 300 ug B g^{-1}. One third of these samples contained less than 20 ug B g^{-1}, while ten percent contained greater than 70 ug B g^{-1}. The average boron concentration of surface materials east of the 96th meridian was slightly higher than the average boron concentration west of the 96th meridian, however, this difference was not significant.

Factors which influence available boron in soils

In their survey of the boron content of soils of the United States, Whetstone et al. (1942) attempted to correlate the boron content of soils with soil properties and classification. These investigators found that acidic soils contained less water soluble boron compared with alkaline soils. In humid regions topsoil had higher boron concentrations than soil from lower horizons. The researchers suggested that soils developed from limestone were relatively high in boron because of soil formation factors.

Several studies found that available boron in acidic soils was positively correlated to the organic matter content of those soils (Parks and White 1952, Page and Paden 1954, Miljkovic et al. 1966). Other studies with alkaline soils found that boron availability was influenced more by the pH of the soil than the organic matter content (Wolf 1940, Berger and Truog 1945, Gestring and Soltanpour 1987, Jin 1988).

Soil texture also influences available boron in the soil. Cartwright et al. (1984) measured lower boron concentrations in the saturated paste extract from coarse textured (sandy) soils compared with fine textured soils. These researchers suggested that the difference in boron concentrations of the soils was due to the length of time required for the saturated paste extraction to equilibrate. A longer equilibration time was necessary for the finer textured soils and this may have allowed more boron to dissolve from the soil minerals. Gestring and Soltanpour (1987) added boron to three soils: silt loam, loam and sandy loam. These investigators found that more of the added boron was available in the coarser textured loam and sandy loam soils than in the silt loam soil. Miljkovic et al. (1966) found that boron absorption by sunflowers (*Helianthus annuus*) in Ontario soils increased as clay content increased up to 15 percent. Absorption by sunflowers decreased in soils as clay content increased from 15 to 20 percent. Kubota et al. (1948) and Wilson et al. (1951) found boron moved more rapidly in coarse textured soils as compared with fine textured soils. Keren et al. (1985) found that the chemical activity of boron is greater in coarse textured soils as compared with fine textured soils.

Boron availability is also affected by moisture content of soils. In their work with sunflowers, Miljkovic et al. (1966) found that boron absorption by sunflowers was higher from soil with higher moisture content than soils with lower moisture content.

Boron adsorption in soils

Sposito (1989) defines adsorption as a process in which two elements coprecipitate at the interface of a host mineral and the soil solution. Two elements which coprecipitate must have some amount of structural compatibility. Adsorption results in a uniform mixing of the two elements at the site of precipitation.

Boron adsorption is dependent on pH of the soil (Hue et al. 1988). As calcium hydroxide is added to soils, the pH increases, calcium ions replace aluminum ions on the exchange sites. Aluminum ions precipitate as aluminum hydroxide, this precipitate adsorbs either boric acid or the borate ion (Sims and Bingham 1967, 1968a, 1968b, Hatcher et al. 1967). The adsorption is a ligand exchange mechanism (Hingston et al. 1972). As the pH increases above nine, adsorption of the borate ion decreases because hydroxyl ions in solution have a greater affinity for the adsorption sites than do the borate ions. The borate ion is repulsed by the negative charge associated with the adsorption sites because of the adsorbed hydroxyl ions in the higher pH solution.

Clay content and clay type influence boron adsorption. Keren et al. (1985) found greater adsorption in soils with higher clay content. Goldberg and Glaubig (1986b) found a significant correlation between clay content and the maximum boron adsorbed by 15 California soils. On a weight basis montmorillonite and kaolinte adsorb more boron than illite (Goldberg and Glaubig 1986a). Based on surface area, illite adsorbed the most boron and kaolinite adsorbed more boron than montmorillonite (Hingston 1964).

Couch and Grim (1968) studied boron adsorption on illite clays. They found that adsorption increased as the concentration of the borate ion ($B(OH)_4^-$) in the solution increased. A greater percentage of the boron was adsorbed from solutions containing low boric acid concentrations compared with solutions containing high boric acid concentrations. They suggested that boron was probably adsorbed to edges of clay minerals where broken bonds created positive charges that would attract the negatively charged borate ion. Boron was also incorporated into the crystalline structure of the illite, either by authigenic processes or through intracrystalline diffusion.

Boron adsorption by amorphous soils of volcanic ash deposits was strongly correlated to amorphous aluminum oxide content of the soil (Hue et al. 1988, Bingham et al. 1971). In calcareous soils, boron adsorption was reduced by 10% after calcite was removed, adsorption on the calcareous soils was similar to adsorption on calcite minerals (Goldberg and Forster 1991).

Adsorption isotherms and other models have been used to predict boron adsorption, with varying degrees of success. For soils of New Mexico the Langmuir adsorption isotherm did not describe boron adsorption, while the Freundlich adsorption isotherm did describe boron adsorption (Elrashidi and O'Connor 1982). Goldberg and Glaubig (1985) used the constant capacitance model to predict boron adsorption on aluminum and iron minerals over changing conditions of pH.

Other elements that may influence boron in soils

Brenchly and Warington (1927) noted that boron uptake may be influenced by calcium in the system. Reeve and Shive (1944) observed that external symptoms of boron deficiency were similar to calcium deficiency and studied the relationship between calcium and boron in a soil system. They found that boron toxicity symptoms decreased with increased calcium in the system. Their results showed that cotton plants grown in a soil with high pH (7.5 - 7.8) and high calcium concentration had fifty percent less boron uptake than plants grown in soil with low pH (5.5 - 5.8) and low calcium concentration. This reduced uptake may indicate boron was removed from the soil solution by adsorption. Cartwright et al. (1984) found that in barley plants the calcium to boron ratio was 28.8 in plants with severe boron toxicity symptoms while this ratio was 159.4 in plants with slight boron toxicity symptoms.

Boron assessment in soils and plants

The hot water soluble (HWS) boron extraction method was first described by Berger and Truog (1940). Bingham (1982) describes more recent modifications. This method entails boiling a 2 to 1 mixture of 0.01 M (molar) $CaCl_2$ and soil for five minutes in a flask equipped with a reflux condenser. The cool mixture is filtered. An aliquot of the filtrate is heated over a flame to destroy organic matter. The residue is dissolved in a weak acid and then analyzed colorimetrically with a spectrophotometer to determine boron concentration. Boron concentration is calculated in ug B g^{-1} soil.

The saturated paste extraction method entails saturating soil with distilled water, allowing this mixture to equilibrate overnight and extracting the liquid using vacuum and filtration. Boron concentration in the extract is determined in ug B mL^{-1} (extract) and converted to boron concentration per unit weight of soil using the saturation percentage of the soil (Bingham 1982, U.S. Salinity Laboratory Staff 1954).

Hot water soluble boron concentrations correlated best with plant boron uptake when compared with total and acid soluble boron concentrations (Berger and Truog 1940). Gestring and Soltanpour (1987) used saturated paste, HWS, mannitol-$CaCl_2$ and AB-DTPA (ammonium bicarbonate diethylenetriaminepentaacetic acid) extraction methods to determine available soil boron of three different soils. They found that none were adequate to predict boron toxicity of alfalfa. According to Bingham (1973) the boron concentration of saturated paste extract is comparable to that of the soil solution. Becic (1983) and Barth et al. (1987) state that hot water soluble extraction may be a less stable extraction technique than the saturated paste extraction to determine available boron in soils, neither author cited published research to support that statement.

Perennial, non-crop species response to boron

Oertli et al. (1961) assessed boron toxicity of several turfgrass species. Kentucky bluegrass and seaside bent (*Agrostis palustris* var seaside) germination and establishment in soil was stimulated by watering with a nutrient solution containing 4.8 ug B mL^{-1}. This boron treatment did not affect their growth rates. Clipping removed excess accumulated boron from those grasses. Boron treatment of 10.1 ug mL^{-1} did not affect growth rate of weeping alkaligrass (*Puccinellia distans*) over a 15 week period in a sand culture compared with growth rate of plants receiving 0.1 and 4.6 ug B mL^{-1} treatments. If not clipped, leaves of weeping alkaligrass treated with 4.6 and 10.1 ug B mL^{-1} developed necrotic areas, the amount of necrotic area increased with higher boron treatment. If clipped, necroses were not different between treatments. As boron level increased the weeping alkaligrass became darker green. Boron concentrations in the leaf tips of weeping alkaligrass were ten times greater than in the overall leaf blade. Plant boron concentrations of bermudagrass (*Cynodon dactylon*) Japanese lawngrass (*Zoysia japonica*), alta fescue (*Festuca arundinacea*), creeping bent (*Agrostis palustris*) perennial ryegrass (*Lolium perenne*) and Kentucky bluegrass were monitored as these grasses were exposed to 10 ug B mL^{-1} in a water culture for two weeks. Plant boron concentrations increased after the plants were exposed to boron in solution, and then plant boron concentrations decreased after boron was removed from the solution. Leaf tips and edges accumulated more boron than other leaf parts.

Chatterton et al. (1969) compared germination and growth of several accessions of desert saltbush (*Atriplex polycarpa*) grown in water cultures containing high levels of boron. Germination was not affected by treatment with solutions of 25 or 50 ug B mL^{-1} compared with 0.25 ug B mL^{-1}. For one accession, roots of plants grown in 80 ug B mL^{-1} were significantly shorter than those grown in 20 or 40 ug B mL^{-1}. Root length of the other desert saltbush accessions was not affected by 80 ug B mL^{-1}.

Schuman (1969) determined the relative boron tolerance of three varieties of tall wheatgrass (*Thinopyrum ponticum*). All varieties exhibited similar degrees of boron tolerance. Shoot growth of all three varieties was reduced by 50 percent in nutrient solution boron concentrations ranging from 33 to 36 ug B mL^{-1}. There was no interaction between boron treatment and varieties. After 60 days the root to shoot ratio for Alkar tall wheatgrass was constant in boron concentrations from 0 through 150 ug mL^{-1}. Germination was faster at higher boron levels. Boron toxicity symptoms were not observed until 10 days after the plants were exposed to boron.

Rollins et al. (1968) studied the relationship of tall wheatgrass seedling survival to physical and chemical properties of surface soils at a greasewood-rabbitbrush range site in Nevada. This site contained small dunes and barren soil areas. The dunes consisted of large soil particles that were not removed by wind blowing across the site. Small windblown particles were deposited in barren soil areas between the dunes. The barren soil areas had higher concentrations of boron (3.7 - 215 ug B g^{-1}, saturated paste extract), sodium and total salts compared with the dune areas. Alkar tall wheatgrass seeded in the spring during two years had good emergence across the site. Plants growing in barren soil areas were smaller leaved, light green with brown tips, and they died by fall of each year. The investigators suspected that the plants may have been killed by excess sodium, boron or total salts. Rollins et al. noted that Alkar tall wheatgrass grew well in soils with boron concentrations (from saturated paste extract) greater than 2 ug g^{-1} and still had good growth in soils with boron concentrations greater than 8 ug g^{-1}.

In California, Pratt et al. (1971) listed tall wheatgrass and fourwing saltbush (*Atriplex canescens*) among several grasses, shrubs and trees that would tolerate spoil with high boron concentrations. They did not measure boron concentrations in the spoil or plants.

Connor et al. (1976) surveyed trace element concentrations in surface and subsurface soils and sagebrush (*Artemisia tridentata*) growing in the Powder River Basin of Montana and Wyoming. They found total boron concentrations in the surface and subsurface soils ranging from less than 20 to 70 ug B g^{-1}. Boron concentrations in the sagebrush across the region ranged from 200 to 500 ug B g^{-1}.

Gough and Severson (1981) compared boron concentrations of fourwing saltbush and alkali sacaton (*Sporobolus airoides*) collected from rehabilitated mine sites with those collected from native undisturbed sites. Boron concentrations in plants from the mine sites were higher than boron concentrations in plants from native sites. While total boron in rehabilitated soils was lower than total boron in native soils of that region extractable boron levels were higher in the mine soils. They attributed the higher plant boron concentrations at the mine sites to higher extractable boron in the spoil material. They suggested that after mining the fractured spoil would have greater surface area exposed to release greater amounts of boron to the extractable pool.

Severson and Gough (1983) surveyed 11 coal mines of the Northern Great Plains, Powder River Basin and Green River regions to assess hot water soluble soil boron availability and plant boron uptake from reclaimed mine soils. Fourwing saltbush was the only plant growing at one site at which HWS boron concentrations of the soil ranged from 2.5 to 9.5 ug B g^{-1}. Boron concentration in the fourwing saltbush ranged from 140 to 420 ug g^{-1}. At a different site, intermediate wheatgrass (*Thinopyrum intermedium*) growing in soil containing 0.5 to 2.0 ug B g^{-1} had plant boron concentrations of 4.0 to 16 ug g^{-1}. At a third site, alfalfa growing in soils with 0.5 to 3.0 ug B g^{-1} had plant boron concentrations ranging from 22 to 130 ug g^{-1}. At another site, fourwing saltbush growing in soils containing 0.5 to 1.0 ug B g^{-1} had plant boron concentrations of 26 to 38 ug g^{-1}. Slender wheatgrass (*Elymus trachycaulus*) growing in soil with 0.5 to 3.0 ug B g^{-1} had 3 to 36 ug g^{-1} boron concentration. Most of these plant boron concentrations are within the range for normal growth (Gupta et al. 1985), however boron concentration in the fourwing saltbush growing at the high boron site may have been above normal.

Kilkelly and Lindsay (1982) measured boron content of western wheatgrass (*Pascopyrum smithii*) growing in soil of different thicknesses over two types (high and low total boron) of leached and unleached retorted oil shale in Colorado. They included a high elevation site and a low elevation site in their study. At both sites, boron concentrations in plants growing over either shale were higher (20 to 180 ug B g^{-1}) than in plants not growing over shale (<20 ug B g^{-1}). Differences in plant boron concentrations between the shales were attributed to the different total boron contents of each shale. Thicker soil layers over the shale tended to reduce plant boron concentrations. Plants at the high elevation site had lower boron concentrations than plants at the low elevation site. Plants growing directly in the high boron shale were stunted and their leaves scorched.

Schwab et al. (1983) measured boron content of Indian ricegrass (*Oryzopsis hymenoides*), fourwing saltbush, western wheatgrass, Shermans big bluegrass (*Poa ampla*), Utah sweetvetch (*Hedysarum boreale*) and winterfat (*Ceratoides lanata*) growing in soil from 0 to 90 cm deep covering retorted oil shale. Total and extractable boron concentrations in the shale were 120 and 1.89 ug B g^{-1}, respectively. They stated that boron levels of these plants were somewhat elevated compared with plants from the surrounding area, yet below toxic levels for most cultivated species. The authors did not report the levels of boron in the plants.

Smith (1984) grew five species of range plants in retorted oil shale which had been adjusted to different boron concentrations. Extractable boron concentrations ranged from 2.2 to 55 ug B g^{-1} (NH_4Ac extractable). Indian ricegrass and Utah sweetvetch did not grow in the shale at any boron concentration. Yield of western wheatgrass grown in shale containing 20 ug B g^{-1} was reduced by 45% from the yield grown in shale containing 2.2 ug B g^{-1}. Yield of winterfat grown in shale containing 7.5 ug B g^{-1} was reduced by 31% compared with its yield grown in shale containing 2.2 ug B g^{-1}. Maximum yield of fourwing saltbush occurred in shale containing 20 ug B g^{-1}. There were no differences in yields of fourwing saltbush grown in shale containing 2.2, 7.5, 10.0 and 20 ug B g^{-1}. In shale containing 33.8 ug B g^{-1}, yield was reduced by 47% compared with the maximum yield. Smith concluded that there was no clear response of fourwing saltbush yield to boron concentration in the shale and that in shale containing up to 20 ug B g^{-1}, plant yield may have been positive with respect to boron.

Marquis et al. (1984) determined boron tolerance of desert saltgrass (*Distichlis stricta*) relative to reed canarygrass (*Phalaris arundinacea*). Seedlings of both species were grown for 28 days in nutrient solution with boron concentration adjusted from trace boron (0.5 ug B mL^{-1}) to 300 ug B mL^{-1}. Growth of the saltgrass was not different among nutrient solutions with boron concentration less than 300 ug mL^{-1}. However, in solution containing 500 ug B mL^{-1} growth was reduced by 50%. Reed canarygrass growth decreased with all boron additions to the nutrient solution. Boron concentrations in shoots of reed canarygrass were four times greater than in shoots of desert saltgrass. Boron concentrations in the roots of the canarygrass were 1.7 times higher than in roots of desert saltgrass. The investigators proposed that the differential boron uptake reflected differences in transpiration or genetics of the two species.

Roundy (1985) measured the effect of boron on germination and seedling growth of Jose tall wheatgrass and Magnar basin wildrye (*Elymus cinereus*). To assess germination and radicle growth of both species, Roundy determined germination and measured radicle growth by placing seeds in boxes containing polystyrene foam and irrigating each with boric acid solutions. Boron concentrations ranged from 0 to 500 ug B mL^{-1}. Germination of the wheatgrass was not affected by any boron concentration up to 500 ug mL^{-1} while the wildrye germination was reduced from 92% to 80% at 200 ug B mL^{-1}. While radicle growth of both species was reduced at boron concentrations greater than 120 ug B mL^{-1}, radicle growth of Jose tall wheatgrass was more reduced than Magnar basin wildrye. To assess seedling growth, Roundy seeded both species into pots containing sandy loam soil. The pots were irrigated every other day with Hoagland's nutrient solution with adjusted boron levels ranging from 0 to 100 ug B mL^{-1}. Roots and shoots were harvested 45 days after seeding. Seedling survival of the wheatgrass was not affected by boron while for wildrye it was reduced in boron concentrations greater than 60 ug mL^{-1}. Both species exhibited pronounced tip burn at 80 ug B mL^{-1} and some chlorosis was apparent in 60 ug B mL^{-1}. While root growth of both species was similar in sensitivity to increased boron concentration this growth was more sensitive to boron than shoot growth. Shoot growth of wildrye was more sensitive to increased boron than shoot growth of the wheatgrass.

