TOLERANCE OF TRITICALE, WHEAT AND RYE TO COPPER AND ZINC DEFICIENCY IN SOILS OF LOW AND HIGH pH

by

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ABSTRACT

The tolerance of triticale to soils of low copper status and low zinc status over a range of pH, both natural and artificially induced, was determined in three glasshouse experiments and compared with its parent species, wheat and rye.

In the first experiment, the tolerance of triticale to low copper status was determined in a neutral soil adjusted to both acid and alkaline pH. Intermediate tolerance of triticale was demonstrated, in that triticale was tolerant like rye at pH 5.0, but sensitive at pH 8.4 like wheat. Rye maintained the highest concentrations of copper and wheat the lowest, and concentration decreased with increasing pH. Uptake of copper showed the same pH dependence as concentration, and again rye had highest uptake of copper and wheat the least.

The second experiment was identical in design to the first experiment, but examined the tolerance of triticale to soil of low zinc status. Again, intermediate tolerance of triticale was demonstrated. At the alkaline pH in this experiment, where zinc was limiting, triticale was sensitive like wheat, although maintaining both a total shoot yield and grain yield intermediate between wheat (least) and rye (highest). Rye was tolerant of zinc deficiency. The concentration and absolute content of zinc in all plant parts of rye and triticale were higher than those of wheat at maturity, irrespective of the zinc status of the soil and in all pH environments.

Three natural soils (pH 5.0, 7.1, and 8.8) deficient in copper and zinc, were chosen for the third experiment in which growth responses of triticale, wheat and rye were compared at low and high levels of the limiting trace elements. Results further established the tolerance of rye to extremes of pH, and to both copper and zinc deficiency whether separately

or together, the relatively greater sensitivity of wheat, and the intermediate performance of triticale. Typically positive interactions between zinc and copper were observed in vegetative yield and grain yield and most strikingly in pollen viability on which the patterns of grain yield were based. A basic difference in the physiological effects of copper and zinc deficiency was on pollen viability: adding zinc alone aggravated copper deficiency and decreased pollen viability and yield, whilst adding copper alone generally increased pollen viability and yield. Genotypic differences in the copper-zinc interaction showed up strongly at higher pH where grain was produced only by rye and triticale in the unfertilised treatment.

Although there were marked differences among genotypes in their sensitivity to a single deficiency of copper or zinc, the copper-zinc interaction was physiologically similar for all genotypes in each soil.

Results of all three experiments were consistent in that rye was most tolerant of copper and zinc deficiency in all soils and that wheat was most sensitive. It was also evident that effects of copper were more on grain yield, whilst effects of zinc were mediated more through effects on general vigour and vegetative yield. Thus, artificial pH adjustment led to the same conclusion as natural extremes of pH.

This study showed conclusively that pH did indeed effect the uptake of copper and zinc, however, pH had a larger influence on the availability of zinc than of copper. This was contrary to the findings of Piper and Beckwith (1949), who found that pH had no effect on the availability of copper.

DECLARATION

This thesis contains no material that has been accepted for the award of any other degree or diploma in any University and, to the best of my knowledge and belief, it contains no material previously published or written by another person, except when due reference is made in the text.

S. P. HARRY

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1.0 INTRODUCTION

Despite many years of research, new reports of micronutrient deficiency in traditional cereals in South Australia still occur, particularly those of copper and zinc. This appears to be due largely to the increased use of macronutrient fertilizers, especially nitrogen, which aggravates copper and zinc deficiency (Chaudhry and Loneragan, 1970).

The pH of the soil is the most important single characteristic governing the availability of trace elements to plants, and is of particular importance in connection with liming, fertilizing and soil management. Peech (1941) found that the amount of exchangeable copper and zinc decreased as the soil pH was raised, and postulated that this was due to a decrease in solubility of copper and zinc compounds at the higher pH values. The effect of pH on availability of copper in general, however, is debated. A study by Piper and Beckwith (1949) considered that availability of copper in soil was not much affected by pH over a wide range.

Copper deficiency has been found in South Australia in sands and other light-textured soils including solodized solonetz soils, solodic soils and lateritic podzolic soils on Eyre Peninsula, in the Murray Mallee and in the Upper and Lower South East of the State (Riceman and Donald, 1938; Tiver, 1955; King and Alston, 1975a; Graham and Nambiar, 1981). Responses to application of copper have also occurred in calcareous and alkaline soils, peat and muck soils, regosols and alluvials (Tiver, 1955; Caldwell, 1971; King, 1974; Graham and Nambiar, 1981).

Occurrences of zinc deficiency are more frequently observed on alkaline and calcareous soils than on acid soils, and are attributed to the low solubility products of zinc complexes and carbonates at high pH (Lucas and Davis, 1961; Udo *et al.*, 1970) and to the formation of insoluble zinc hydroxides (Lucas and Davis, 1961). Zinc deficiencies that occur on

acid soils are usually associated with low total soil zinc content (Lucas and Davis, 1961), although acid soils may show high total zinc and low available zinc. In high rainfall areas where acidic conditions prevail, weathered minerals release zinc which is soon removed by leaching (Lucas and Davis, 1961).

Vose (1963) has reported that cereals differ markedly in their sensitivity to such nutrient deficiencies in soils. Differences between genotypes in copper nutrition among cereals have been reported by Smilde and Henkens (1967), Piper (1942) and others. They found that susceptibility to copper deficiency fell into the order: wheat > oats > rye. Barley has a position intermediate between wheat and oats (Nambiar, 1976b). Toms (1958) working in Western Australia, concluded, as a result of field observations, that oats was much more sensitive to zinc deficiency than was wheat or barley. Wheat was found to be sensitive to zinc deficiency, although differential response occurred among varieties (Shukla and Raj, 1974). Little is known about rye in this regard, although it was found by Gladstones and Loneragan (1967) to have the highest zinc content of the cereals.