Hanson et al. (1990) planted pregerminated thickspike wheatgrass (*Elymus lanceolatus*) seeds into sand, clay and shale soils. Boron levels in these soils were adjusted to range from 1.3 to 57.9 ug g^{-1} (HWS). After a 100 day growing period 10 and 20% reduction in shoot growth corresponded to HWS soil boron concentrations of 11.6 and 20.5 ug B g^{-1}, respectively. Root growth in their study was more sensitive to boron than shoot growth. Root growth was reduced 10% and 20% at 3.8 and 6.6 ug B g^{-1}. Boron injury to thickspike wheatgrass occurred at lower soil boron concentrations in sandy soil than in clay or shale soils. They proposed that this lower boron tolerance in sandy soil might be related to lower soil moisture in the sandy soil compared with clay and shale soils.

In summary, the research of boron nutrition of non-crop species is limited to a few species under varied research conditions. A general consensus is not possible. As with the crop species, some non-crop species are very sensitive to excess boron, others are tolerant of higher boron concentrations and some species fall between these two extremes.

Nutrient solution culture

Plants require nutrients for normal growth and reproduction. Carbon, hydrogen and oxygen are obtained from air and water, other nutrients (nitrogen, potassium, calcium, magnesium, phosphorus, sulfur, chlorine, iron, boron, manganese, zinc, copper, and molybdenum) are obtained from the growing medium (Salisbury and Ross 1985).

Plants grow well in solutions with elemental concentrations similar to those in the soil solution as long as an adequate supply of all elements is applied and maintained (Hewitt 1966, Asher and Edwards 1983, Salisbury and Ross 1985). Hoagland and Arnon (1938) developed a formula for a nutrient solution which contains all of these minerals. Elemental proportions were based approximate proportions of the elements as they were found to be absorbed by the tomato plant (Arnon and Hoagland 1940). Most nutrient solutions are more concentrated than soil solutions.

The nutrient solution or water culture method is a technique in which plants are grown with roots submersed in nutrient solution. The roots must be aerated to provide for root respiration. The pH of the nutrient solution must be monitored and adjusted accordingly. Periodically the solution must be replaced. In the sand culture method plants are grown in sand that is irrigated with nutrient solution. The sand culture method provides for more efficient natural aeration of roots than the water culture method. Minute quantities of elements in the sand may alter elemental concentrations in the nutrient solution and thus pose a problem to quantitative studies of micronutrients (Hewitt 1966, Salisbury and Ross 1985).

Nutrient solution and sand solution methods are important in plant nutrition research (Asher and Edwards 1983). An important role for these studies is the determination of critical tissue concentrations for diagnosis of plant toxicities. Gupta et al. (1985) stated that:

> "Universal criteria for determining any boron deficiency or toxicity can be obtained from sand culture studies. These boron concentrations can be easily related to soil solution concentrations and all roots are exposed to the same level of boron concentration."

MATERIALS AND METHODS

Fourwing saltbush, basin wildrye, thickspike wheatgrass, alfalfa, yellow sweetclover (*Melilotus officinalis*), Indian ricegrass, western wheatgrass and bluebunch wheatgrass (*Pseudoroegneria spicata*) were grown from seed for 96 days in a sand culture that was treated with six boron concentrations (0.25, 1, 5, 10, 20, and 40 ug B mL^{-1}). Thickspike wheatgrass was also seeded in soil to which boron was added by weight to equal boron concentrations used in the sand culture study. Emergence, plant height, aboveground biomass, and plant boron concentration were measured and compared for each species grown in sand and soil.

Sand culture

Thirty seeds of eight species (Table 1) were planted 1 cm deep in pots that were 10 cm wide and 40 cm deep. Each pot had been filled with sand which had been previously washed to remove fine material. A 2 cm layer of perlite was placed on top of the sand in each pot after seeding to minimize evaporation from the surface of the sand. Twenty-eight days after seeding plants were thinned if possible to ten average-sized plants which were evenly spaced in each pot. For those species with poor seedling emergence, it was not possible to have 10 plants in each pot.

Pots were watered with Hoagland's nutrient solution diluted 1:4 with tap water (Table 2). Boric acid was added to the nutrient solution to create six boron concentrations (trace, 1, 5, 10, 20 and 40 ug B

ml^{-1}). Trace boron concentration was equal to the boron concentration normally present in tap water, meaning no boric acid was added for this treatment. Each treatment was replicated four times for each species.

Table 1. Species used in the sand culture study.

Scientific Name	Common Name
Atriplex canescens	fourwing saltbush
Elymus cinereus	basin wildrye 'Magnar'
Elymus lanceolatus	thickspike wheatgrass
Medicago sativa	alfalfa
Melilotus officinalis	yellow sweetclover
Oryzopsis hymenoides	Indian ricegrass 'Nezpar'
Pascopyrum smithii	western wheatgrass
Pseudoroegneria spicata	bluebunch wheatgrass

Table 2. Hoagland's nutrient solution*.

compound	mol compound L^{-1}	ug compound L^{-1}
$NH_4H_2PO_4$	2.5×10^{-4}	29
KNO_3	1.5×10^{-3}	152
$Ca(NO_3)_2$	1.0×10^{-3}	164
$MgSO_4$	5.0×10^{-4}	60
$MnCl_2 \cdot 4H_2O$	2.3×10^{-6}	0.46
$ZnSO_4 \cdot 7H_2O$	1.9×10^{-7}	0.06
$CuSO_4 \cdot 5H_2O$	8.0×10^{-8}	0.02
$H_2MoO_4 \cdot H_2O$	1.3×10^{-7}	0.02
FeEDTA**	-	10

* Hoagland and Arnon (1938).
** This compound was added after the dilution was made.

Boron concentrations in the nutrient solutions were measured 12 times throughout the study using the colorimetric curcumin analysis described by Bingham (1982). Three samples of each boron concentration were analyzed at each time. Boron concentrations measured in the nutrient solutions varied slightly from calculated values (Table 3).

Table 3. Measured boron concentrations in the nutrient solutions.

Calculated concentrations (ug B mL^{-1})	Mean concentrations (ug B mL^{-1})	Standard error	Number of sample dates	Number of samples per date
0	0.2	0.03	12	3
1	1.1	0.06	12	3
5	5.6	0.2	12	3
10	10.9	0.4	12	3
20	21.2	0.8	12	3
40	41.6	1.4	12	3

For the first eight weeks pots were watered every 6 days, for the remainder of the period pots were watered every 3 to 4 days. Pots were watered with a volume of nutrient solution equal to 1.2 times the pore volume determined for the sand in the pots. Pore volume was determined using equations 1 and 2 (Brady 1974).

$$\text{total pore volume} = \%\ \text{pore space of sand} \times \text{volume of pot} \qquad (1)$$

$$\%\ \text{pore space of sand} = \left(1 - \frac{\text{bulk density of sand}}{\text{density of solids}}\right)(100) \qquad (2)$$

where:

$$\text{bulk density of the sand} = 1.55\ g\ cm^{-3}$$

$$\text{density of solids} = 2.65\ g\ cm^{-3}$$

Soil culture

A greenhouse soil mixture consisting of equal parts of top soil, sand and peatmoss was used for the root medium in the soil culture. The amount of boric acid necessary to adjust boron concentrations in the soil (by weight) similar to levels in the nutrient solutions was calculated. The appropriate amount of boric acid was added to the soil. Each pot was lined with plastic to avoid boron leaching from the soil. Thirty seeds of thickspike wheatgrass were planted 1 cm deep into pots filled with the boron adjusted soil. Perlite was placed on top after seeding to minimize evaporation from the soil surface. Pots in the soil culture were watered at the same time as pots in the sand culture.

Soils were analyzed for hot water soluble and saturated paste extractable boron (Bingham 1982) after plants were harvested. For the hot water extraction, plastic freezer bags were used in place of reflux condensers (Jacobson, personal communication). Twenty grams of air dried soil were mixed with 40 mL of 0.01 M $CaCl_2$ in a sealed plastic freezer bag. The bag was immersed in boiling water for 10 minutes and then cooled. The contents were filtered and the extract was analyzed for boron concentration with the colorimetric curcumin method. Results of these analyses are summarized in Table 4.

Plants were grown and watered in a greenhouse located in the Plant Growth Center at Montana State University. Full spectrum lamps were used to extend the daylight period to 14 hours. Over the time of the growing period, average temperature during the daytime period was 19°C, it ranged from 10°C to 33°C. Average night temperature for this period was 16°C ranging from 9°C to 23°C.

Table 4. Extractable boron concentration of soil.

Calculated boron concentration ($\mu g\ B\ g^{-1}$)	Saturated paste extract ($\mu g\ B\ g^{-1}$)	Standard deviation	Number of samples	Hot water extract ($\mu g\ B\ g^{-1}$)	Standard deviation	Number of samples
0	0.6	0.3	4	1.2	0.2	4
1	0.4	0.0	4	1.5	0.4	4
5	0.9	0.2	4	3.8	1.0	4
10	2.4	0.1	4	6.0	0.0	4
20	5.9	0.2	4	7.0	1.2	4
40	12.9	0.9	4	16.0	0.0	3

Measurements

Seedlings in all pots were counted 20 days after seeding to determine emergence, seedlings that emerged later were not included in the emergence measurement. Height of the tallest plant in each pot was measured 28, 68 and 96 days after seeding. Boron injury symptoms were observed and recorded at these times. At the end of the study (day 96) plants in each pot were counted and above-ground biomass was harvested. Plant tissues were dried 24 hrs at 47°C. Dried material from each pot was ground in a Wiley mill to pass a 20 mesh screen. Three subsamples (0.500 g) of ground plant material from each pot were heated for 12 hrs at 540°C in silica or quartz crucibles. The ash was dissolved in 0.1 N hydrochloric acid and analyzed for boron content using the colorimetric curcumin procedure (American Public Health Association 1976, Bingham 1982). Average boron concentration of National Institute of Standards and Technology reference material (#1570, non-certified value) was 30 ug

g^{-1}. The boron concentration of these spinach leaves determined in this study was 29.2 ug g^{-1} (N=9, Std=18.6).

Statistical Design

Eight plant species were treated with six boron concentrations in a randomized complete block design using four blocks. Emergence, plant height on days 28, 68, and 96, total dry weight per pot and plant boron concentration were the measured variables for each species in each boron concentration. Mean dry weight per plant was calculated by dividing the total dry weight per pot by the number of plants in that pot. For each species and boron concentration, a relative mean dry weight was determined by dividing the average mean dry weight per plant (across the four blocks) by the maximum mean dry weight per plant (of all the treatments) for that species and multiplying the quotient by 100.

Residuals ($Y-\bar{Y}$) and predicted values ($\hat{Y}$) for each measured variable across all the boron treatments were calculated for each species. A probability plot of residuals was used to determine if the data fit a normal curve. It was necessary to remove one outlier from the Indian ricegrass data set in order to have all the data for all the variables fit the normal distribution. For the bluebunch wheatgrass data set, for plant height on day 28 it was necessary to remove one data point in order for the data to fit the normal distribution. Data from two variables of the western wheatgrass did not fit the normal curve. The non-normality was not due to a single outlier. The variance of the plant boron concentrations was not equal across the treatments.

For those data with a normal distribution and equal variance, a two-way analysis of variance (ANOVA) was used to detect effects of boron treatment and block on emergence, plant height on all three days, and mean dry weight per plant (Snedecor and Cochran 1989). Using two-way ANOVA the variation across the blocks (replication) was calculated and subtracted from the total variation to determine the variation due to the treatment. In this way, variation due to the treatment was not masked by variation across the blocks. Friedmans's nonparametric test was used to detect treatment effect on plant boron concentration data, and the non-normal western wheatgrass data (Sokal and Rohlf 1981, Snedecor and Cochran 1989).

The least significant differences (LSD) test with $p<0.05$ was used to determine differences between treatment means of those variables which had a significant treatment effect as determined by ANOVA and Freidman's test. Each variable was also analyzed across all species to determine species effect and species by treatment interaction. Linear regression was used to determine the relationship between relative mean dry weight and boron concentration in the nutrient solution for each species.

Data were analyzed with Montana State University Statistical Computer program (MSUSTAT, Lund 1988) and SAS software (SAS Institute 1988).

RESULTS

Sand culture

Atriplex canescens

Data from fourwing saltbush measurements are presented in Table 17 (Appendix B). Toxicity symptoms were observed on seedlings in two pots receiving 40 ug B mL^{-1} when emergence was measured (Table 26, Appendix C). At the end of the study yellow or burned leaf edges were present on some of the plants in all of the treatments. Plants irrigated with solution containing 40 ug B mL^{-1} exhibited the greatest amount of leaf burn, they also appeared yellow. None of the plants flowered. No differences were observed in plant roots among the different boron concentrations.

There was no significant effect of boron treatment on emergence of fourwing saltbush (Table 5). There was a significant treatment effect on plant height. Except for early in the study, plant height in pots receiving 40 ug B mL^{-1} was reduced compared with plant height in pots receiving lower boron concentrations. At the conclusion of the study, plant height was greatest for plants irrigated with solution containing 10 ug B mL^{-1}. There was no significant treatment effect on mean dry weight per plant. Plant boron concentrations tended to increase with boron treatment.

The relative mean dry weight per plant of fourwing saltbush grown in each boron concentration was plotted against boron concentration in the nutrient solution (Figure 1). Although there was no significant treatment effect on yield of fourwing saltbush, linear regression indicates a negative response in the relative mean dry weight of this species to boron concentration of the nutrient solution. Fifty percent

Table 5. Treatment means of *Atriplex canescens* grown in sand culture.

Boron in solution	N	Percent emergence	Plant height (mm)			Mean dry weight per plant	Relative mean dry weight	Plant boron concentration
(ug B mL^{-1})			day 28	day 68	day 96	(g)	(%)	(ug B g^{-1})
0	4	12.5	43 c*	208 b	351 cb	2.06	100	15.0 a
1	4	13.2	34 bc	188 b	304 b	1.24	60	56.0 a
5	4	12.8	30 ab	220 b	373 cb	1.21	59	183.3 b
10	4	19.0	36 bc	225 b	393 c	1.30	63	260.0 b
20	4	25.0	44 c	223 b	375 cb	1.18	57	366.7 c
40	4	11.8	19 a	116 a	202 a	0.27	13	695.5 d
P(trt)		0.181	0.004	0.023	0.002	0.168	-	0.0001
P(blk)		0.070	0.209	0.734	0.454	0.549	-	1.0

* Means within each column followed by the same letter are not statistically different at the 5% level as determined by the LSD test of significance.

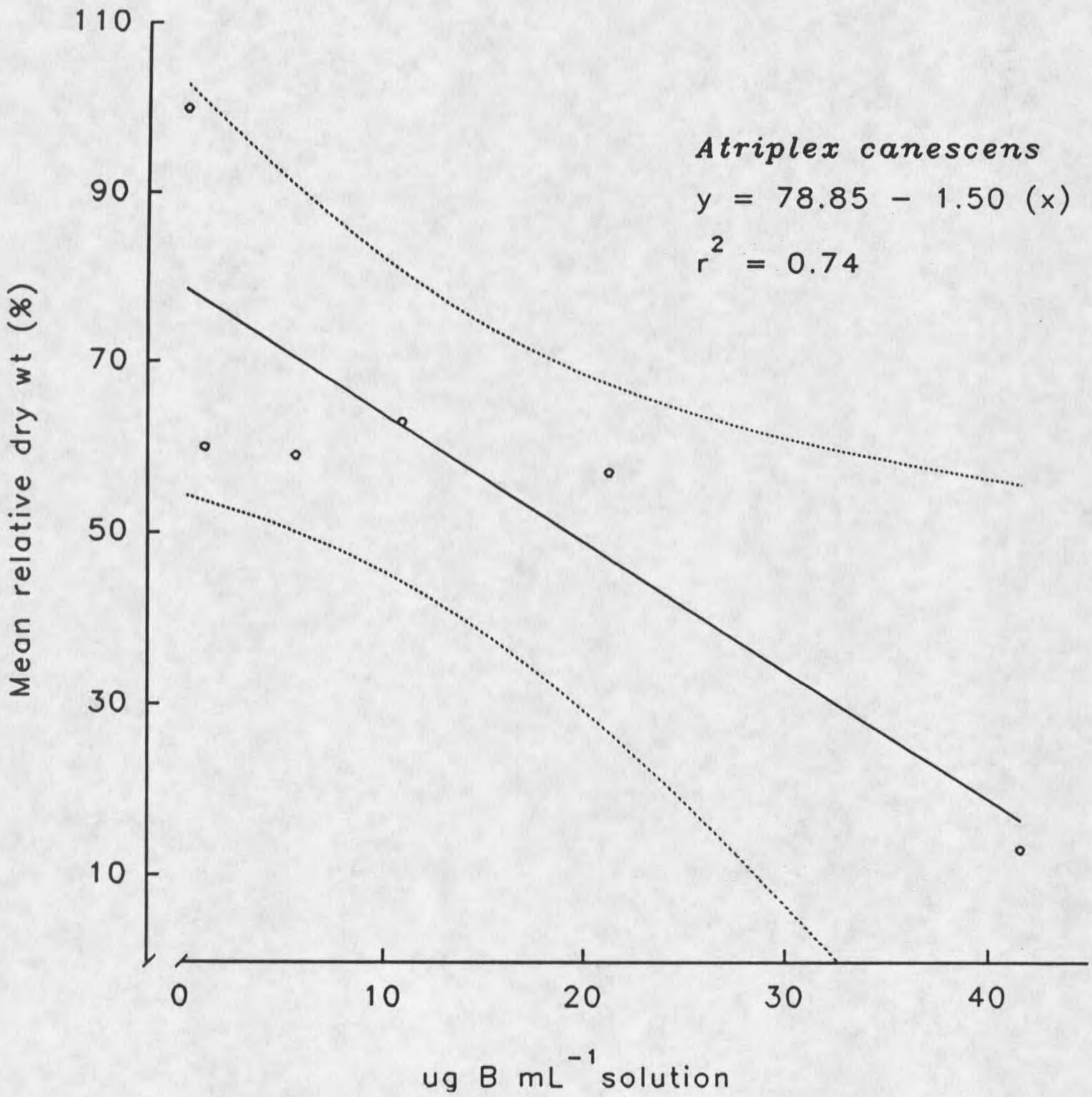

Figure 1. Linear regression of relative mean dry weight of fourwing saltbush to boron concentration in nutrient solution. Dotted lines indicate 95% confidence interval.

of maximum growth was estimated to occur when boron concentration in the nutrient solution was 19.2 ug mL^{-1}. Smith (1984) found no clear response in the growth of fourwing saltbush to boron in retorted coal shale. He suggested that the response of fourwing saltbush to boron concentration may have been positive.

Severson and Gough (1983) found 140 to 420 ug B g^{-1} in fourwing saltbush growing in reclaimed minesoil that contained HWS boron ranging from 2.5 to 9.5 ug g^{-1}. Boron concentrations in the fourwing saltbush at that site are slightly higher than boron concentrations of plants grown in this sand culture study. They also reported boron concentrations ranging from 26 to 38 ug B g^{-1} of fourwing saltbush from minesoils with lower HWS boron concentrations (0.5 to 1.0 ug B g^{-1}). These plant boron concentrations are similar to those determined here.

Smith (1984) grew fourwing saltbush in retorted oil shale to which boron had been added. In that study, plants grown in shale containing 7.2 ug B mL^{-1} (NH_4Ac extractable) contained 76 ug B g^{-1}. Plant boron concentrations from Smith's study appear to be lower than those determined in this sand culture.

A related species, desert saltbush is tolerant of high boron concentrations (Chatterton et al. 1969). Desert saltbush grown in nutrient solution containing 80 ug B mL^{-1} contained 552 ug B g^{-1}. They suggested that the low level of boron in the plants may be due to a slow rate of boron uptake. They proposed that desert saltbush prevents excessive salt accumulation in living tissue by pushing up or breaking off of older trichomes that continually develop from the epidermis of desert saltbush. The trichomes may be sinks for the deposition of excessive salts and contribute to the tolerance of this species to boron.

Elymus cinereus

Data from basin wildrye measurements are summarized in Table 18 (Appendix B). Toxicity symptoms were evident on seedlings irrigated with solution containing 40 ug B mL^{-1} when emergence was measured (Table 27, Appendix C). After 28 days, symptoms were observed on plants irrigated with more than 1 ug B mL^{-1}. By day 68, symptoms were evident on plants irrigated with solutions containing greater than trace concentrations of boron. At the end of the study, only plants irrigated with trace boron solution had leaves without tip burn. Root growth appeared to be reduced for plants irrigated with solution containing 40 ug B mL^{-1}. Tillers were present on plants irrigated with all boron solutions. Plants irrigated with solutions containing 5, 10 and 20 ug B mL^{-1}, were dark green, while those irrigated with solutions containing trace, 1 and 40 ug B mL^{-1} were light green.

There was no significant treatment effect on emergence of basin wildrye nor on plant height early in the study (Table 6). On day 68, plants irrigated with solution containing 40 ug B mL^{-1} were shorter than plants irrigated with solutions containing less than 20 ug B mL^{-1}. At the end of the study there was no significant effect of boron on plant height. Mean dry weight per plant was greater for plants irrigated with solution containing 5 ug B mL^{-1} than for plants irrigated with solutions containing 10, 20, and 40 ug B mL^{-1}. Plant boron concentrations increased in plants irrigated with solutions containing greater than 1 ug B mL^{-1}.

While maximum above-ground growth of basin wildrye occurred in plants receiving 5 ug B mL^{-1}, boron toxicity symptoms appeared on plants in pots receiving greater than trace amounts of boron. In this study, maximum above-ground yield of basin wildrye corresponded with boron

Table 6. Treatment means of *Elymus cinereus* grown in sand culture.

Boron in solution	N	Percent emergence	Plant height (mm)			Mean dry weight per plant	Relative mean dry weight	Plant boron concentration
(ug B mL^{-1})			day 28	day 68	day 96	(g)	(%)	(ug B g^{-1})
0	4	31.0	154	670 b*	729	0.99 cb	79	16.8 a
1	4	40.8	177	700 b	752	1.06 cb	85	110.0 a
5	4	21.8	157	658 b	796	1.25 c	100	793.3 b
10	4	31.8	154	688 b	769	0.84 b	67	1417 c
20	4	31.5	156	607 ab	656	0.74 b	59	2133 d
40	4	28.2	101	503 a	662	0.30 a	24	2733 e
P(trt)		0.160	0.069	0.013	0.134	0.002	-	0.0001
P(blk)		0.126	0.017	0.722	0.380	0.566	-	1.0

* Means within each column followed by the same letter are not statistically different at the 5% level as determined by the LSD test of significance.

concentrations of 793.3 ug g^{-1} in the plant tissue (dry weight).

The relative mean dry weight of plants decreased as boron concentration in the nutrient solution increased (Figure 2). Using the linear regression equation fifty percent reduction in mean dry weight corresponded to 25.9 ug B mL^{-1} in the nutrient solution.

Roundy (1985) reported that germination of Magnar basin wildrye was not affected by boron levels less than 250 ug mL^{-1}. He found that seedlings of this grass grown in sandy loam soil irrigated with 60 ug B mL^{-1} had pronounced tip burn. He also found that root growth of basin wildrye after 45 days was more sensitive to boron treatment than shoot growth.

Elymus lanceolatus

Data from thickspike wheatgrass measurements are presented in Table 19 (Appendix B). By mistake thickspike wheatgrass seeds were not seeded into three pots. Toxicity symptoms were observed as yellow leaf tips on seedlings in pots receiving 40 ug B mL^{-1} when emergence was determined (Table 28, Appendix C). On day 28, yellow leaf tips were observed on plants irrigated with solutions containing greater than 1 ug B mL^{-1}. Symptoms developed as leaf burn on day 68 and necrotic areas at the end of the study. Some plants irrigated with solutions containing 1, 5 and 10 ug B mL^{-1} were dark blue-green, plants were light green and yellow green, respectively for plants irrigated with solution containing trace and 40 ug B mL^{-1}. Root growth was decreased and fewer rhizomes were observed on plants irrigated with solution containing 40 ug B mL^{-1}.

There was no significant treatment effect on emergence of thickspike wheatgrass (Table 7). On days 28 and 68, height of plants irrigated with 40 ug B mL^{-1} was reduced compared with plants irrigated

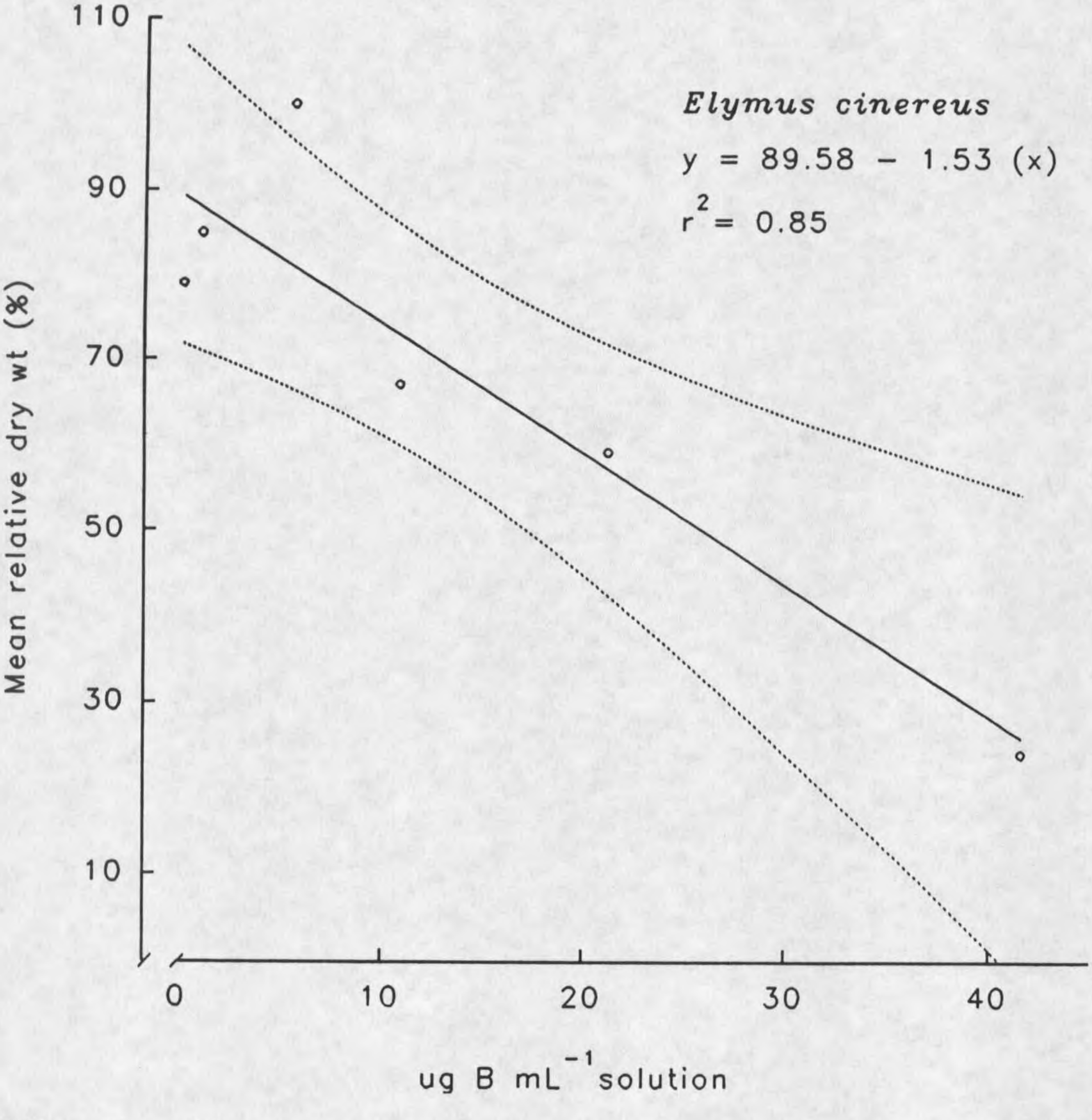

Figure 2. Linear regression of relative mean dry weight of basin wildrye to boron concentration in nutrient solution. Dotted lines indicate 95% confidence interval.

Table 7. Treatment means of *Elymus lanceolatus* grown in sand culture.

Boron in solution	N	Percent emergence	Plant height (mm)			Mean dry weight per plant	Relative mean dry weight	Plant boron concentration
(ug B mL^{-1})			day 28	day 68	day 96	(g)	(%)	(ug B g^{-1})
0	3	76.7	191 b*	566 b	615	1.13 c	100	22.4 a
1	4	72.5	165 b	486 b	561	1.04 c	92	185.0 a
5	4	75.0	166 b	484 b	565	0.86 cb	76	1138 b
10	4	76.0	175 b	500 b	553	0.63 b	56	1767 c
20	2	73.5	166 b	430 b	568	0.58 b	51	2600 d
40	4	69.0	120 a	276 a	438	0.19 a	17	3200 e
P(trt)		0.932	0.005	0.003	0.085	0.0005	-	0.0001
P(blk)		0.851	0.001	0.489	0.305	0.690	-	0.0001

* Means within each column followed by the same letter are not statistically different at the 5% level as determined by the LSD test of significance.

with solutions containing lower boron concentrations. At the end of the study there was no significant treatment effect on plant height. Mean dry weight per plant was reduced for plants irrigated with solutions containing 10, 20 and 40 ug B mL^{-1} compared with plants irrigated with solutions containing trace and 1 ug B mL^{-1}. Plant boron concentrations increased in plants irrigated with solutions containing greater than 1 ug B mL^{-1}. A significant reduction of above-ground yield corresponded with 1767 ug B g^{-1} in plant tissues.

The relative growth of thickspike wheatgrass decreased with increased boron concentration in the nutrient solution (Figure 3). Using the linear regression equation, the estimated boron concentration in the nutrient solution that corresponded with a fifty percent reduction in above-ground growth was 21.7 ug B mL^{-1}. Hanson et al. (1990) found that 10 and 20 percent reduction in shoot growth of thickspike wheatgrass corresponded to 11.6 and 20.5 ug B g^{-1} (HWS), respectively.

Medicago sativa

Data from alfalfa measurements are presented in Table 20 (Appendix B). Yellow cotyledons were observed when emergence was measured in two pots receiving 20 ug B mL^{-1} and in all pots receiving 40 ug B mL^{-1} (Table 29, Appendix C). On day 28, yellow leaves were evident on plants in one pot receiving 10 ug B mL^{-1} and all plants irrigated with solutions containing higher boron concentrations. On day 68 leaf edges appeared white on all plants irrigated with solutions containing greater than 1 ug B mL^{-1}. Plants flowered in all treatments. While all plants lost some leaves, more leaves were lost from plants irrigated with solutions containing higher boron concentrations. At the end of the study, all

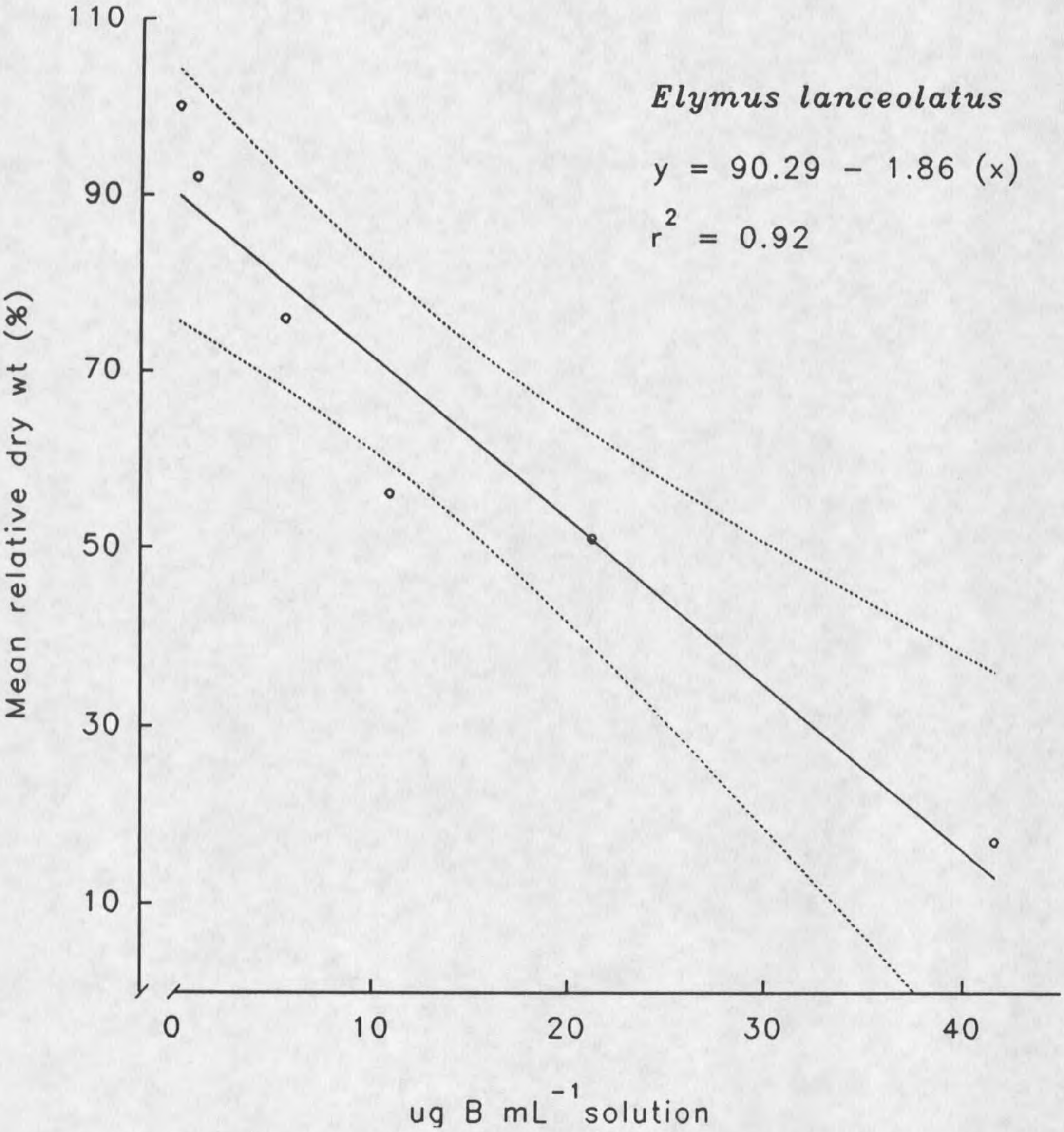

Figure 3. Linear regression of relative mean dry weight of thickspike wheatgrass to boron concentration in nutrient solution. Dotted lines indicate 95% confidence interval.

plants except those irrigated with solution containing trace boron concentration exhibited leaf burn that was greater with increased boron concentration in the nutrient solution.