Cereal rye, adaptable to a range of climatic conditions and soil types, has gained recognition because of its ability to grow on acid soils which are ordinarily too acid for wheat plants to thrive (Herriot, 1948). In addition, rye has long been sown as the cereal for the impoverished soils in South Australia and has been used to stabilize sand dunes (Blencowe, 1957). These soils cover large areas of southern and western Australia and are naturally deficient in trace elements (King and Alston, 1975a).

As early as the 19th century the idea of producing a hybrid between wheat (Triticum) and rye (Secale) was conceived; this hybrid

now being known as triticale. A major objective in triticale development was to introduce a well adapted crop on to marginal lands such as light, sandy and acid soils, to which rye is well adapted but wheat and other traditional cereals are ill-adapted. Muntzing (1961) established that triticale was best suited to conditions of soil and climate that were intermediate between those for wheat and rye. Triticale is now sown throughout the world and shows promise of high yield, high lysine content and like rye, good performance on sandy soils.

A high degree of tolerance to soil acidity was found in triticale by Slootmaker (1974) and attributed to the addition of the rye genome in that genotype. Triticale was also observed to be intermediate between wheat (sensitive) and rye (tolerant) in tolerance of aluminium toxicity in soils (Mugwira *et al.*, 1976) and Mugwira and Patel (1977). However, many of the nutritional needs of triticale have not been established because of the relatively short history of the crop. Little is known about the tolerance of triticale to low concentrations of available trace elements in soils over a wide range of soil acidities.

Graham and Pearce (1979) have shown that the difference in response of wheat and rye in copper-deficient soils is due to the ability of rye to maintain a higher concentration of copper in the shoot. In their study, the yield of hexaploid triticale without added copper was comparable to that of wheat with the highest level of copper. Clearly, the hexaploid triticale had followed its rye parentage in its tolerance of low copper supply. It is of interest, then, to know if triticale has inherited the tolerance of rye to copper deficiency under other soil (pH) conditions.

The object of this thesis has been to examine the tolerance of triticale, in comparison to wheat and rye, to low concentrations of

available copper and zinc, both separately and together over a range of soil acidities in both natural and pH-adjusted soils, and to examine the nature of the copper-zinc interaction amongst the genotypes.

2.0 LITERATURE REVIEW

2.1 COPPER AND ZINC IN SOILS

2.1.1 Content and Distribution of Copper and Zinc in Soils

Eight of the seventeen elements essential for growth of plants and microorganisms are required in minute quantities and occur in soils in small amounts (Leeper, 1970; Russell, 1973). The trace elements (micronutrients) as they are called are iron, manganese, zinc, copper, boron, molybdenum, cobalt and chlorine.

Copper

The copper content of soils ranges from traces to 250 ppm but generally lies between 2 and 100 ppm (Tisdale and Nelson, 1975). Steenbjerg (1940) determined total copper in surface soils of different parental origin and attributed variations to:

(1) the different copper contents of the parent rocks on which the soils had been formed,

(2) the type of soils corresponding to the differences which exist between the principal climatic zones and geographic regions.

Copper content of the surface soil is usually higher than that of the parent material due to eluviation of other materials and the addition of plant residues to the upper horizons of the soil profile (Tisdale and Nelson, 1975). King and Alston (1975a) examined a number of soil profiles and found that EDTA-[1] extractable copper decreased with depth in the soil profile, as did the total copper content.

Zinc

The content of zinc in lithosphere rock is generally between 10 and 250 ppm, but an average surface soil usually contains about 100 ppm zinc (Mitchell, 1972). Variations in soil zinc content that

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[1] ethylenediaminetetraacetic acid

occur are due primarily to the different concentrations in the parent material from which the soils were derived. Soils originating from basic igneous rocks are higher in zinc, while soils derived from more siliceous parent materials are particularly low (Udo and Fagbami, 1979).

Follett and Lindsay (1970) reported that total zinc is uniform throughout the soil profile (37 profiles) and does not accumulate at the surface to any extent, but that DTPA-[1] extractable zinc decreased with depth. Alston and McConaghy (1965) also showed that the amount of EDTA- extractable zinc decreased sharply with depth in the profile.

2.1.2 Copper and Zinc Minerals in Soils

Trace elements may replace a proportion of the major ions constituting rock and clay silicates, or may be occluded when precipitates are formed during decomposition and soil formation (Le Riche and Weir, 1963).

Copper

Copper occurs in its native state 99.9 % pure, but more frequently as sulphides and oxides (Sauchelli, 1969). Sulphide minerals include chalcopyrite, chalcosine, bornite and copper mica, whilst oxides are red copper ore, cuprite and tenorite.

In sedimentary rocks, copper minerals occur as sparse grains or as widely dispersed patches although occasionally they are abundant enough to form ore deposits (Krauskopf, 1972). In igneous rocks, copper is more heavily concentrated in basalt than granite (Krauskopf, 1972), and occurs mainly in the following forms:

(1) as submicroscopic grains of sulphide between the silicate minerals,

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[1] diethylenetriaminepentaacetic acid

(2) as a trace metal substituting for the major elements in ferromagnesian silicates,

(3) as ions or salts adsorbed in films on the surfaces of silicate crystals.

Copper has a high ionization potential and occurs in soil almost exclusively in divalent form (+2), although it also shows +1 valence under reducing conditions (Krauskopf, 1972). The Cu^{2+} ion is the common species in the environment of higher plants. Weathering of primary ore deposits produces the blue and green secondary minerals; the carbonates, malachite and azurite, and the hydrous silicate, chrysocolla being most common (Krauskopf, 1972).

Zinc

Zinc has a single valence state of +2 and commonly shows 4-coordination in mineral structures, although 6- coordination with oxygen is not unusual (Krauskopf, 1972).

Zinc is scattered throughout the mineral fraction of soils, its ions being held in crystal lattices and as occluded ions (Lindsay, 1972b). Zinc substitutes for Mg^{2+} and Fe^{2+} in silicate minerals since the ionic radius of the Zn^{2+} is similar to that of the aforementioned ions (Goldschmidt, 1954). These minerals make up the bulk of zinc in soils. Zinc also forms three silicate minerals of its own, but natural occurrences of these minerals are rare (Krauskopf, 1972). A number of zinc salts exist, including zinc sulphide (ZnS), sphalerite (ZnFeS), zincite (ZnO) and smithsonite ($ZnCO_3$), but these salts are too soluble to persist in soils for any length of time (Lindsay, 1972b).

In igneous rocks, zinc does not form independent silicate minerals nor does it occur to any extent in quartz or feldspars (Lindsay,

1972b). Zinc occurs in ferromagnesian and magnetite minerals in basic rocks, while in acid rocks it appears in hornblende and biotite minerals (Sullivan, 1972).

2.1.3 Adsorption of Copper and Zinc in Soils

Adsorption may be defined as the adhesion of the elements, in an aqueous medium, to the surface of solid materials including clay minerals, organic matter, and iron and aluminium oxides (Ellis and Knezek, 1972).

Copper

Copper in the adsorbed state in soils occurs primarily as a consequence of the tendency of copper atoms to form strong covalent bonds (Northmore, 1959). Copper adsorption is usually strong enough to keep the concentration of copper in soil solution low; however, where the conditions are acid and oxidizing, abundant copper may be present in solution (Krauskopf, 1972). Assuming adsorption as the cupric ion, copper may be adsorbed by soil colloids in amounts in excess of their conventional exchange capacities, that is, adsorption of copper by these colloids can take place in the presence of concentrations of calcium and other major nutrient cations large enough to prevent adsorption on normal cation exchange sites (Sauchelli, 1969).

Heydemann (1959) showed that copper is adsorbed by quartz and, appreciably more strongly, by clays. Adsorption by the clays increased as pH was increased and the adsorption capacity of the clays increased from kaolin to illite to montmorillonite. Heydemann also found that adsorption on calcite, as a function of the copper concentration was not described by the Freundlich adsorption isotherm, unlike that on quartz and the clay minerals. This was interpreted to be the result

of a chemical reaction with the carbonate, although no specific compound could be identified.

Organic matter contributes significantly to the cation exchange capacity of soils and consequently contributes to the capacity to fix copper (McLaren and Crawford, 1973). The higher the percentage of organic matter in mineral soils, the greater is the capacity for fixation of copper. Organic matter will preferentially adsorb copper on negative sites until its cation exchange capacity is saturated (Tisdale and Nelson, 1975).

The influence of soil organic matter on the adsorption of copper in soils is discussed in more detail in Section 2.2.2.3.

Zinc

Zinc is adsorbed to solid surfaces. In experiments with clays (Bingham *et al.*, 1964; Reddy and Perkins, 1974) and organic matter (Randhawa and Broadbent, 1965; Tan *et al.*, 1971), more zinc was adsorbed in basic environments than in acidic environments. Udo *et al.* (1970) and Singh and Sekhon (1977) showed that in calcareous soils zinc can be adsorbed by calcium carbonate and that this follows the Langmuir isotherm in its linear form.

Elgabaly and Jenny (1943) found that the reaction of zinc with montmorillonite resulted in some adsorbed zinc becoming non-extractable. This was due to the zinc entering the octahedral layer of the mineral and being fixed in holes normally occupied by aluminium ions. Elgabaly (1950) extended this work to include many minerals and reported that vermiculite, brucite and talc all combined with large amounts of zinc. Nelson and Melsted (1955) made similar observations

with montmorillonite and noted that strongly-bound zinc was desorbed according to first-order chemical kinetics.

2.1.4 Solubility and Mobility of Copper and Zinc in Soils

The solubility of the trace element cations are significantly affected by soil pH, organic matter content and the nature and strength of the adsorption by soil surfaces (Norvell and Lindsay, 1969).

Copper

Norvell and Lindsay (1969) expressed the solubility of copper minerals in soils by the relationship

$$(Cu^{2+}) = 10^{3.2} (H^{+})^{2}$$

which depends on the temperature and pH of the medium. Copper can be eluted below pH 4.5, however, above that pH, sparingly soluble copper hydrates may be formed, although the cupric ion still predominates (Lindsay, 1972a). When the pH exceeds 7.3, $CuOH^{+}$ is abundant, although precipitates appear together with copper bound as phosphates, sulphates and carbonates (Lindsay, 1972a). Copper may also be bound in the soil as oxalate, citrate and as salts of other acids, which being water-soluble, increase the mobility of copper at higher pH.

Nearly all copper in the soil solution is in complexed form. Complexing increases the total copper concentration in solution, but the mechanism by which complexing affects the nutrition of plants is not fully understood. Total copper in the soil solution is relatively high compared with the amounts required by plants (Hodgson *et al.*, 1966; Graham, 1978b).

It is known that complexing agents compete to some degree with the root for the metal, and therefore a continual equilibrium between cation and complexing agent in solution at various distances from the root must exist (Cavallaro and McBride, 1980).

Mobility of copper may be considerable in light soils, but is low in heavy loams and even less in peaty soils, depending on the extent and nature of the adsorption on soil surfaces (Ermolenko, 1972). In non-acid and non-oxidizing solutions the movement of copper is restricted (Krauskopf, 1972). Mobile copper is encountered in the soil solution as soluble salts since the water insoluble copper sulphides are slowly oxidized to soluble sulphates by atmospheric oxygen. Copper which forms part of the alumino-silicate lattice is difficult to dissolve in comparison to the copper sorbed by ion exchange (Brady, 1978).

Zinc

Zinc is sparingly soluble in soils (Lindsay, 1972b). The solubility of Zn^{2+} in soils is expressed by the relationship

$$(Zn^{2+}) = 10^{6}(H^{+})^{2}$$

as determined by Norvell and Lindsay (1969), which shows a significant effect of pH on zinc ion solubility in soils. The soil matrix of iron, aluminium, manganese and other oxides, carbonates and silicates impose some control on the solubility of zinc in soils (Lindsay, 1972b). Similarly, the solid phase minerals and adsorption reactions prevent a high concentration of zinc from persisting (Lindsay, 1972b).