There was no significant treatment effect on emergence of alfalfa (Table 8). Early in the study, plants irrigated with solution containing 1 ug B mL^{-1} were significantly taller than plants irrigated with the other solutions. On day 68, plants irrigated with solution containing 40 ug B mL^{-1} were shorter than plants irrigated with the other solutions. At the end of the study, there was no significant treatment effect on plant height of alfalfa. Mean dry weight per plant was significantly greater in pots receiving 1 ug B mL^{-1} than in pots receiving other boron treatments. This may indicate a positive response of alfalfa to a small addition of boron. Plant boron concentrations increased with boron treatment level up to 10 ug B mL^{-1}. The lack of differences among plants irrigated with solutions containing 10, 20 and 40 ug B mL^{-1} may be due to the amount of boron that was lost as leaves dropped off plants. Maximum above-ground yield of alfalfa corresponded to 183.3 ug B g^{-1} (dry weight) in the plant tissue.

Although there was an initial positive effect of boron on the relative growth of alfalfa, overall, the relative growth decreased as the boron concentration in the nutrient solution increased (Figure 4). Using the equation derived from the linear regression, the relative growth of alfalfa is reduced by fifty percent when the boron concentration in the nutrient solution is 29.7 ug B mL^{-1}.

In Eaton's (1944) sand culture study, alfalfa yield was greatest in those plants watered with nutrient solution containing 10 ug B mL^{-1} while plants grown in sand receiving 15 ug B mL^{-1} exhibited boron injury

Table 8. Treatment means of *Medicago sativa* grown in sand culture.

Boron in solution	N	Percent emergence	Plant height (mm)			Mean dry weight per plant	Relative mean dry weight	Plant boron concentration
(ug B mL^{-1})			day 28	day 68	day 96	(g)	(%)	(ug B g^{-1})
0	4	81.5	66 b*	407 ab	489	0.76 bc	71	14.1 a
1	4	78.5	91 c	488 b	467	1.07 d	100	183.3 a
5	4	74.2	71 b	448 b	520	0.82 c	77	479.2 b
10	4	82.2	74 b	430 b	532	0.80 c	75	987.5 c
20	4	83.5	77 b	434 b	560	0.56 ab	52	1083 c
40	4	88.2	49 a	315 a	470	0.42 a	39	1175 c
P(trt)		0.233	0.0001	0.040	0.650	0.0003	-	0.0001
P(blk)		0.718	0.0001	0.599	0.587	0.2335	-	1.0

* Means within each column followed by the same letter are not statistically different at the 5% level as determined by the LSD test of significance.

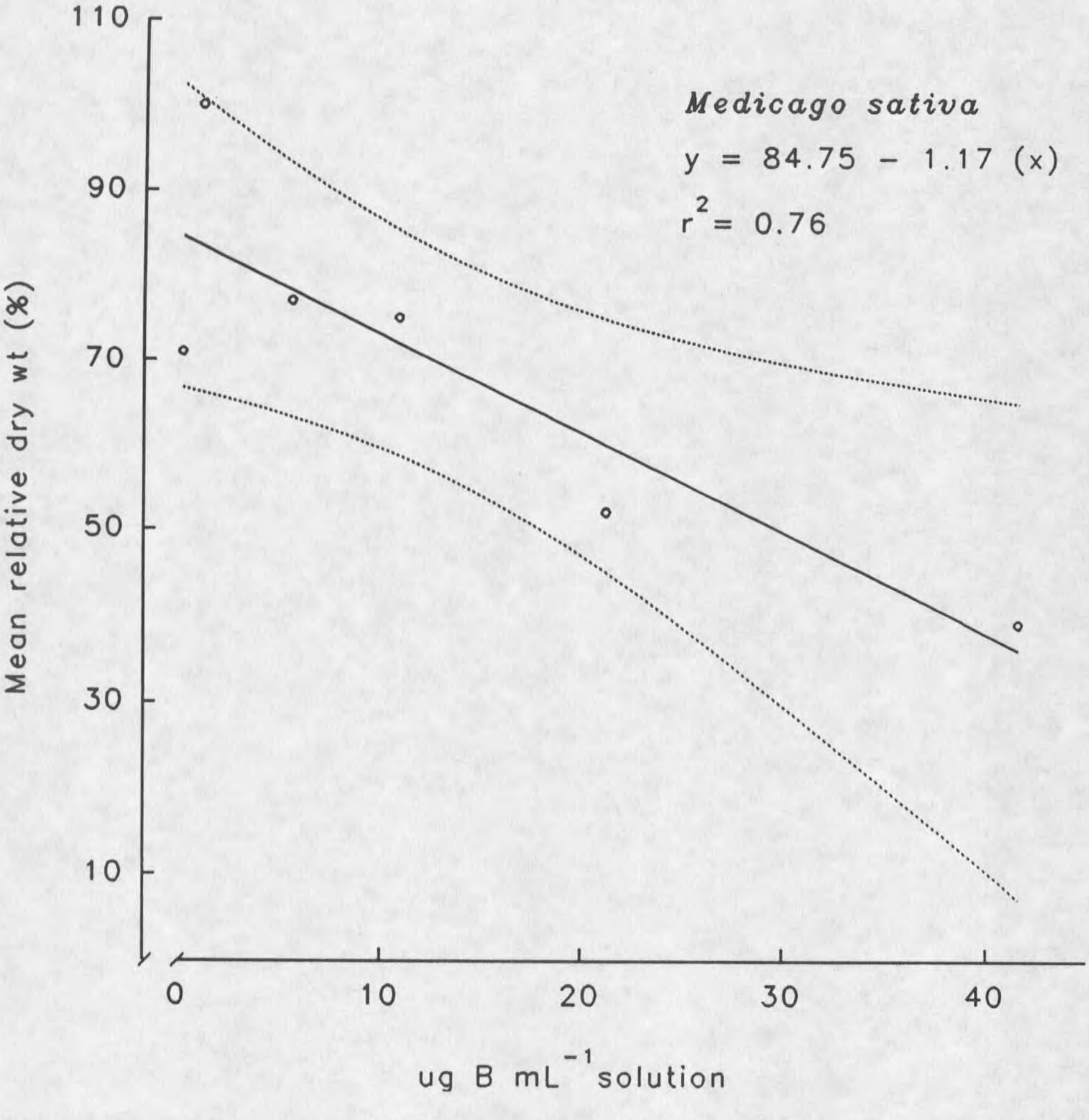

Figure 4. Linear regression of relative mean dry weight of alfalfa to boron concentration in nutrient solution. Dotted lines indicate 95% confidence interval.

symptoms, fifty percent of the plants grown in sand receiving 25 ug B mL^{-1} died by the end of his study.

Boron concentration of alfalfa ranged from 31 to 91 ug g^{-1} for plants grown in reclaimed minesoils with HWS boron ranging from 0.5 to 3.5 ug B g^{-1} (Severson and Gough 1983). Gestring and Soltanpour (1987) reported that alfalfa yield decreased when plant boron concentrations exceeded 850 to 975 ug B g^{-1}. Their plant boron concentrations were much higher than those corresponding to reduced alfalfa yield in this study. Boron uptake by alfalfa grown in coarse-textured soil was greater than boron uptake by alfalfa grown in fine-textured soil (Wear and Patterson 1962). Keren et al. (1985) proposed that differences in boron uptake by plants in soils with different textures may be attributed to chemical activity of boron in the soil solution.

Melilotus officinalis

Yellow sweetclover measurements are summarized in Table 21 (Appendix B). Boron toxicity symptoms appeared as yellow cotyledons on seedlings irrigated with solution containing 40 ug B mL^{-1} when emergence was measured (Table 30, Appendix C). By day 28 yellow leaf tips were observed on plants irrigated with solutions containing 20 and 40 ug B mL^{-1}. On day 68, leaf burn had developed on plants in one pot receiving 5 ug B mL^{-1} and on all plants irrigated with solutions containing higher boron concentrations. At the end of the study, only plants irrigated with solutions containing trace and 1 ug B mL^{-1} did not have leaf burn. All plants lost leaves, and more were lost from plants irrigated with solutions containing higher boron concentrations.

There was no significant treatment effect on emergence of yellow sweetclover (Table 9). Early in the study plant height was

Table 9. Treatment means of *Melilotus officinalis* grown in sand culture.

Boron in solution ($ug\ B\ mL^{-1}$)	N	Percent emergence	Plant height (mm) day 28	Plant height (mm) day 68	Plant height (mm) day 96	Mean dry weight per plant (g)	Relative mean dry weight (%)	Plant boron concentration ($ug\ B\ g^{-1}$)
0	4	89.2	56 b*	250	286	0.70 bc	80	10.8 a
1	4	88.5	70 c	283	355	0.87 c	100	186.7 b
5	4	90.2	58 b	301	382	0.74 c	85	686.7 c
10	4	85.0	48 ab	272	317	0.51 ab	59	883.3 d
20	4	90.0	52 b	256	346	0.49 ab	56	966.7 d
40	4	83.2	40 a	218	303	0.35 a	40	1250 e
P(trt)		0.717	0.0007	0.212	0.436	0.002	-	0.0001
P(blk)		0.139	0.0021	0.132	0.481	0.397	-	1.0

* Means within each column followed by the same letter are not statistically different at the 5% level as determined by the LSD test of significance.

significantly greater in pots receiving 1 ug B mL^{-1}, this may indicate that boron deficiency occurred in plants irrigated with trace boron solution. Later in the study, there were no differences in plant height among boron treatments but mean dry weight per plant was reduced in pots receiving more than 5 ug B mL^{-1}. Plant boron concentrations increased with boron treatment. The above-ground yield of yellow sweetclover was not significantly reduced in plants containing 686 ug B g^{-1} in the plant tissue. Mean dry weight per plant was not different for plants receiving trace, 5 or 10 ug B mL^{-1}, this also may indicate that plants receiving trace amounts of boron may have been boron deficient.

There may be an initial stimulatory affect of boron on the above-ground growth of yellow sweetclover. However, overall, the effect of boron on the relative growth of yellow sweetclover is negative (Figure 5). Using the linear regression equation, the estimated boron concentration at which the growth of yellow sweetclover is reduced by fifty percent is 29.4 ug B mL^{-1} in the nutrient solution.

Oryzopsis hymenoides

Data from measurements of Indian ricegrass are summarized in Table 22 (Appendix B). In block 2, there was no emergence in the pot receiving 10 ug B mL^{-1} at the time that this characteristic was determined. However, one seedling emerged after that date and it was measured from that time onward. Data from this pot were deleted from statistical analyses because they were outliers which caused skewness in the data for most of the measurements of this species.

Boron toxicity symptoms appeared as yellow leaf tips on seedlings in one pot receiving 40 ug B mL^{-1} when emergence was measured (Table 31, Appendix C). By day 28, symptoms appeared as tip burn on all plants

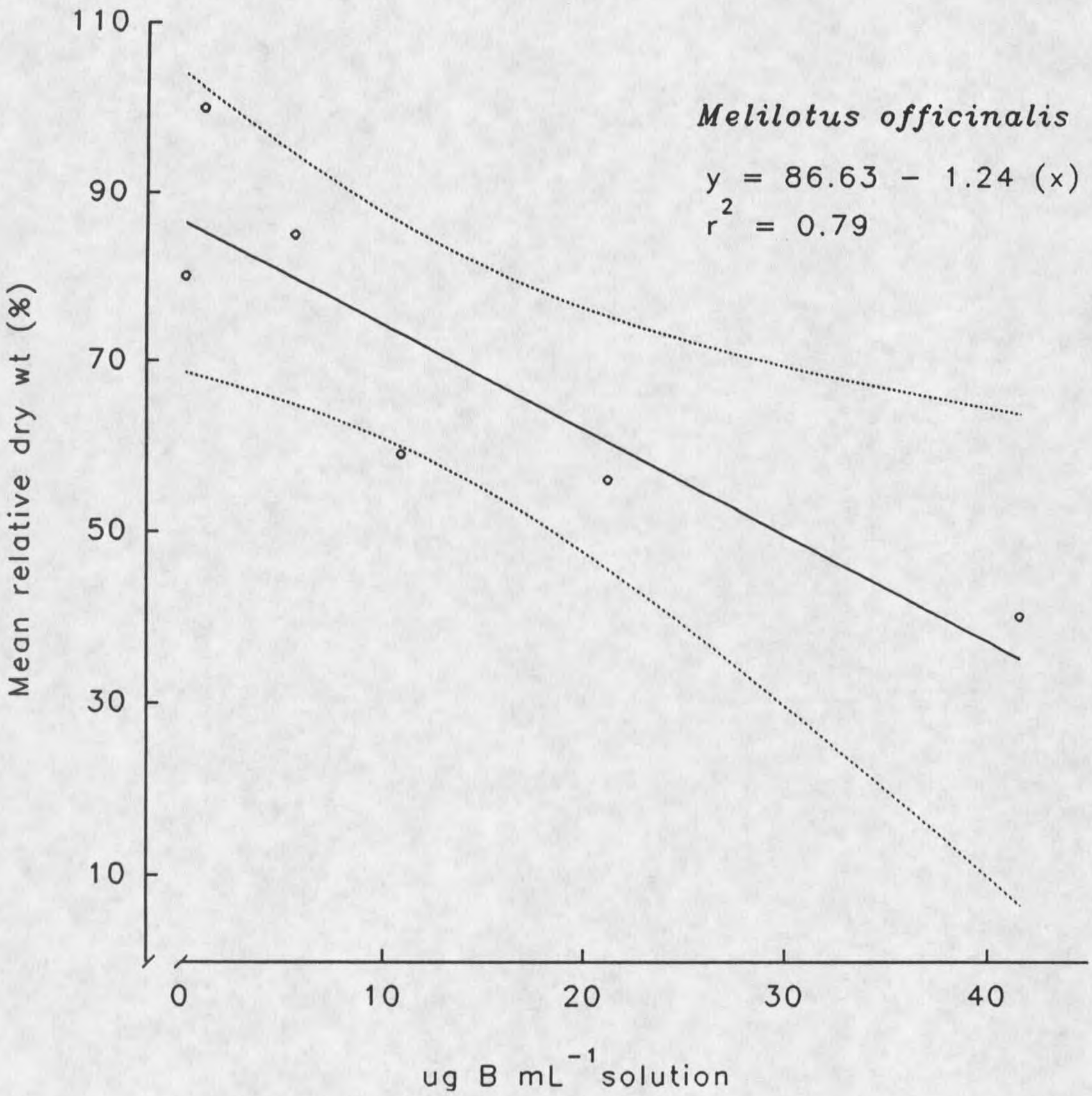

Figure 5. Linear regression of relative mean dry weight of yellow sweetclover to boron concentration in nutrient solution. Dotted lines indicate 95% confidence interval.

irrigated with solutions containing more than 1 ug B mL^{-1}. On day 68 plants irrigated with solution containing 20 and 40 ug B mL^{-1} also appeared yellow. At the end of the study only plants irrigated with solution containing trace boron concentration were without tip burn. Plants irrigated with solutions containing trace and 1 ug B mL^{-1} flowered. Root growth was apparently reduced in pots receiving higher boron treatments.

There was no significant treatment effect on emergence of Indian ricegrass (Table 10). Height of plants irrigated with solution containing 20 and 40 ug B mL^{-1} was reduced each time that it was measured. Mean dry weight per plant was decreased in pots receiving more than 5 ug B mL^{-1} compared with pots receiving trace 1 or 5 ug B mL^{-1}. Plant boron concentration increased with boron treatment, above-ground yield was not reduced by concentrations of 763.7 ug B g^{-1} in the plant tissue.

The relative growth of Indian ricegrass decreased as the boron concentration in the nutrient solution increased (Figure 6). Using the linear regression equation for this relationship, fifty percent reduction in growth was estimated to occur at 17.5 ug B mL^{-1} in the nutrient solution.

Pascopyrum smithii

Data from measurements of western wheatgrass are presented in Table 23 (Appendix B). Toxicity symptoms were observed as yellow leaf tips of seedlings in two pots receiving 40 ug B mL^{-1} when emergence was measured (Table 32, Appendix C). On day 28, symptoms were observed on plants in one pot receiving 5 ug B mL^{-1}, and all plants in pots

Table 10. Treatment means of *Oryzopsis hymenoides* grown in sand culture.

Boron in solution (ug B mL^{-1})	N	Percent emergence	Plant height (mm) day 28	Plant height (mm) day 68	Plant height (mm) day 96	Mean dry weight per plant (g)	Relative mean dry weight (%)	Plant boron concentration (ug B g^{-1})
0	4	21.8	140 c	592 c	751 cd	1.42 d	100	11.3 a
1	4	36.0	156 c	621 c	838 de	1.19 d	84	131.4 ab
5	4	23.5	150 c	613 c	794 cde	1.26 d	89	763.7 bc
10	3	17.7	167 c	646 c	847 cde	0.84 c	59	833 bc
20	4	18.2	108 b	438 b	569 b	0.32 b	23	1150 bc
40	4	16.8	67 a	72 a	79 a	0.00 a	0	4304 d
P(trt)		0.145	0.0001	0.0001	0.0001	0.0001	-	0.0001
P(blk)		0.347	0.0041	0.1294	0.7889	0.8844	-	0.1907

* Means within each column followed by the same letter are not statistically different at the 5% level as determined by the LSD test of significance.