Weathering of zinc minerals gives Zn^{2+} in solution and this ion remains dominant to pH values about neutrality (Krauskopf, 1972). Soil solutions also contain hydrolysed species of the zinc ion (Lindsay,

1972a and b). Above neutrality, the neutral species $Zn(OH)_2$ aq is abundant, but at high concentrations of sulphate in the soil, the formation of $(ZnSO_4)$ aq occurs. This complex can increase the solubility of zinc since it is expected to be highly mobile in soils (Lindsay, 1972a).

2.2 AVAILABILITY OF COPPER AND ZINC TO PLANTS

2.2.1 Patterns of Copper and Zinc Deficiency

Copper and zinc are present in most soils in quantities sufficient for the needs of crops; however, some soil conditions exist which reduce their availability as plant nutrients. Graham (1978b) has calculated that even deficient soils contain absolute amounts of trace elements sufficient for thousands of crops, and pointed out that the problem may be viewed as one of the ability of the plants to extract their requirements from the soil.

Copper

Responses to application of copper occur in sandy soils, calcareous and alkaline soils, peat and muck soils, regosols and alluvials (Tiver, 1955; Caldwell, 1971; King, 1974). Deficiency is exacerbated in deficient soils heavily fertilized with nitrogen (Graham and Nambiar, 1981) and is common in leached acid soils (Truog, 1946). In South Australia, copper deficiency occurs in sands and other light-textured soils, including solodized solonetz soils, solodic soils and lateritic podzolic soils on Eyre Peninsula, in the Murray Mallee and in the Upper and Lower South East of the State (Riceman and Donald, 1938; Tiver, 1955; King and Alston, 1975a).

For many crops in mineral soils, values of 0.5 to 3.0 ppm extractable copper and 7.0 to 8.0 ppm total copper are considered as the deficiency limits (Reuther and Labanauskas, 1966).

Zinc

Deficiencies of zinc are not common on acid soils and when they do occur, it is an indication of very low levels of total zinc (Lucas and Davis, 1961). However, acid soils may have higher than usual total zinc and low available zinc because that zinc which is released by weathering is lost from the profile (Lindsay, 1972b). In arid and semi-arid regions also, sandy soils are frequently deficient in available zinc, this being a consequence of a low total zinc content of the quartz from which the sand is derived (Lindsay, 1972b).

The total zinc content in the soil is poorly correlated with the amount of zinc that is available to the growing crop. Most of the zinc in soil is present in combined form either in organic complexes or in various minerals. It is therefore not readily available to plants, since they mainly take up zinc from water-soluble or exchangeable forms of zinc (Sauchelli, 1969). Water-soluble zinc is often as high in sandy soils as in finer textured soils, however, the labile zinc content is much lower so that more extensive depletion zones of zinc occur in the immediate vicinity of roots in sand (Lindsay, 1972b).

2.2.2 Factors Affecting Availability of Copper and Zinc

2.2.2.1 Restricted Root Zones

Lack of oxygen curtails the absorption of water and nutrients (Lucas and Knezek, 1972). Poor soil aeration is usually caused by excess water; however factors such as microbial activity, temperature, and bulk density can also affect the diffusion and composition of soil air.

Zinc deficiency frequently occurs on soils with restricted root zones which can be caused by hardpans and high water tables (Lindsay, 1972b). Areas of compacted soils caused by tractor wheels may

also result in deficiency on some soils (Lucas and Knezek, 1972). Occasionally however, this type of effect may be more pronounced on another element, leading to less competition on zinc absorption. Thus, Labanauskas *et al.* (1966) reported that a decrease in soil oxygen supply to roots of orange seedlings reduced copper in the roots while zinc, manganese, boron and iron were increased.

2.2.2.2 Soil pH

The availability of trace elements to plants is affected by pH changes, whether induced by liming, chemical or biological effects (Truog, 1951). Even small changes in pH values may markedly influence the availability of trace elements in the soil because pH is a logarithmic function (Stolen and Andersen, 1978). It is not easy, however, to decide whether the observed effect of pH on trace element uptake is due to the pH change alone or to factors associated with it. Such factors include increased calcium status, enhanced bacterial activity or the presence of the bicarbonate ion (DeKock and Cheshire, 1968).

The influence of soil reaction (pH) on the availability of plant nutrients is of tremendous importance in connection with liming, fertilizing and soil management (Truog, 1946). With the exception of molybdenum, the availability of all trace elements increases with a decrease in pH (Tisdale and Nelson, 1975).

Soil reaction is a principal factor influencing fixation and leaching of many fertilizer constituents and therefore plays an important role in governing the availability and utilization of ions in light sandy soils (Peech, 1941). Likewise, the availability of the native supplies of the more insoluble nutrients, is influenced by soil reaction. Under acid soil conditions the native supplies of many soil nutrients become

depleted more rapidly because of greater rates of dissolution and leaching of soil minerals (Peech, 1941).

Though comparatively little hydrogen ion is exchanged by cations from their neutral salts, it is readily replaced by lime and other basic materials commonly used to correct soil acidity (Peech, 1941):

$$2H^{+}\ (soil) + CaCO_3 \rightleftharpoons Ca^{2+}\ (soil) + H_2O{+}CO_2$$

Addition of lime to correct excessive soil acidity reduces losses by leaching and helps to conserve the fertilizer constituents applied in the form of neutral salts. Raising pH, however, by the indiscriminate use of lime to the point favourable to fixation of ions into nonexchangeable or more insoluble forms may offset any benefits derived from liming (Peech, 1941) by inducing deficiencies of trace elements such as Mn, Cu, Zn.

Copper

Peech (1941) found that the amount of copper recovered by single extraction with 1M sodium chloride solution from three soils decreased rapidly with increase in pH of the soil and postulated that this was due to a decrease in solubility of copper compounds at higher pH values. Where availability for a given copper content was compared at various pH levels, Lucas and Davis (1961) showed that soils with a pH of 7.0 to 8.0 released the smallest amounts of copper.