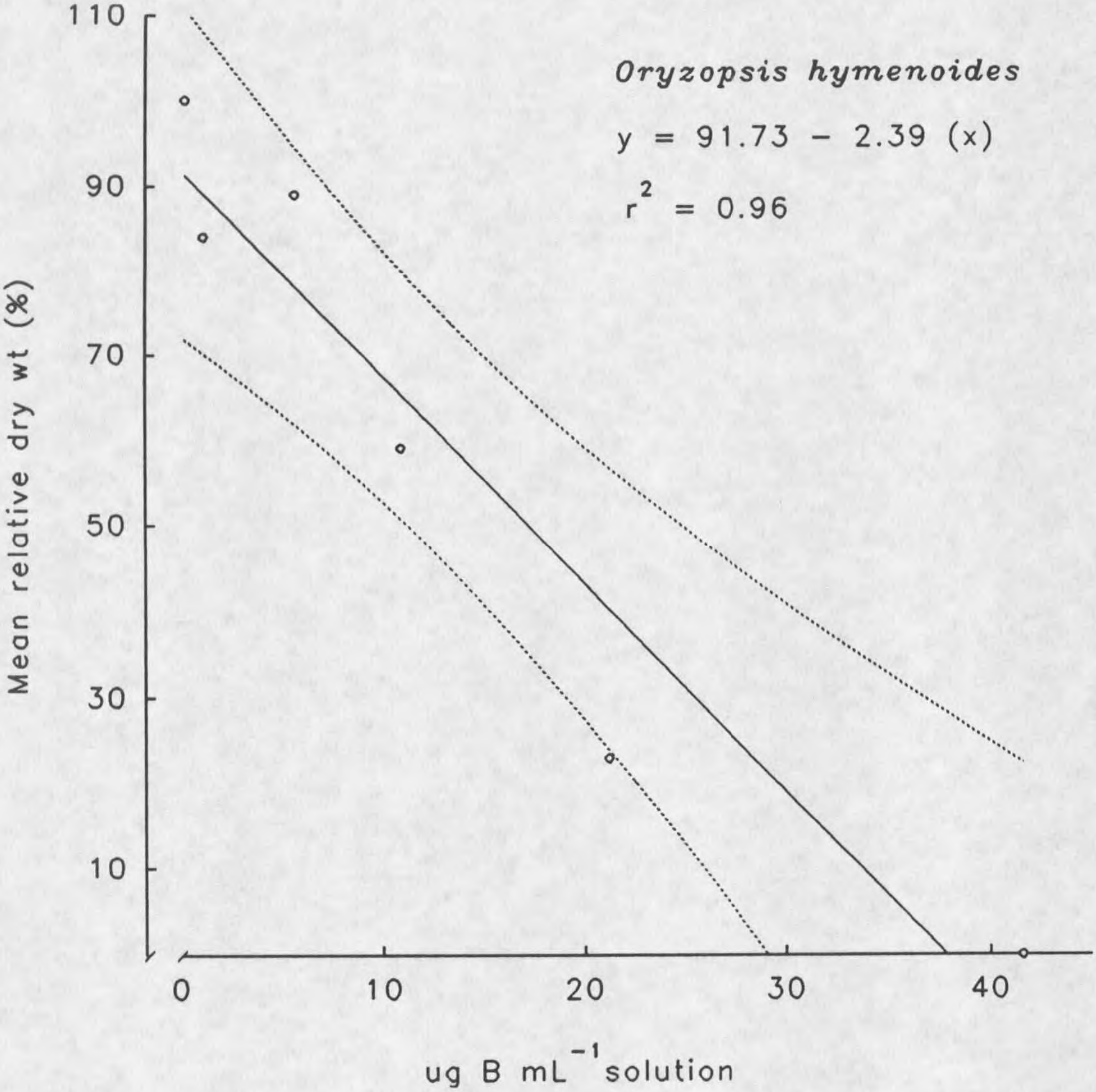

Figure 6. Linear regression of relative mean dry weight of Indian ricegrass to boron concentration in nutrient solution. Dotted lines indicate 95% confidence interval.

receiving higher boron concentrations. By day 68 tip burn had developed on plants irrigated with solutions containing greater than 1 ug B mL^{-1}. At the end of the study, tip burn was evident on plants in all treatments. Plants were generally dark green except those irrigated with 40 ug B mL^{-1}. These plants were light green. Reduced root growth and smaller rhizomes were observed for plants irrigated with solutions containing 20 and 40 ug B mL^{-1}.

There was no significant treatment effect on emergence of western wheatgrass (Table 11). Plant height was reduced in pots receiving 40 ug B mL^{-1} at the beginning and end of the study. Mean dry weight per plant was reduced in pots receiving 10 or more ug B mL^{-1} compared with plants in pots receiving trace and 1 ug B mL^{-1} solutions. Plant boron concentrations increased in plants irrigated with more than 1 ug B mL^{-1}. Above-ground yield of western wheatgrass was not reduced by boron concentrations of 700 ug g^{-1} in the plant tissue.

The relative growth of western wheatgrass decreased as the boron concentration of the nutrient solution increased (Figure 7). Based on the linear regression expression, fifty percent reduction in relative growth is estimated to occur with boron concentration of 23.5 ug B mL^{-1} in the nutrient solution.

In retorted oil shale with adjusted boron concentrations, yield of western wheatgrass decreased with increased boron concentration. Ten percent reduction in yield corresponded to 8.5 ug B g^{-1} (NH_4Ac extractable). Plant boron concentration of western wheatgrass grown in that shale was 569 ug B g^{-1} (Smith 1984).

Table 11. Treatment means of *Pascopyrum smithii* grown in sand culture.

Boron in solution	N	Percent emergence	Plant height (mm)			Mean dry weight per plant	Relative mean dry weight	Plant boron concentration
(ug B mL^{-1})			day 28	day 68	day 96	(g)	(%)	(ug B g^{-1})
0	4	57.5	166 b*	544 cb	623 b	0.92 c	94	7.3 a
1	4	64.8	174 b	562 c	620 b	0.98 c	100	65.8 a
5	4	51.5	152 b	520 cb	620 b	0.79 cb	81	700 b
10	4	51.0	158 b	458 b	595 b	0.64 b	65	1150 c
20	4	51.8	163 b	480 cb	636 b	0.61 b	62	1767 d
40	4	56.5	91 a	268 a	402 a	0.14 a	14	3400 e
P(trt)		0.541	0.006	0.014	0.0006	0.0001	-	0.00000
P(blk)		0.295	0.571	0.445	0.4183	1.0	-	-

* Means within each column followed by the same letter are not statistically different at the 5% level as determined by the LSD test of significance.

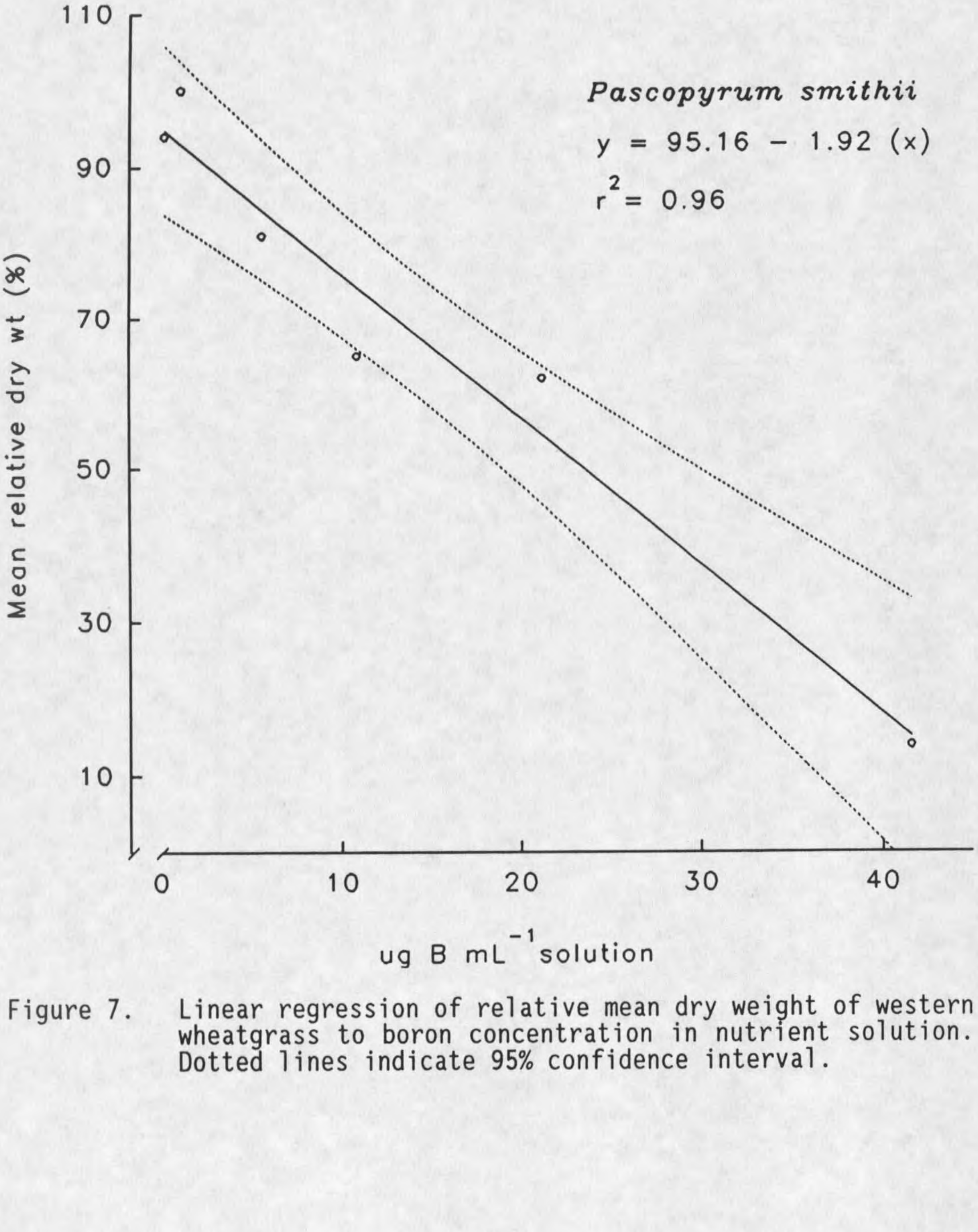

Figure 7. Linear regression of relative mean dry weight of western wheatgrass to boron concentration in nutrient solution. Dotted lines indicate 95% confidence interval.

Pseudoroegneria spicata

Data from measurements of bluebunch wheatgrass are summarized in Table 24 (Appendix B). No bluebunch wheatgrass seedlings established in four pots. In the pot receiving trace boron in block 2, one seedling established after the date on which establishment was determined. Although the plant was not counted as part of establishment, it was measured. Except for the height measurement on day 28, data from this plant was included for statistical analyses. For statistical analyses of height on day 28, this data point was deleted because it was an outlier which skewed the data set.

Seedlings in all three pots irrigated with solution containing 40 ug B mL^{-1} had yellow leaf tips when emergence was determined (Table 33, Appendix C). On day 28, plants irrigated with solutions containing more than 1 ug B mL^{-1} had yellow leaf tips. On day 68, this became tip burn. At the end of the study, only plants receiving trace boron concentration were without tip burn. Plants irrigated with solutions containing trace, 1 and 5 ug B mL^{-1} were dark green. Plants irrigated with solutions containing higher boron levels were light green. Tillers of plants irrigated with solution containing 40 ug B mL^{-1} appeared to be smaller than tillers of plants irrigated with solutions containing lower boron concentrations.

Boron treatment did not significantly affect emergence of bluebunch wheatgrass (Table 12). On day 28, plant height was reduced in pots receiving 40 ug B mL^{-1}. On day 68 plant height was reduced in pots receiving 40 ug B mL^{-1} compared with plant height in pots receiving 1, 5, and 10 ug B mL^{-1}. Mean dry weight per plant was greater in pots receiving trace, 1 and 5 ug B mL^{-1} than in pots receiving 20 and 40 ug B mL^{-1}. Plant boron concentrations increased in plants irrigated with

Table 12. Treatment means of *Pseudoroegneria spicata* grown in sand culture.

Boron in solution (ug B mL^{-1})	N	Percent emergence	Plant height (mm) day 28	Plant height (mm) day 68	Plant height (mm) day 96	Mean dry weight per plant (g)	Relative mean dry weight (%)	Plant boron concentration (ug B g^{-1})
0	4	10.0	162[1] de*	399 b	492	1.35 c	100	9.8 a
1	3	18.7	154 bde	417 b	532	1.27 c	94	174.7 a
5	4	14.5	152 bde	386 b	460	1.20 c	89	890.9 b
10	4	11.8	124 bc	364 b	524	1.02 bc	76	1317 c
20	2	11.5	131 bcd	332 ab	464	0.46 ab	34	2266 d
40	3	13.3	89 a	253 a	340	0.13 a	10	3689 e
P(trt)		0.578	0.0007	0.040	0.130	0.011	-	0.0001
P(blk)		0.413	0.0011	0.109	0.344	0.622	-	0.0371

[1] The mean for this treatment is based on three replications, the fourth was considered an outlier and was deleted for statistical analyses.

* Means within each column followed by the same letter are not statistically different at the 5% level as determined by the LSD test of significance.

solutions containing greater than 1 ug B mL^{-1}. Above-ground yield of bluebunch wheatgrass was not significantly reduced by plant boron concentration of 1317 ug B g^{-1}.

As boron concentration in the nutrient solution increased the relative growth of bluebunch wheatgrass decreased (Figure 8). Fifty percent reduction of growth is estimated to occur at 21.1 ug B mL^{-1} in the nutrient solution.

Soil culture

Elymus lanceolatus

Data summarized from measurements of the soil grown thickspike wheatgrass are presented in Table 25 (Appendix A). Plants in all treatments appeared similar at emergence (Table 34). When the plants were measured on day 68, a small amount of tip burn was apparent on plants in two pots containing soil adjusted to 20 ug B g^{-1} and in three pots with soil adjusted to 40 ug B g^{-1}. Plants in all treatments had leaves with tip burn and blotches at the end of the study.

There was no significant treatment effect on emergence of thickspike wheatgrass (Table 13). There are significant differences among plant height treatment means throughout the study, but there are no apparent trends to those differences. There was no significant treatment effect on mean dry weight per plant. Boron concentrations increased in plants from pots containing soil with greater than 5 ug g^{-1} added boron.

Mean dry weight per plant of thickspike wheatgrass grown in soil was much less than mean dry weight of this species grown in the sand culture. This may reflect differences in nutrient supply, since no nutrients were added to the soil. Boron concentrations of plants grown

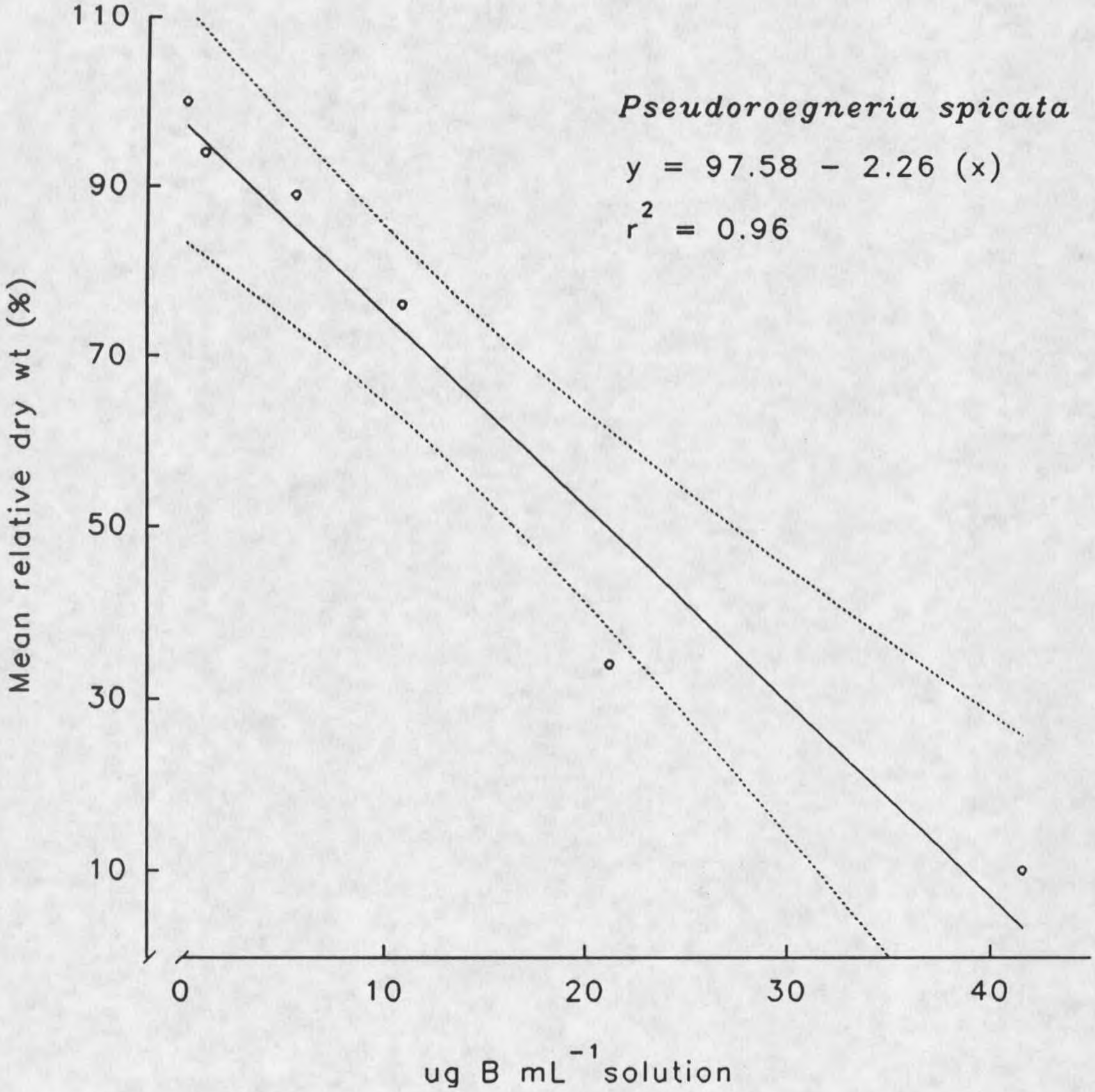

Figure 8. Linear regression of relative mean dry weight of bluebunch wheatgrass to boron concentration in nutrient solution. Dotted lines indicate 95% confidence interval.