Early investigations indicated that on some soils copper is slightly more available to plants under acid soil conditions than under neutral or alkaline conditions (Piper, 1942; Piper and Walkley, 1943; Oertel *et al.*, 1946). However, Piper and Beckwith (1949) examining

amounts of copper taken up by three plant species (*Medicago denticulata, Erodium cygnorum* and *Hordeum leporinum*) in a study on two neutral soils adjusted to acid and alkaline extremes by addition of sulphur and calcium carbonate, respectively, found otherwise: the effect of soil pH on the availability of copper was very small and insignificant. All three species of plants showed that nearly as much copper was taken up from neutral and alkaline soils as from acid soil.

In a study on an acid soil (pH 4.3) adjusted to three pHs by the addition of various rates of dolomitic limestone, both the concentration and uptake of copper by *Zea mays* were greater at the higher pHs (Lutz *et al.*, 1972). This was unexpected since it had previously been reported that copper availability decreased with increased pH (Piper, 1942; Piper and Walkley, 1943; Oertel *et al.*, 1946). The data obtained was in partial agreement with the work of other investigators (Piper and Beckwith, 1949; Blevins and Massey, 1959; McKenzie, 1966), who found no relationship between soil pH and copper uptake. Blevins and Massey (1959) did find, however, that increasing the aluminium concentrations in solution-culture at levels greater than 0.1 ppm decreased the copper uptake by wheat plants. Lutz *et al.* (1972) found in their study that KC1-extractable aluminium was higher at acid pH than neutral pH, and postulated that the concentrations of aluminium in the soils were the cause of the unexpected results.

The effect of pH on the availability of copper to plants in general is debated, and requires further examination to verify findings reached to date. In addition, little is known about the effect of pH on the uptake of copper by triticale, the hybrid of wheat and rye, because of the relatively short history of the crop.

Zinc

For a given zinc content the availability is increased as the soil becomes more acid (Wear, 1956; Lucas and Davis, 1961; Lutz *et al.*, 1972). When the pH was increased, the solubility of Zn^{2+} decreased and above neutrality the availability of zinc declined considerably (Wear, 1956; Melton *et al.*, 1973). Wear (1956) concluded from data presented in his study that decreased uptake of zinc by plants from the use of lime was the result of a pH effect and not a calcium effect. It seemed likely that a soluble form of zinc at lower pH was converted to a less soluble and less available form in the soil at higher pH values. Brown and Jurinak (1964) examined the effect of lime on zinc availability and reached the same conclusion as Wear (1956), and also observed that copper followed a similar pattern to zinc. Working on an acid soil (pH 4.3) adjusted to three pHs by the addition of various rates of dolomitic limestone, Lutz *et al.* (1972) found that the average zinc concentration and uptake in *Zea mays* decreased with increased pH, but uptake values were not significantly different at pH 5.1 and 6.1.

Most zinc disorders occur on calcareous soils and highly limed soils, and are attributed to the low solubility products of zinc soil complexes and carbonates (Udo *et al.*, 1970), or hydroxides (Lucas and Davis, 1961). Zinc also combines with phosphorus in the soil under neutral to alkaline conditions to form insoluble zinc phosphates (Udo *et al.*, 1970). The minimum zinc solubilities coincide with the pH values of 6.0 to 8.0 and it is within this region that most deficiencies are recorded (Tisdale and Nelson, 1975).

The amount of copper and zinc extracted from three soils decreased rapidly with increase in pH of the soil (Peech, 1941). In addition, the amount of copper extracted was considerably lower than the

amount of zinc extracted at any given pH, indicating that copper is the more strongly fixed of the two cations, despite the fact that both are precipitated as hydroxides. Similarly, Dolar and Keeney (1971b), MacLean and Langille (1976) and Sedberry *et al.* (1980) all showed conclusively that the amounts of zinc extracted from soils using various chemical extractants decreased with increases in soil pH.

As is the case for copper, little is known about the effect of pH on the uptake of zinc by cereals, but more particularly triticale, because of its short history. Nothing is known about rye in this regard.

2.2.2.3 Soil Organic Matter

Organic matter is an important secondary source of trace elements which are held as complexes not always available to plants, their release through decomposition of organic matter being undoubtedly an important fertility factor (Brady, 1978). Stevenson and Ardakani (1972) and McLaren and Crawford (1973) concluded that insoluble metal combinations are most likely bound to the humic fraction (particularly humic acids), while soluble metal complexes are mainly associated with individual biochemical molecules (e.g. organic acids and amino acids). Metal complexes with fulvic acids also have high water solubilities (Stevenson and Ardakani, 1972; Lindsay, 1972b).

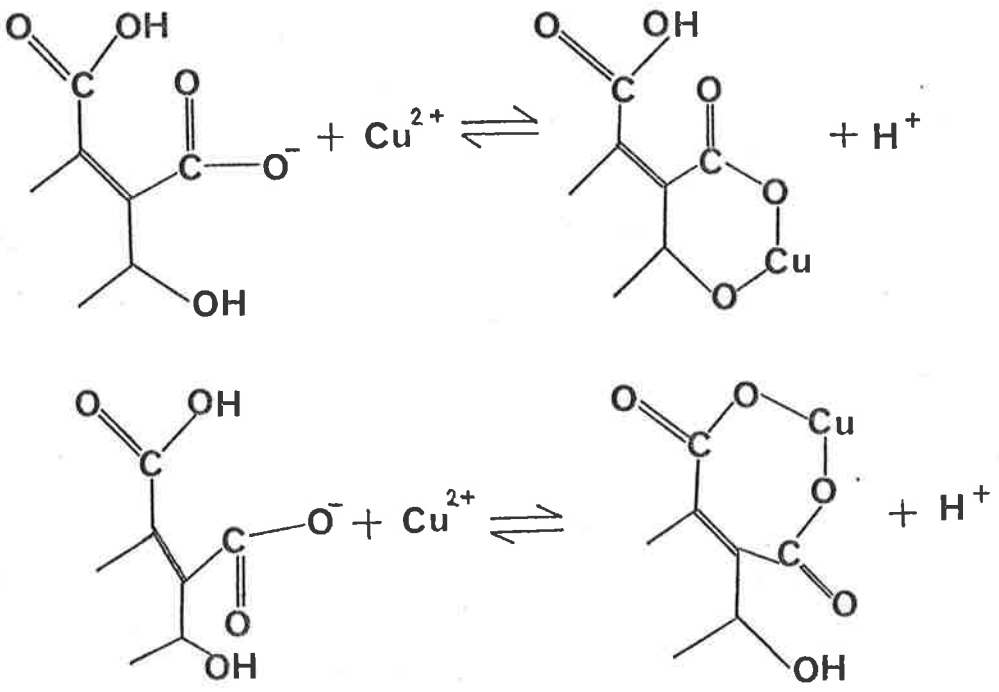
Copper

Petruzelli and Guidi (1976) suggested that native copper, and some of the copper added to soils is strongly linked to humic substances and not available to plants. They found, however, that copper linked to lower molecular weight fulvic substances was absorbed by plants and the functional groups involved in binding copper were weak acids whose configurations offered opportunity for chelation. Broadbent

(1957), using a chromatographic technique, observed that four types of sites were responsible for the retention of copper by humic acids; however, he only identified one of the four: carboxylic groups. Lewis and Broadbent (1961) found that retention of metals involved phenolic-hydroxy groups of varying acidities, normal carboxylic groups, and a group of sites more acidic than the normal carboxylic groups.

Goodman and Cheshire (1973) found that complexes which were stable to successive washings with hydrochloric acid contained copper coordinated to porphyrin derivatives in the humic acid. Hodgson, Lindsay and Trierweiler (1966) and Geering and Hodgson (1969) showed that 98 percent of copper in displaced soil solutions of calcareous soils was present as organic complexes.

Equilibrium reactions between cupric ions and functional groups of fulvic acids were postulated by Gamble *et al.* (1970) and were as follows:



Zinc

Zinc is closely associated with the organic fraction of soils, although organic matter does not influence the availability of zinc as much as it does the availability of copper (Leeper, 1970). High levels of organic matter in the upper horizons of soils are important in maintaining adequate supply of available zinc, particularly in calcareous soils, since zinc released from decomposing plant material is in available form (Martens *et al.*, 1966; Follett and Lindsay, 1970).

Randhawa and Broadbent (1965) showed that although zinc was less strongly bound on humic acids than copper or ferrous ions, this organic matter fraction was still important in the retention of zinc and three or more sites of adsorption were involved. The least stable fraction, which accounted for most of the zinc, was associated with phenolic-hydroxy groups and weakly acidic carboxylic groups. The more stable fraction of zinc was bound by strongly acidic carboxylic groups.

About 75 percent of soluble zinc is chelated to organic matter (Hodgson, Lindsay and Trierweiler, 1966).

2.2.2.4 Micro-organisms

Micro-organisms are highly efficient concentrators of trace elements (Lucas and Knezek, 1972) and compete with higher plants. Zinc deficiency is often quite pronounced on old corral sites and barnyards where it is believed to be the result of rapid microbial growth which causes biological fixation (Lindsay, 1972b). Copper is also fixed in microbial cells in the soil. Soil sterilization released significant amounts of copper to higher plants (Piper, 1942).

2.2.2.5 Soil Temperature

Copper

Reddy (1976) found that increasing soil temperature raised the copper concentration in the tops of subterranean clover. He proposed that increasing soil temperature would result in more rapid decomposition of the soil organic materials with accompanying release of copper. Results of Cheng and Pesant (1977) contradict this earlier finding. They found that copper contents were higher in oat plants grown at the lower temperature, for both aerial and root portions of the plant.

In an incubation study, Harry and Alston (1981) showed that EDTA-extractable copper increased or decreased with increasing temperature depending on the soil and how it was treated. In addition, less copper was extracted from soils incubated at fluctuating temperature than from those where incubation temperature was constant.

Zinc

Zinc deficiencies often encountered in field crops during the early growing season tend to disappear by midseason (Ferres, 1949; Millikan, 1953). In Colorado, Bauer and Lindsay (1965) observed that zinc deficiencies were often severe during cool, wet spring seasons and disappeared by mid-July; they concluded that decreased solubility of soil zinc rather than a biological effect was the main reason for this. Higher temperature rendered more available the zinc in the soil.

Other explanations for the effect of temperature on zinc have been proposed:

(1) the root system of the plants are not well developed in cool soils such that their feeding zone is restricted (Lindsay, 1972b);

more roots are developed when soil temperature is increased (Viets and Lindsay, 1973).

(2) available zinc may come from organic matter, and in cool soils reduced microbial activity may be such that insufficient available zinc is released (Lindsay, 1972b).

2.2.3 Movement of Trace Elements to Plant Roots

Ions move in the soil water to the root surface by two distinct processes, mass flow or convection and diffusion (Barber, 1962). Mass flow is the movement of dissolved nutrients carried by the water flow through the soil to the plant root, which occurs as a result of transpiration (Barber, 1962; Barley, 1970). Movement by diffusion occurs over short distances as a result of a concentration gradient arising when the ions are being taken up faster than they can be carried to the surface by mass flow (Barber, 1962; Barley, 1970).

Combining these two processes, a simple equation for the flow of an ion to a plant root is:

$$F = -D_e \left(\frac{\delta C}{\delta r}\right) + VC$$

where C is the total concentration of diffusible metal i.e. labile pool (moles/cm^3 of soil), r is the radial distance from the root axis (cm), V is the inward flux of water into the root (cm^3 cm^{-2} sec^{-1}), F is the inward radial flux of the ion (moles cm^{-2} sec^{-1}) and D_e is the effective diffusion coefficient (cm^2 sec^{-1}) (Barber, 1974).

Mass flow and diffusion are complemented by root interception, an additional process by which roots run into or intercept nutrients in their path (Barley, 1970; Wilkinson, 1972). Consequently, the intensity of soil exploration by roots will have an influence on the total supply

of nutrients. The ions absorbed from the soil by a root arrive at the root surface because:

(1) they have moved through the soil,

(2) the root has grown into a previously unexploited region (Barley, 1970).