Table 13. Treatment means of *Elymus lanceolatus* grown in soil.

Boron added	Measured SPE	Measured HWS	N	Percent emergence	Plant height (mm) day 28	Plant height (mm) day 68	Plant height (mm) day 96	Mean dry weight per plant	Relative mean dry weight	Plant boron concentration
($ug\ B\ g^{-1}$)									(%)	($ug\ B\ g^{-1}$)
0	0.6	1.2	4	54.0	116 a	287 a	409 a	0.18	69	9.9 a
1	0.4	1.5	4	58.0	115 a	344 abc	480 b	0.22	85	8.7 a
5	0.9	3.8	4	61.0	150 c	383 bc	494 b	0.26	100	21.0 ab
10	2.4	6.0	4	53.2	118 a	336 ab	406 a	0.20	77	32.1 b
20	5.9	7.0	4	44.2	145 bc	402 c	477 b	0.26	100	77.0 c
40	12.9	16.0	4	67.5	124 ab	321 ab	452 ab	0.20	77	156.7 d
P(trt)				0.159	0.0215	0.015	0.014	0.244	-	0.0001
P(blk)				0.878	0.0004	0.004	0.003	0.015	-	1.0

* Means within each column followed by the same letter are not statistically different at the 5% level as determined by the LSD test of significance.

in boron treated soil are much lower than boron concentrations of plants grown in the sand culture. This may be due to the lower boron concentrations in the soil solution. It may also be an effect of lower nutrient levels in the soil culture. With less nutrients in the soil, plants would grow more slowly and take up less boron from the soil.

The relative growth of thickspike wheatgrass in soil has no linear relationship to either the hot water soluble or the saturated paste extractable boron concentration (Figures 9 and 10).

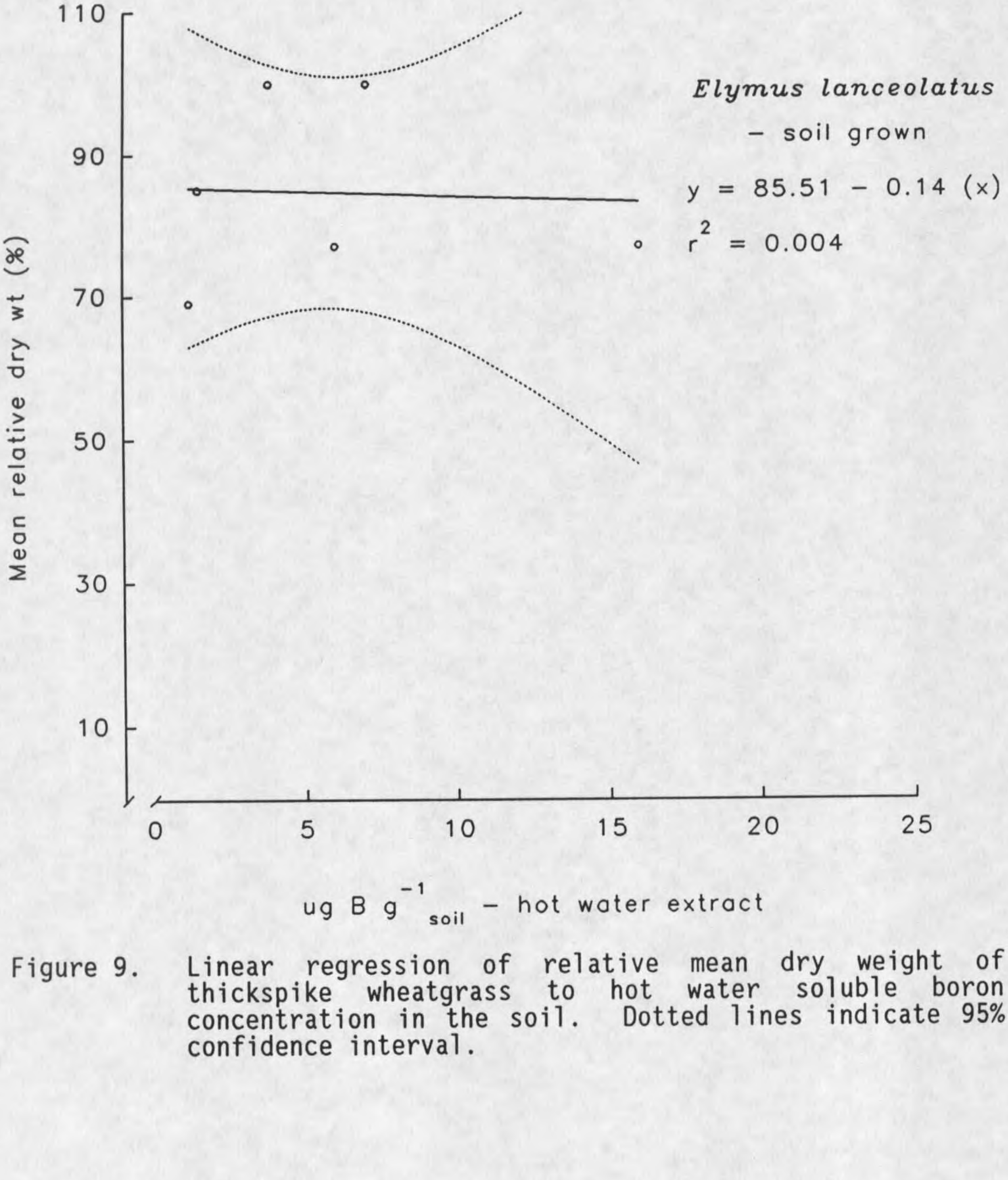

Figure 9. Linear regression of relative mean dry weight of thickspike wheatgrass to hot water soluble boron concentration in the soil. Dotted lines indicate 95% confidence interval.

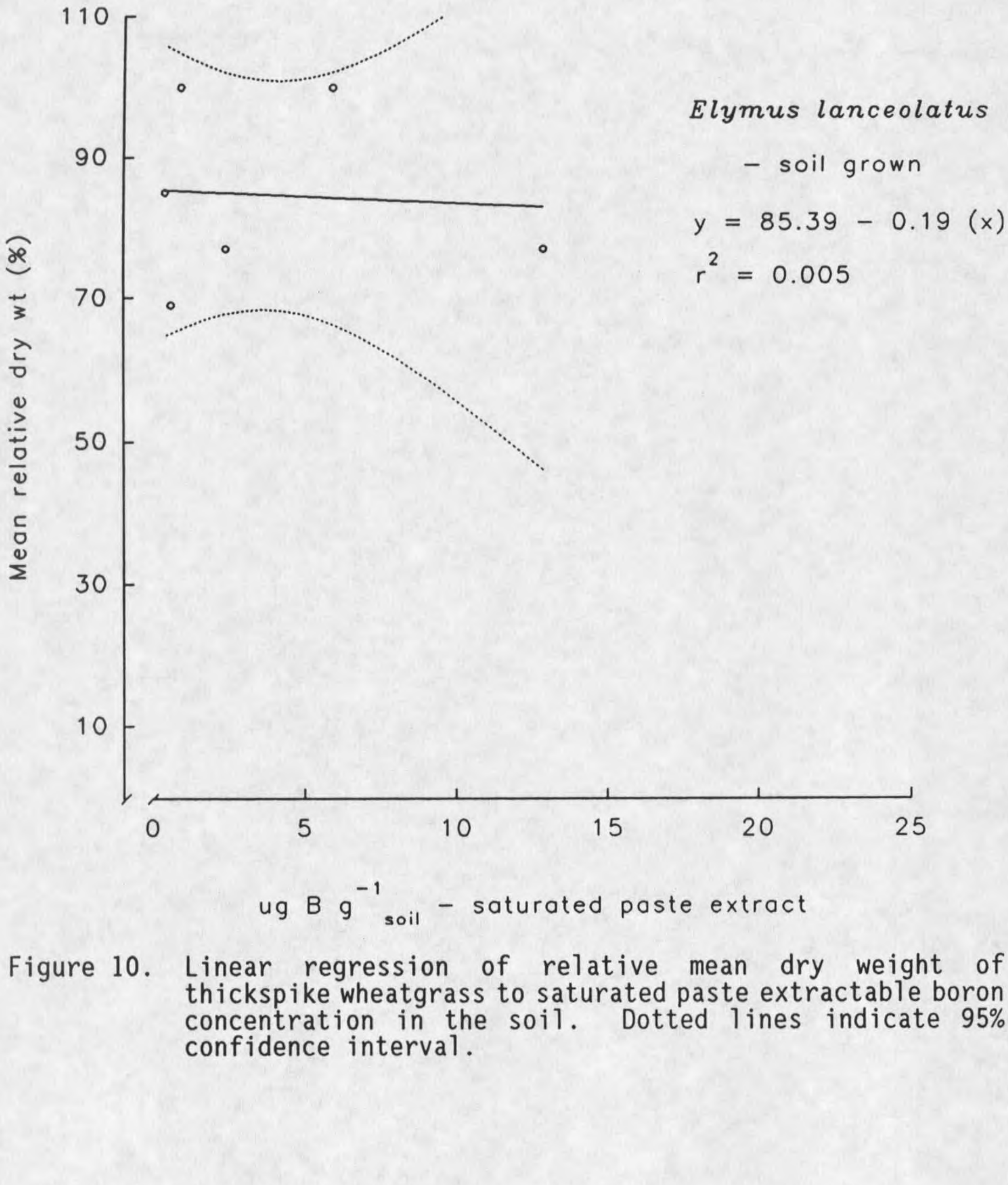

Figure 10. Linear regression of relative mean dry weight of thickspike wheatgrass to saturated paste extractable boron concentration in the soil. Dotted lines indicate 95% confidence interval.

Comparison of species

The significant species effect for all the measured variables indicates that there were differences among species (Table 14). The lack of significant species by treatment interaction for plant height on day 28 indicates that plant height response to boron was similar for all species early in the study. Later during the growing period plant height response to boron was not similar for all species. This may reflect different inherent growth characteristics of each species.

Table 14. Summary of analysis of variance across all species.

Source	Emergence	Height			Mean dry weight per plant
		day 28	day 68	day 96	
Species	***[1]	***	***	***	***
Block	NS	***	**	NS	NS
Treatment	NS	***	***	***	***
Spp*Trt	NS	**	***	***	***

[1]*** indicates F value with $p<0.01$, ** indicates F value with $p<0.05$, NS indicates F value is not significant.

Except for Indian ricegrass, fourwing saltbush had the lowest boron concentration in nutrient solution that corresponded to fifty percent reduction in relative mean dry weight (as determined with the linear regression equations, Table 15). However, the highest boron concentration in nutrient solution did not cause significant reduction in yield of fourwing saltbush. The response of alfalfa is the reverse of that expressed by fourwing saltbush. The boron concentration in the nutrient solution that corresponded to fifty percent reduction in yield of alfalfa was the highest of all the species in the sand culture study, whereas the boron concentration in the nutrient solution which caused significant reduction in yield was the lowest of all the species.

Table 15. Summary of yield reduction for all species.

Species	Fifty percent	Significant yield reduction*	Maximum plant boron concentration with no yield reduction
	($\mu g\ B\ mL^{-1}$)		($\mu g\ B\ g^{-1}$)
Atriplex canescens	19.2	none	695.5
Elymus cinereus	25.9	10	793.3
Elymus lanceolatus	21.7	10	1138
Medicago sativa	29.7	5	183.3
Melilotus officinalis	29.5	10	686.7
Oryzopsis hymenoides	17.5	10	763.7
Pascopyrum smithii	23.5	10	700
Pseudoroegneria spicata	21.1	20	1317

*$p<0.05$.

Using the slopes of the lines of regression of relative mean dry weight to boron concentration in the nutrient solution to compare species, alfalfa (-1.17) and yellow sweetclover (-1.24) were most tolerant to boron. Fourwing saltbush (-1.50) and basin wildrye (-1.53) were less tolerant than the legumes. The wheatgrasses, thickspike (-1.86), western (-1.92) and bluebunch (-2.26) appeared to be less tolerant than the legumes, saltbush and wildrye. Indian ricegrass (-2.39) was the least tolerant of the species in the sand culture study.

CONCLUSIONS

Fourwing saltbush, basin wildrye, thickspike wheatgrass, alfalfa, yellow sweetclover, Indian ricegrass, western wheatgrass and bluebunch wheatgrass were grown in sand and irrigated with six concentrations of boron (0.25, 1, 5, 10, 20, and 40 ug B mL^{-1}) in diluted nutrient solution. Thickspike wheatgrass was also grown in soil to which boron had been added. Plants were grown for 96 days in a greenhouse. Emergence, plant height, yield and boron concentration in the plant tissue were measured for each species. Plants were observed for boron toxicity symptoms.

For all species boron injury symptoms appeared earliest on plants that were treated with the highest boron concentration. Plants irrigated with solutions containing lower boron concentrations (5, 10 and 20 ug B mL^{-1}) developed symptoms of boron toxicity later during the study period. Boron injury symptoms were more severe as boron treatment increased. In general the boron injury symptoms did not correspond with a significant reduction of above-ground yield.

Boron treatment did not affect emergence of any of the species.

There was no effect of boron treatment on yield of fourwing saltbush. Bluebunch wheatgrass yield was significantly reduced by boron concentration of 20 ug B mL^{-1}. Yields of basin wildrye, thickspike wheatgrass, yellow sweetclover, Indian ricegrass and western wheatgrass were reduced by irrigation with solution containing 10 ug B mL^{-1}. Alfalfa yield was reduced by irrigation with solution containing 5 ug B mL^{-1}. The maximum boron concentrations of plants that did not cause significant yield reduction were generally higher than normal boron concentrations found in crop plants. They were also generally higher than boron concentrations considered to be toxic to crop plants.

The mean relative growth of all species in the sand culture decreased as boron concentration in the nutrient solution increased. This was indicated by the negative slope in the equation of the linear regression for mean relative growth to boron concentration in the nutrient solution. Comparison of the rate of decrease (slope) by each species to boron concentration in the nutrient solution indicates that alfalfa and yellow sweetclover were most tolerant to boron concentration in the nutrient solution. Fourwing saltbush and basin wildrye were less tolerant than the legumes and more tolerant than the wheatgrasses. Indian ricegrass was least tolerant of the species.

In the sand culture study, the response by the species was similar to crop species in that some were very susceptible to boron while others were more tolerant. Fourwing saltbush and basin wildrye warrant future research to determine their tolerance to boron treatment under field conditions that would be encountered in minedland reclamation.

There was no relationship between yield of thickspike wheatgrass grown in soil and boron concentration in the soil solution. Yield of thickspike wheatgrass was not reduced by 16 ug B g^{-1} (HWS). The average yield of thickspike wheatgrass from the soil study was three times less than the average yield of thickspike wheatgrass grown in the sand culture study.

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APPENDICES

APPENDIX A

Nomenclature of plant species cited in the text.

Table 16. Nomenclature of plant species cited in the text*.

Common Name	Scientific Name
alfalfa	*Medicago sativa L.*
alkali sacaton	*Sporobolus airoides* (Torrey) Torrey
alta fescue	*Festuca arundinacea* Schreb.
american elm	*Ulmus americana* L.
apricot	*Prunus armeniaca* L.
artichoke	*Cynara scolymus* L.
asparagus	*Asparagus officinalis* L.
barley	*Hordeum vulgare* L.
basin wildrye	*Elymus cinereus* Leymus
bermudagrass	*Cynodon dactylon* (L.) Pers
blackberry	*Rubus* sp.
bluebunch wheatgrass	*Pseudoroegneria spicata* (Pursh) Love
corn	*Zea mays* L.
cotton	*Gossypium hirsutum* L.
creeping bent	*Agrostis palustris* Huds.
desert saltgrass	*Distichlis stricta* (Torrey) Rydb.
desert saltbush	*Atriplex polycarpa* (Torrey) S. Wats
fourwing saltbush	*Atriplex canescens* (Pursh) Nutt.
grape	*Vitis vinifera* L.
Indian ricegrass	*Oryzopsis hymenoides* (R. & S.) Ricker
intermediate wheatgrass	*Thinopyrum intermedium* (Podp.) Barkworth & Dewey
Japanese lawngrass	*Zoysia japonica* Steud
Kentucky bluegrass	*Poa pratensis* L.
kidney bean	*Phaseolus vulgaris* L.
lemon	*Citrus limon* (L.) Burm.
lupine	*Lupinus hartwegii* Lindl. Ann.
milo	*Sorghum vulgare* Pers.
oats	*Avena sativa* L.
perennial ryegrass	*Lolium perenne* L.
reed canarygrass	*Phalaris arundinacea* L.
sagebrush	*Artemisia tridentata* Nutt.

Table 16. -Continued.