The concentration of ions at the root surface can change from that in the bulk solution, depending on the relative rates of absorption by the roots and mass flow in the soil solution (Milthorpe and Moorby, 1974). Copper and zinc do not reach the root surface under the influence of conventional water flow as fast as they are absorbed by roots: consequently, zones of zinc depletion are known to occur in the vicinity of plant roots (Chaney, 1975). It appears that these ions move to the plant root predominantly by diffusion.

2.2.4 Absorption and Translocation of Copper and Zinc by Plants

Nutrient uptake can be resolved into a metabolic and a non-metabolic component (Jacobson *et al.*, 1958) and metabolically mediated nutrient uptake occurs in all actively metabolizing tissue. Nutrients absorbed are accumulated in root cells as well as being translocated to aerial parts of the plant (Jarvis, 1978; Graham, 1979; Jarvis and Robson, 1982).

Absorption of ions by active processes, including simple and Donnan diffusion, exchange adsorption into cytoplasm and active metabolic accumulation into symplasm, is selective, involving selectivity of uptake and selectivity of translocation (Russell, 1972). Selectivity depends completely on the presence of calcium, in the absence of which selectivity breaks down (Epstein, 1972).

If ion uptake is considered simply as the transfer of ions across the root surface, the rate of ion uptake can be written as:

$$dQ/dt = 2\pi \alpha \eta C, \text{ where } C = Co$$

where Q is the uptake per unit length of root (moles cm^{-1}), α is the apparent surface conductance of the root (cm sec^{-1}), η is radius of root zone (cm) and Co is the initial concentration for a particular ion species in the soil solution (Barley, 1970). The rate of ion uptake per unit area of root surface changes with time and along the length of the root axis and between axes within the root system (Milthorpe and Moorby, 1974); however, not all roots are concerned primarily with the absorption of water or nutrients.

The magnitude of the resistance that the soil offers to the transfer of nutrients depends on whether the dominant transfer process is diffusion or convection, the values of the transfer coefficients existing in the soil and on the lengths of the paths along which nutrients move to the root surface (Barley, 1975). Rooting density, defined as the length of root operative in nutrient uptake per unit volume of the soil, exerts a strong influence on nutrient uptake, particularly when transference is not efficient (Barley, 1970). Barley (1970) also showed that root elongation affects uptake, especially in the uptake of less mobile nutrients. Although root hairs increase the surface area of roots available for absorption, the restricted movement of ions through the soil results in the concentration of ions within the root zone being depleted. Hence, the overall effect of root hairs is to increase the effective diameter of the root (Barley, 1970; Milthorpe and Moorby, 1974).

Copper

Copper and zinc are taken up readily by plants in ionic form but not so readily in chelated form (DeKock and Mitchell, 1957; Loneragan, 1975). DeKock and Mitchell (1957) obtained data at high concentrations of trace elements which showed a five- to ten-fold reduction in the rate of absorption of copper and zinc by plant roots when the chelate EDTA was present. They suggested that the charge on the chelate molecule governed its uptake by plants and that there were physiological problems associated with the absorption of large molecules by plants. Evidence obtained by DeKock and Mitchell (1957) and Dragun *et al.* (1976) support the view that copper is absorbed as Cu^{2+} since the addition of chelates of copper to the external medium reduced the rate of its absorption. The evidence that copper is absorbed as the Cu^{2+} ion was reviewed by Graham (1981).

Graham (1979) followed the absorption of copper in sunflower and showed that the total copper in the fibrous roots was linearly related to the concentration of copper in the external solution. The concentration of copper released to the xylem exudate was buffered against the changes made externally. Calculation of the electrochemical potential gradient for free cupric ions showed that a large driving force existed to move the Cu^{2+} ion into the plant. Wheat plants obtained their requirements from solutions with less than 0.01 μM Cu^{2+}; however, at concentrations nearing 0.001 μM wheat plants showed signs of copper deficiency (Loneragan, 1975).

The mobility of copper is variable and limited (Loneragan, 1975). Leaves of sugar cane lost most of their copper to the stem during senescence (Mukherjee, 1969), whilst leaves of oats lost 25 percent of their copper to developing grain (Williams and Moore, 1952). Loneragan *et al.* (1976) found that leaves of plants given a luxury supply of copper

lost more than 70 percent of their copper during grain development, and that leaves of copper-deficient plants lost less than 20 percent. For all treatments, however, loss of copper from the oldest leaf paralleled senescence.

Mobility of copper was shown by Hill *et al.* (1978, 1979a, b) and Loneragan *et al.* (1980) to be highly correlated with mobility of nitrogen. Nitrogen moved predominantly when senescence occurred. Similarly, copper was highly mobile under conditions favouring senescence. Both senescence and remobilization of copper are delayed in copper deficient wheat plants. However, Hill *et al.* (1979a) induced mobility of copper from old leaves of deficient plants by shading the leaf to enhance senescence.

Zinc

Rathore *et al.* (1970) found that zinc uptake by bean tissues was typical of non-metabolic processes; rapid absorption occurred which was strongly dependent on external zinc concentration and pH. Zinc absorption was not inhibited by respiratory inhibitors, nor was it light or temperature dependent (Rathore *et al.*, 1970); thus supporting the view that zinc uptake occurs primarily by a passive mechanism.

Schmid *et al.* (1965) found that although there was a large non-metabolic exchange-absorption of zinc, zinc absorption by barley roots showed a sustained steady state rate typical of a metabolically controlled process. Bowen (1969) reported that zinc absorption by sugar cane leaf discs was characteristic of an active process being inhibited by low temperatures and metabolic poisons. Zinc concentrations in xylem exudates from decapitated tomatoes and soybeans were found to be considerably higher than the nutrient solution by Tiffin (1972) and Ambler *et al.* (1970). Such accumulation against a concentration gradient suggests an active absorption of zinc (Lindsay, 1972b).

The majority of data collected to date support the view that the absorption of zinc is metabolically controlled, but the subject is still clearly controversial.