Common Name	Scientific Name
saltcedar	*Tamarix chinensis* Lour.
seaside bent	*Agrostis palustris* Huds. var seaside
Sherman's big bluegrass	*Poa ampla* Merr.
slender wheatgrass	*Elymus trachycaulus* (Link) Gould
strawberry	*Fragaria* sp.
sugar beets	*Beta vulgaris* L.
sunflower	*Helianthus annuus* L.
sweetclover	*Melilotus indica* (L.) All.
tall wheatgras	*Thinopyrum ponticum* (Podp.) Barkworth & Dewey
thickspike wheatgrass	*Elymus lanceolatus* (Scribner & Smith) Gould
tomato	*Lycopersicon esculentum* L.
Utah sweetvetch	*Hedysarum boreale* Nutt.
weeping alkaligrass	*Puccinellia distans* (L.) Parl.
western wheatgrass	*Pascopyrum smithii* (Rydberg) Love
winterfat	*Ceratoides lanata* (Pursh) Howell
yellow sweetclover	*Melilotus officinalis* (L.) Pall.

* Nomenclature follows Rumley and Lavin (1991) for grasses, Hitchcock and Cronquist (1976) for native forbs and shrubs and Bailey and Bailey (1976) for crop species.

APPENDIX B

Measurements

Table 17. Measurements of *Atriplex canescens* grown in sand culture.

Block	Boron in solution	Emergence	Number of plants	Plant height (mm)			Total dry weight per pot	Mean dry weight per plant	Plant boron conc.*
	(μg B mL^{-1})	(%)		day 28	day 68	day 96	(g)	(g)	(μg B g^{-1})
1	0	20	6	37	170	275	2.21	0.37	20.0
2	0	7	2	49	265	441	7.72	3.86	8.0
3	0	20	4	56	205	348	4.60	1.15	16.0
4	0	3	1	29	193	340	2.88	2.88	16.0
1	1	13	4	30	189	309	3.72	0.93	60.0
2	1	17	5	30	210	350	5.63	1.13	33.3
3	1	13	3	40	170	279	6.63	2.21	61.3
4	1	10	6	38	183	276	4.10	0.68	69.3
1	5	10	6	25	174	329	2.93	0.49	226.7
2	5	17	4	26	231	400	4.95	1.24	213.3
3	5	7	2	40	281	440	4.07	2.04	160.0
4	5	17	5	31	192	323	5.38	1.08	133.3
1	10	33	1	20	270	452	1.89	1.89	160.0
2	10	13	4	35	140	385	4.87	1.22	346.7
3	10	20	6	39	264	384	6.67	1.11	293.3
4	10	10	4	49	225	350	3.95	0.99	240.0
1	20	47	3	43	176	286	2.91	0.97	400.0
2	20	20	7	42	232	404	3.97	0.57	266.7
3	20	10	3	46	270	449	6.66	2.22	400.0
4	20	23	7	47	215	360	6.58	0.94	400.0
1	40	20	4	24	165	278	1.13	0.28	600.0
2	40	10	3	16	89	165	0.45	0.15	841.0
3	40	10	2	15	92	164	0.54	0.27	641.0
4	40	7	2	22	116	203	0.76	0.38	700.0

*For samples with sufficient dry material, plant boron concentration is the average of three analyses.

Table 18. Measurements of *Elymus cinereus* grown in sand culture.

Block	Boron in solution	Emergence	Number of plants	Plant height (mm)			Total dry weight per pot	Mean dry weight per plant	Plant boron conc.*
	(ug B mL^{-1})	(%)		day 28	day 68	day 96	(g)	(g)	(ug B g^{-1})
2	0	30	7	141	731	780	7.27	1.04	18.0
3	0	27	8	178	571	671	8.36	1.05	14.0
4	0	27	9	179	661	684	8.25	0.92	18.0
1	1	37	6	162	724	736	8.87	1.48	93.3
2	1	43	10	150	676	715	9.26	0.93	126.7
3	1	40	12	212	712	751	11.28	0.94	153.3
4	1	43	12	185	690	808	10.41	0.87	66.7
1	5	10	3	104	640	849	5.42	1.81	560.0
2	5	37	9	176	626	750	8.61	0.96	986.7
3	5	17	6	132	669	714	7.70	1.28	853.3
4	5	23	9	216	696	871	8.51	0.95	773.3
1	10	27	9	125	709	756	6.46	0.72	1200.0
2	10	27	10	180	793	929	10.05	1.00	1266.7
3	10	30	9	145	660	666	8.70	0.97	1400.0
4	10	43	11	167	591	724	7.53	0.68	1800.0
1	20	33	10	127	531	621	5.55	0.56	1600.0
2	20	40	10	98	562	650	4.30	0.43	1600.0
3	20	13	6	150	702	763	5.64	0.94	2533.3
4	20	40	8	250	632	590	8.32	1.04	2800.0
1	40	43	10	98	521	639	2.76	0.28	2666.7
2	40	30	9	101	585	794	3.27	0.33	2400.0
3	40	10	3	71	376	546	0.74	0.25	3200.0
4	40	30	10	135	530	667	3.41	0.34	2666.7

*For samples with sufficient dry material, plant boron concentration is the average of three analyses.

Table 19. Measurements of *Elymus lanceolatus* grown in sand culture.

Block	Boron in solution	Emergence	Number of plants	Plant height (mm)			Total dry weight per pot	Mean dry weight per plant	Plant boron conc.*
	(ug B mL^{-1})	(%)		day 28	day 68	day 96	(g)	(g)	(ug B g^{-1})
2	0	80	10	150	576	589	10.91	1.09	27.3
3	0	70	11	191	540	652	13.01	1.18	16.0
4	0	80	11	231	581	606	12.46	1.13	24.0
1	1	77	10	135	496	556	7.73	0.77	153.3
2	1	60	10	155	412	531	8.81	0.88	173.3
3	1	73	10	163	513	571	13.22	1.32	320.0
4	1	80	10	207	525	587	11.85	1.19	93.3
1	5	77	9	160	574	704	9.32	1.04	1153.3
2	5	63	10	150	425	454	6.33	0.63	1100.0
3	5	77	11	174	505	600	10.27	0.93	1000.0
4	5	83	10	178	430	502	8.57	0.86	1300.0
1	10	70	10	136	537	683	8.97	0.90	1466.7
2	10	90	12	163	409	550	7.65	0.64	1733.3
3	10	57	11	206	660	466	2.50	0.23	2333.3
4	10	87	10	195	395	512	7.62	0.76	1533.3
2	20	77	10	151	403	489	4.93	0.49	2666.7
4	20	70	8	180	458	646	5.38	0.67	2533.3
1	40	63	10	79	259	395	0.96	0.10	3200.0
2	40	73	10	132	315	467	2.74	0.27	2666.7
3	40	80	8	117	206	372	1.01	0.13	3200.0
4	40	60	10	153	323	517	2.54	0.25	3733.3

*For samples with sufficient dry material, plant boron concentration is the average of three analyses.

Table 20. Measurements of *Medicago sativa* grown in sand culture.

Block	Boron in solution	Emergence	Number of plants	Plant height (mm)			Total dry weight per pot	Mean dry weight per plant	Plant boron conc.*
	(ug B mL^{-1})	(%)		day 28	day 68	day 96	(g)	(g)	(ug B g^{-1})
1	0	80	10	52	430	541	7.24	0.72	16.0
2	0	83	11	51	384	472	8.32	0.76	18.3
3	0	83	10	70	390	441	9.32	0.93	10.0
4	0	80	9	91	423	502	5.49	0.61	12.0
1	1	77	10	89	587	353	11.47	1.15	190.0
2	1	77	10	72	355	365	8.29	0.83	210.0
3	1	87	10	110	558	664	12.54	1.25	173.3
4	1	73	10	94	452	486	10.57	1.06	160.0
1	5	77	10	68	470	548	7.44	0.74	380.0
2	5	80	10	61	434	533	7.21	0.72	350.0
3	5	73	10	67	488	552	8.92	0.89	506.7
4	5	67	10	87	400	445	9.52	0.95	680.0
1	10	73	9	73	427	534	7.40	0.82	750.0
2	10	90	10	57	436	526	7.40	0.74	1200.0
3	10	83	10	81	456	606	9.87	0.99	1000.0
4	10	83	10	85	401	462	6.26	0.63	1000.0
1	20	97	11	72	393	440	6.49	0.59	1100.0
2	20	70	9	62	429	503	2.94	0.33	1100.0
3	20	90	10	80	404	631	6.69	0.67	1066.7
4	20	77	10	94	509	665	6.63	0.66	1066.7
1	40	83	10	39	311	456	3.29	0.33	1000.0
2	40	83	10	39	305	513	5.00	0.50	1000.0
3	40	90	9	41	214	366	2.17	0.24	1200.0
4	40	97	10	77	430	545	6.25	0.63	1500.0

*For samples with sufficient dry material, plant boron concentration is the average of three analyses.

Table 21. Measurements of *Melilotus officinalis* grown in sand culture.

Block	Boron in solution ($\mu g\ B\ mL^{-1}$)	Emergence (%)	Number of plants	Plant height (mm) day 28	Plant height (mm) day 68	Plant height (mm) day 96	Total dry weight per pot (g)	Mean dry weight per plant (g)	Plant boron conc.* ($\mu g\ B\ g^{-1}$)
1	0	90	10	59	279	340	7.18	0.72	8.0
2	0	93	10	45	200	224	4.28	0.43	12.0
3	0	97	10	69	308	325	10.73	1.07	11.0
4	0	77	9	52	214	254	5.14	0.57	12.0
1	1	87	10	69	270	328	9.43	0.94	200.0
2	1	93	10	65	276	329	7.91	0.79	186.7
3	1	97	10	69	290	421	7.39	0.74	173.3
4	1	77	10	76	296	343	10.22	1.02	186.7
1	5	90	10	52	256	408	5.69	0.57	666.7
2	5	87	10	48	268	291	7.34	0.73	666.7
3	5	87	10	64	361	399	7.61	0.76	693.3
4	5	97	10	69	319	431	8.81	0.88	720.0
1	10	70	10	46	276	347	5.86	0.59	800.0
2	10	93	10	39	222	275	3.94	0.39	933.3
3	10	87	10	50	340	373	5.25	0.53	733.3
4	10	90	10	59	252	274	5.23	0.52	1066.7
1	20	90	10	46	325	472	4.87	0.49	800.0
2	20	90	10	33	209	340	5.24	0.52	933.3
3	20	100	10	54	196	230	3.90	0.39	1133.3
4	20	80	10	74	296	341	5.46	0.55	1000.0
1	40	90	10	36	162	180	1.76	0.18	1333.3
2	40	80	11	38	186	296	3.61	0.33	1200.0
3	40	90	10	40	247	362	4.24	0.42	1066.7
4	40	73	10	48	278	376	4.58	0.46	1400.0

*For samples with sufficient dry material, plant boron concentration is the average of three analyses.

Table 22. Measurements of *Oryzopsis hymenoides* grown in sand culture.

Block	Boron in solution	Emergence	Number of plants	Plant height (mm)			Total dry weight per pot	Mean dry weight per plant	Plant boron conc.*
	(ug B mL^{-1})	(%)		day 28	day 68	day 96	(g)	(g)	(ug B g^{-1})
1	0	17	5	117	591	754	7.29	1.46	12.6
2	0	23	9	107	523	706	11.80	1.31	12.0
3	0	27	9	160	577	731	12.63	1.40	8.7
4	0	20	6	177	676	813	8.95	1.49	12.0
1	1	20	9	147	632	855	7.91	0.88	109.3
2	1	40	10	126	572	848	12.57	1.26	154.7
3	1	37	10	171	581	794	11.89	1.19	122.7
4	1	47	10	181	700	855	14.35	1.44	138.7
1	5	10	3	117	576	796	4.80	1.60	666.7
2	5	17	6	115	560	771	6.68	1.11	760.7
3	5	27	8	151	580	820	9.85	1.23	626.7
4	5	40	10	216	737	790	10.99	1.10	1000.7
1	10	30	8	151	636	841	6.51	0.81	966.7
2	10	0	1	0	0	210	0.01	0.01	935.7
3	10	6	6	170	649	846	4.67	0.78	766.7
4	10	17	5	179	653	856	4.65	0.93	766.7
1	20	13	4	94	332	461	1.03	0.26	1200.0
2	20	23	9	117	541	648	3.09	0.34	1000.0
3	20	10	3	108	431	611	1.14	0.38	1000.0
4	20	27	7	115	446	555	2.18	0.31	1400.0
1	40	7	2	62	79	85	0.02	0.01	3000.0
2	40	20	6	62	56	72	0.01	0.00	4098.0
3	40	30	11	74	78	84	0.01	0.00	4348.0
4	40	10	3	70	74	76	0.01	0.00	5769.0

*For samples with sufficient dry material, plant boron concentration is the average of three analyses.

Table 23. Measurements of *Pascopyrum smithii* grown in sand culture.

Block	Boron in solution	Emergence	Number of plants	Plant height (mm)			Total dry weight per pot	Mean dry weight per plant	Plant boron conc.*
	(ug B mL^{-1})	(%)		day 28	day 68	day 96	(g)	(g)	(ug B g^{-1})
1	0	63	10	135	472	591	8.94	0.89	6.7
2	0	57	10	159	594	621	9.07	0.90	7.3
3	0	53	9	160	554	656	9.07	1.01	6.0
4	0	57	11	212	556	625	9.73	0.88	9.3
1	1	63	10	176	511	605	9.22	0.92	26.7
2	1	83	10	164	523	619	8.82	0.88	66.7
3	1	73	10	200	660	702	10.40	1.04	46.7
4	1	40	10	156	556	555	10.99	1.10	123.3
1	5	53	10	157	584	719	9.78	0.98	720.0
2	5	43	13	164	498	582	9.20	0.71	533.3
3	5	53	10	145	485	606	7.29	0.73	666.7
4	5	57	10	144	515	575	7.48	0.75	880.0
1	10	57	10	141	464	614	6.09	0.61	800.0
2	10	57	9	151	401	480	4.09	0.45	1266.7
3	10	53	10	162	398	566	6.06	0.61	1333.3
4	10	37	10	180	567	719	9.06	0.91	1200.0
1	20	70	10	195	477	650	4.71	0.47	1600.0
2	20	40	10	116	423	611	5.29	0.53	1866.7
3	20	40	10	211	575	667	9.57	0.96	1600.0
4	20	57	10	130	445	616	4.79	0.48	2000.0
1	40	73	10	93	251	399	1.16	0.12	3200.0
2	40	43	9	89	229	374	1.41	0.14	3600.0
3	40	57	11	97	275	397	1.81	0.16	3600.0
4	40	53	10	85	318	436	1.49	0.15	3200.0

*For samples with sufficient dry material, plant boron concentration is the average of three analyses.

Table 24. Measurements of *Pseudoroegneria spicata* grown in sand culture.

Block	Boron in solution	Emergence	Number of plants	Plant height (mm)			Total dry weight per pot	Mean dry weight per plant	Plant boron conc.
	(ug B mL^{-1})	(%)		day 28	day 68	day 96	(g)	(g)	(ug B g^{-1})
1	0	13	5	142	343	426	5.12	1.02	10.7
2	0	0	1	5	367	576	2.19	2.19	12.0
3	0	20	7	163	450	483	7.16	1.02	8.0
4	0	7	5	182	437	482	5.87	1.17	8.7
1	1	13	3	111	434	560	4.09	1.36	137.3
2	1	20	6	152	373	505	5.32	0.89	80.0
4	1	23	7	198	444	532	10.87	1.55	306.7
1	5	15	5	146	371	529	5.95	1.19	1066.7
2	5	13	4	157	319	360	4.81	1.20	710.0
3	5	10	2	115	371	420	2.76	1.38	906.7
4	5	20	6	192	481	531	6.10	1.02	880.0
1	10	10	5	110	310	448	2.28	0.46	1800.0
2	10	10	2	126	316	491	2.73	1.37	1200.0
3	10	7	2	110	330	408	2.47	1.24	1133.3
4	10	20	6	151	500	750	6.01	1.00	1133.3
1	20	10	5	118	325	440	2.34	0.47	2400.0
2	20	13	5	144	338	488	2.24	0.45	2133.3
1	40	6	3	65	220	296	0.26	0.09	3649.0
2	40	17	5	101	310	393	1.00	0.20	3200.0
4	40	17	3	102	230	332	0.28	0.09	4219.0

*For samples with sufficient dry material, plant boron concentration is the average of three analyses.

Table 25. Measurements of *Elymus lanceolatus* grown in soil culture.

Block	Boron added to soil	Emergence	Number of plants	Plant height (mm)			Total dry weight per pot	Mean dry weight per plant	Plant boron conc.*
	(ug B g^{-1})	(%)		day 28	day 68	day 96	(g)	(g)	(ug B g^{-1})
1	0	50	10	98	295	490	1.89	0.19	12.0
2	0	60	10	112	296	354	1.62	0.16	10.7
3	0	53	10	105	210	356	1.32	0.13	8.0
4	0	53	10	149	346	435	2.23	0.22	9.3
1	1	53	8	99	386	512	2.04	0.26	8.0
2	1	63	10	110	292	458	2.18	0.22	8.0
3	1	63	11	110	319	441	1.72	0.16	8.0
4	1	53	10	140	380	508	2.42	0.24	10.7
1	5	77	12	163	365	499	1.80	0.15	16.0
2	5	47	6	100	312	446	1.78	0.30	16.0
3	5	53	10	146	435	529	2.32	0.23	16.0
4	5	67	10	191	420	501	3.43	0.34	36.0
1	10	37	9	106	377	469	1.91	0.21	29.3
2	10	40	9	97	295	372	1.48	0.19	32.7
3	10	73	10	114	294	353	1.66	0.17	37.3
4	10	63	10	153	380	431	2.35	0.24	29.3
1	20	53	9	170	484	565	2.81	0.31	80.0
2	20	47	10	112	286	399	2.15	0.22	72.0
3	20	37	11	125	370	424	1.82	0.17	60.0
4	20	40	10	174	466	519	3.24	0.32	96.0
1	40	80	11	142	355	480	2.20	0.20	153.3
2	40	63	9	101	299	470	1.92	0.19	146.7
3	40	57	10	116	296	439	2.12	0.21	146.7
4	40	70	10	139	335	419	2.24	0.22	180.0

*For samples with sufficient dry material, plant boron concentration is the average of three analyses.

APPENDIX C

Boron injury symptoms

Table 26. Observations of *Atriplex canescens* plants grown in sand culture.

Block	Boron in solution (μg B mL^{-1})	Emergence	Day 28	Day 68	End of study: leaf burn	End of study: color	End of study: flowers	End of study: roots
1	0	-*	-	-	-	-	none	-
2	0	-	-	-	(7)†	-	none	-
3	0	-	-	-	b‡	-	none	-
4	0	-	-	-	-	-	none	-
1	1	-	-	-	(7)	-	none	-
2	1	-	-	-	-	-	none	-
3	1	-	-	-	(7)	-	none	-
4	1	-	-	-	(7)	-	none	-
1	5	-	-	-	-	-	none	-
2	5	-	-	-	(7)	-	none	-
3	5	-	-	-	(7)	-	none	-
4	5	-	-	-	(7)	-	none	-
1	10	-	y§	-	-	-	none	-
2	10	-	y	-	(10)	-	none	-
3	10	-	y	-	(7)	-	none	-
4	10	-	-	-	-	-	none	-
1	20	-	-	-	(7)b	-	none	-
2	20	-	-	-	(7)b	-	none	-
3	20	-	-	y(3)	(10)b	-	none	-
4	20	-	-	-	(7)b	-	none	-
1	40	y	y	y(3)	(10)	-	none	-
2	40	-	y	-	(10)b	yellow	none	-
3	40	-	y	-	(10)b	-	none	-
4	40	y	y	-	(30)	-	none	-

* - indicates that plants appeared normal.

† number in parentheses indicates the approximate percentage of leaf area with leaf burn.

‡ b indicates that blotches were present on leaves.

§ y indicates that plants had yellow leaf tips (number in parentheses indicates approximate percentage of leaf area that appeared yellow).

Table 27. Observations of *Elymus cinereus* plants grown in sand culture.

Block	Boron in solution (μg B mL^{-1})	Emergence	Day 28	Day 68	End of study			
					leaf burn	color	flowers	roots
1	0	-*	-	-	-b†	dark green	none	L**
2	0	-	-	-	-b	light green	none	L
3	0	-	-	-	-	dark green	none	L
4	0	-	-	-	-	dark green	none	L
1	1	i‡	-	i	(7)§b	green	none	L
2	1	-	-	y‖	(7)b	light green	none	L
3	1	-	-	y	(7)b	dark green	none	L
4	1	-	-	y	(7)	dark green	none	L
1	5	-	-	-	(7)b	light green	none	L
2	5	-	-	y(25)	(7)b	dark green	none	L
3	5	-	y	y(25)	(7)b	dark green	none	L
4	5	-	y	y(25)	(7)b	dark green	none	L
1	10	-	-	-	(7)b	light green	none	L
2	10	-	-	y(15)	(7)b	dark green	none	L
3	10	-	-	y(15)	(10)b	green	none	L
4	10	-	y	y(15)	(7)b	dark green	none	L
1	20	-	y	y(25)	(10)b	light green	none	L
2	20	-	-	y(25)	(10)b	dark green	none	M
3	20	-	-	y(25)	(10)b	light green	none	L
4	20	-	y	y(25)	(10)b	dark green	none	M
1	40	y	y	-	(10)b	light green	none	S
2	40	y	y	y(25)	(10)b	light green	none	S
3	40	y	y(15)	y(25)	(30)b	light green	none	S
4	40	y	y(10)	y(25)	(10)b	light green	none	M

* - indicates that plants appeared normal.

† b indicates that blotches were present on leaves.

‡ i indicates that insect damage was evident on at least one plant in that pot.

§ number in parentheses indicates the approximate percentage of leaf area with leaf burn.

‖ y indicates that plants had yellow leaf tips (number in parentheses indicates approximate percentage of leaf area that appeared yellow).

**L=large, M=medium, S=small.

Table 28. Observations of *Elymus lanceolatus* plants grown in sand culture.

Block	Boron in solution (μg B mL^{-1})	Emergence	Day 28	Day 68	End of study			
					leaf burn	color	flowers	roots
2	0	-*	-	-	-	light green	none	-
3	0	-	-	-	-	-	none	-
4	0	-	-	-	-	light green	none	-
1	1	-	-	-	-	-	none	-
2	1	-	-	-	-	blue green	none	-
3	1	-	-	-	(7)†	b‡	none	-
4	1	-	-	lb§(7)	y	dark green	none	-
1	5	-	y‖	lb(7)	(10)	b	none	-
2	5	-	y	lb(7)	(10)	blu-green b	none	-
3	5	-	y	lb(7)	(15)	yellow	none	-
4	5	-	y	lb(7)	(15)	yellow b	none	-
1	10	-	y	lb(7)	(10)	yellow b	none	-
2	10	-	y	lb(7)	(10)	blu-green b	none	-
3	10	-	y	lb(7)	(10)	blue green	none	-
4	10	-	y	lb(7)	y	yellow b	none	-
2	20	-	-	lb(7)	(10)	yel-green b	none	-
4	20	-	y	lb(7)	(10)	yellow b	none	-
1	40	y	y(30)	lb(25)	(30)	yellow b	none	few rhizomes
2	40	y	y(20)	lb(25)	(10)	yellow b	none	no rhizomes
3	40	y	y(20)	lb(25)	(10)	yellow b	none	no rhizomes
4	40	y	y(10)	lb(25)	(10)	yellow b	none	few rhizomes

* - indicates that plants appeared normal.

† number in parentheses indicates the approximate percentage of leaf area with leaf burn.

‡ b indicates that blotches were present on leaves.

§ lb indicates that leaf burn was evident on plants (number in parentheses indicates approximate percentage of leaf area with leaf burn).

‖ y indicates that plants had yellow leaf tips (number in parentheses indicates approximate percentage of leaf area that appeared yellow).

Table 29. Observations of *Medicago sativa* plants grown in sand culture

Block	Boron in solution (μg B mL^{-1})	Emergence	Day 28	Day 68	End of study: leaf burn	leaf loss	flowers	roots
1	0	-*	-	-	-	<10†	yes‡	-
2	0	-	-	-	-	<10	yes	-
3	0	-	-	-	-	<10	yes	-
4	0	-	-	-	-	<10	yes	-
1	1	-	-	-	(7)§	10-50	yes	-
2	1	-	-	-	(7)	<10	none	-
3	1	-	-	-	(7)	<10	yes	-
4	1	-	-	-	(7)	<10	yes	-
1	5	-	-	y‖(7)	(10)	10-50	yes	-
2	5	-	-	y(7)	(10)	>50	yes	-
3	5	-	-	y(7)	(20)	>50	yes	-
4	5	-	-	-	(30)	>50	yes	-
1	10	-	-	y(7)	(40)	>50	yes	-
2	10	-	-	y(7)	(40)	>50	yes	-
3	10	-	-	y(7)	(40)	>50	yes	-
4	10	-	y	-	(30)	10-50	yes	-
1	20	-	y	y(7)	(50)	>50	none	-
2	20	-	y	y(7)	(40)	>50	yes	-
3	20	y	y(10)	y(7)	(40)	>50	yes	-
4	20	y	y	y(7)	(40)	>50	yes	-
1	40	y	y(20)	y(7)w#	(50)	>50	yes	-
2	40	y	y(20)	y(7)w	(40)	>50	yes	-
3	40	y	y(20)	y(7)w	(40)	>50	none	-
4	40	y	y(15)	y(7)w	(45)	>50	yes	-

* - indicates that plants appeared normal.

† approximate number of leaves lost from all plants in the pot.

‡ yes indicates that flowers were present on at least one plant in the pot.

§ number in parentheses indicates the approximate percentage of leaf area with leaf burn.

‖ y indicates that plants had yellow leaf tips (number in parentheses indicates approximate percentage of leaf area that appeared yellow).

w indicates that some leaves had white edges.

Table 30. Observations of *Melilotus officinalis* plants grown in sand culture.

Block	Boron in solution (ug B mL^{-1})	Emergence	Day 28	Day 68	End of study: leaf burn	leaf loss	flowers	roots
1	0	-*	-	-	-	10-50†	none	-
2	0	-	-	-	-	<10	none	-
3	0	-	-	-	-	10-50	none	-
4	0	-	-	-	-	<10	none	-
1	1	-	-	-	-	10-50	none	-
2	1	-	-	-	-	10-50	none	-
3	1	-	-	-	-	10-50	none	-
4	1	-	-	-	-	10-50	yes‡	-
1	5	-	-	y§	(7)‖	10-50	none	-
2	5	-	-	-	(7)	10-50	none	-
3	5	-	-	-	(7)	>50	none	-
4	5	-	-	-	(7)	10-50	yes	-
1	10	-	-	y	(7)	10-50	none	-
2	10	-	-	y	(7)	>50	none	-
3	10	-	-	y	(7)	>50	none	-
4	10	-	-	y	(7)	>50	none	-
1	20	-	y	y	(10)	>50	none	-
2	20	-	y	y	(7)	>50	none	-
3	20	-	y	y	(10)	>50	none	-
4	20	-	y	y	(7)	>50	none	-
1	40	y	y	y	(20)	10-50	none	-
2	40	y	y	y	(7)	>50	none	-
3	40	y	y	y	(7)	>50	none	-
4	40	y	y	y	(7)	>50	none	-

* - indicates that plants appeared normal.

† approximate number of leaves lost from all plants in the pot.

‡ yes indicates that flowers were present on at least one plant in the pot.

§ y indicates that plants had yellow leaf tips.

‖ number in parentheses indicates the approximate percentage of leaf area with leaf burn.

Table 31. Observations of *Oryzopsis hymenoides* plants grown in sand culture.

Block	Boron in solution (ug B mL^{-1})	Emergence	Day 28	Day 68	End of study			
					leaf burn	color	flowers	roots
1	0	-*	-	-	-	green	yes†	-
2	0	-	-	-	-	green	yes	-
3	0	-	-	-	-	green	yes	-
4	0	-	-	-	-	green	yes	-
1	1	-	-	-	(7)‡	green	none	-
2	1	-	-	-	(7)	green	none	-
3	1	-	-	-	(7)	green	yes	-
4	1	-	-	y§	(7)	green	yes	-
1	5	-	y	-	(15)	green	none	-
2	5	-	y	y	(15)	green	none	-
3	5	-	y	y	(15)	green	none	-
4	5	-	y	y(25)	(15)	green	none	-
1	10	-	y	y	(20)	green	none	-
2	10	no plant	no plant	y	(20)	green	none	-
3	10	-	y	y	y	green	none	-
4	10	-	y	y	(15)	green	none	-
1	20	-	y(5)	y	(25)	yellow	none	few
2	20	-	y	y	(15)	yellow	none	few
3	20	-	y	y	(30)	yellow	none	few
4	20	-	y	y	(20)	yellow	none	few
1	40	-	y	y	-	yellow	none	few
2	40	-	y	y(5)	-	yellow	none	few
3	40	-	y(10)	y(25)	-	yellow	none	few
4	40	y	y(10)	y(25)	-	yellow	none	few

* - indicates that plants appeared normal.

† yes indicates that flowers were present on at least one plant in the pot.

‡ number in parentheses indicates the approximate percentage of leaf area with leaf burn.

§ y indicates that plants had yellow leaf tips (number in parentheses indicates approximate percentage of leaf area that appeared yellow).

Table 32. Observations of *Pascopyrum smithii* plants grown in sand culture.

Block	Boron in solution (μg B mL^{-1})	Emergence	Day 28	Day 68	End of study			
					leaf burn	color	flowers	roots
1	0	-*	-	-	(7)[†]b[‡]	dark green	none	-
2	0	-	-	-	-	dark green	none	-
3	0	-	-	-	(7)	dark green	none	-
4	0	-	-	-	(7)b	dark green	none	-
1	1	-	-	-	(7)b	dark green	none	-
2	1	-	-	-	(7)b	dark green	none	-
3	1	-	-	-	(7)	dark green	none	-
4	1	-	-	-	(7)b	dark green	present	-
1	5	-	-	lb[§](3)	(7)b	dark green	none	-
2	5	-	-	lb(7)	(7)b	dark green	none	-
3	5	-	y[‖]	lb(7)	(7)b	dark green	none	-
4	5	-	-	lb(7)	(7)b	dark green	none	-
1	10	-	y	lb(7)	(7)b	dark green	none	-
2	10	-	y	lb(7)	(7)b	light green	none	-
3	10	-	y	lb(7)	(7)b	light green	none	-
4	10	-	y	lb(3)	(7)b	dark green	none	-
1	20	-	y	lb(7)	(10)b	light green	none	-
2	20	-	y	lb(3)	(7)b	light green	none	small
3	20	-	y	lb(7)	(10)b	light green	none	small
4	20	-	y	lb(3)	(7)b	dark green	none	small
1	40	y	y(40)	lb(25)	(20)b	light green	none	no rhizomes
2	40	-	y(20)	lb(25)	(10)b	light green	none	small
3	40	y	y(30)	lb(25)	(7)b	light green	none	small
4	40	-	y(25)	lb(25)	(10)b	light green	none	very small

* - indicates that plants appeared normal.

† number in parentheses indicates the approximate percentage of leaf area with leaf burn.

‡ b indicates that blotches were present on leaves.

§ lb indicates that leaf burn was present on leaves (number in parentheses indicates approximate percentage of leaf area with leaf burn).

‖ y indicates that plants had yellow leaf tips (number in parentheses indicates approximate percentage of leaf area that appeared yellow).

Table 33. Observations of *Pseudoroegneria spicata* plants grown in sand culture.

Block	Boron in solution (ug B mL^{-1})	Emergence	Day 28	Day 68	End of study			
					leaf burn	color	flowers	roots
1	0	-*	i[†]	-	-	dark green	none	-
2	0	-	-	-	-	dark green	none	-
3	0	-	-	-	-	dark green	none	-
4	0	-	-	-	-	dark green	none	-
1	1	-	-	-	-	dark green	none	-
2	1	-	-	-	(7)[‡]	dark green	none	-
4	1	-	-	-	(7)	green	none	-
1	5	-	y[§]	y	-	dark green	none	-
2	5	-	y	y	(7)	dark green	none	-
3	5	-	y	y	(7)	dark green	none	-
4	5	-	y	y	(7)	green	none	-
1	10	-	y	lb[‖](7)	(7)	light green	none	-
2	10	-	y	lb(7)	(7)	green	none	-
3	10	-	y	lb(7)	(7)	dark green	none	-
4	10	-	y	lb(7)	(7)	light green	none	-
1	20	-	y	lb(25)	(10)	light green	none	-
2	20	-	y	lb(25)	(10)	light green	none	-
1	40	y	lb(30)	lb(25)	(10)	light green	none	small
2	40	y	lb(30)	lb(25)	(10)	light green	none	small
4	40	y	lb(30)	lb(25)	(10)	light green	none	small

* - indicates that plants appeared normal.

† i indicates that insect damage was evident on at least one plant in that pot.

‡ number in parentheses indicates the approximate percentage of leaf area with leaf burn.

§ y indicates that plants had yellow leaf tips.

‖ lb indicates that leaf burn was present on leaves (number in parentheses indicates approximate percentage of leaf area with leaf burn).

Table 34. Observations of *Elymus lanceolatus* plants grown in soil.

Block	Boron added to soil (ug B g^{-1})	Emergence	Day 28	Day 68	End of study: leaf burn	color	flowers	roots
1	0	-*	y†	-	(5)‡	dark green	none	-
2	0	-	-	-	-	dark green	none	-
3	0	-	-	i§	(5)	green	none	-
4	0	-	-	-	(5)	green	none	-
1	1	-	-	-	(5)	dark green	none	-
2	1	-	-	-	(5)	green	none	-
3	1	-	-	-	(5)	green	none	-
4	1	-	-	-	(5)	green	none	-
1	5	-	-	-	(5)	green	none	-
2	5	-	-	-	(5)	green	none	-
3	5	-	-	-	(5)	light green	none	-
4	5	-	-	-	(5)	green	none	-
1	10	-	-	-	(5)	green	none	-
2	10	-	-	-	(5)	green	none	-
3	10	-	-	-	(5)	dark green	none	-
4	10	-	-	-	(5)	green	none	-
1	20	-	-	-	(5)	light green	none	-
2	20	-	-	lb‖(3)	(5)	green	none	-
3	20	-	-	lb(3)	(5)	green	none	-
4	20	-	y	-	(5)	green	none	-
1	40	i	-	lb(3)	(5)	light green	none	-
2	40	-	-	lb(3)	(5)	green	none	-
3	40	-	-	-	(5)	green	none	-
4	40	y	-	lb(3)	(5)	green	none	-

* - indicates that plants appeared normal.

† y indicates that plants had yellow leaf tips.

‡ number in parentheses indicates the approximate percentage of leaf area appearing burned.

§ i indicates that insect injury was evident on at least one plant in the pot.

‖ lb indicates that leaf burn was present on leaves (number in parentheses indicates approximate percentage of leaf area with leaf burn).