Zinc is intermediate in its mobility within plants compared to that of other nutrients (Lindsay, 1972b). When ^{65}Zn was introduced into the rooting media of plants, translocation of the radioactive tracer to other parts of the plant usually occurred within a few hours (Lindsay, 1972b). The movement of zinc was influenced by its concentration in the plant, the presence or absence of other elements and the acidity of the nutrient medium.

Plants with an adequate zinc supply mobilized appreciable quantities of zinc from old leaves to developing inflorescence and grain, however plants under conditions of zinc deficiency mobilized very little zinc from old leaves (Riceman and Jones, 1958; Williams and Moore, 1952). Young leaves of zinc-deficient plants retained high concentrations of zinc (Rosell and Ulrich, 1964) while roots only accumulated high levels of zinc if the supply was adequate (Lindsay, 1972b). Riceman and Jones (1956) showed that reducing the zinc supply to plants, caused zinc to move from the roots to the tops until the zinc level in the roots approached that of the tops.

2.3 COPPER AND ZINC IN PLANTS

All plants require copper or zinc in small amounts, but genotypes differ in their sensitivity to soils low in them and vary markedly in the degree to which they show deficiency symptoms, and in many instances, varietal differences within species have been found to be greater than differences between related species and genera (Millikan, 1961).

2.3.1 Copper deficiency

Copper deficiency has been observed in monocotyledons (cereals, sugar cane, corn) and dicotyledons (fruit trees, sunflowers, tomatoes, subclover) (Tisdale and Nelson, 1975). Symptoms of the deficiency depend to some degree on the genotype and on the severity of the deficiency, and can be characteristic of the stage of growth of the plant (King, 1974).

The common symptoms of copper deficiency in cereals (King, 1974; Graham and Nambiar, 1981) are outlined below:

(1) 'Wilting' occurs at an early stage of growth, the plants lose turgidity, the foliage tends to flag and subsequent growth is retarded. The time of appearance and severity of wilting depends on the genotype. It is believed that wilting occurs due to a structural weakness in the stem (Graham, 1976a) and as a result of reduced root development (Pizer *et al.*, 1966).

(2) Young leaves often bend at right angles to the stem and spiralling and twisting of the leaves is common. The plants become chlorotic, wither and then die - a condition known as 'dieback'.

(3) Growth is severely retarded: normal elongation in the growth of nodes of tillers is restricted and, in severe cases, subsequent tillers may die. However, usually the lower leaves remain green for a considerable time and numerous secondary tillers are produced (Piper, 1940). Heading is delayed, the extent of the delay being dependent on the genotype.

(4) In severe cases, ears may not be produced at all, whilst in other cases ears may develop, but be affected by the deficiency. When ears do emerge they remain practically empty of grain, deficient grain-formation being one of the most characteristic features of the deficiency in the field. The top of the ear may be yellow and dry, while the remainder of the ear stays green (King, 1974).

(5) The copper-deficient plants remain green with succulent stems well after normal healthy plants have dried off (King, 1974).

(6) Heads sometimes bend towards the ground close to maturity: further evidence of structural weakness in copper-deficient plants (Schutte and Mathews, 1969; King, 1974; Graham, 1976a). Head bending occurs in mild to moderate deficiency conditions where grain set is sufficient to make the heads heavy but lignification is impaired enough that the penduncles will bend under their weight (Graham and Nambiar, 1981).

(7) In ripe crops, blackening of the leaves, stem and grain is observed (King, 1974), and becomes more pronounced as the stubble ages. Darkening may be the result of deposits of melanin, an amino acid precursor (Hooper and Davies, 1968) and to optical effects resulting from the cavitation inside (Graham and Nambiar, 1981).

2.3.1.1 Sensitivity to Copper Deficiency

Differences between genotypes in copper nutrition among cereals have been reported by Smilde and Henkens (1967), Piper (1942) and others, who observed that wheat was generally higher in susceptibility to copper deficiency than barley or oats, while rye proved to be insensitive to copper deficiency. Halberd wheat and Clipper barley were the least sensitive cultivars of wheat, barley and oats (Nambiar, 1976a). Graham (1978a, b) and Graham and Pearce (1979) have found that triticale is tolerant of copper deficiency. However, interpretation is restricted if the tolerance of triticale to copper deficiency is examined at only one soil pH. To determine the potential advantages of triticale over wheat in tolerance to copper deficiency, studies need to be performed over a range of soil pH and levels of deficiency.

Greaves and Anderson (1936) and Rademacher (1937) found that resistant cultivars of wheat and oats had higher copper concentrations than susceptible cultivars when grown on soil low in copper. Mulder (1938) showed that cereals differed in ability to extract copper from soil substrates in which copper was not readily available. Sensitivity to copper deficiency was governed both by the specific copper requirement and by the ability of the root system to release copper from the substrate (Smilde and Henkens, 1967; Nielsen, 1976).

Smilde and Henkens (1967) did not get a response to application of copper in the field although a response occurred in the greenhouse on the same soil. They concluded that roots were able to extract copper from a larger area in the field, whilst in pots in the greenhouse uptake was restricted by the volume of soil. When root systems are crowded, Stevenson (1967) postulated that each root interferes with the water and nutrient supply of nearby roots, and water intake, nutrient uptake and growth of the whole plant are restricted.

Epstein (1972) reviewed trace element efficiency and showed it to be under single gene control in a number of cases. Graham (1978a, b) showed that genetic differences in micronutrient efficiency existed among crop plants and that these may be exploited in breeding programmes for crop cultivars suited to impoverished sandy soils.

2.3.1.2 Copper Requirement of Crops

Some studies showed grazed pasture legumes and associated non-legumes to have similar copper concentrations, although others mainly involving ungrazed situations reported that cereals and grasses contained less copper than legumes (Gladstones *et al.*, 1975). Cereals generally maintained low concentrations of copper in their tops (Piper, 1942).

Gladstones *et al.* (1975) also showed that botanical groups reacted differently to variations in copper supply and found that species varied greatly in their copper concentrations. Critical levels show this well: 1 ppm for wheat (Gartrell *et al.*, 1979a, b), 2 - 3 ppm for subclover (Reuter *et al.*, 1981), in young leaves in both cases.

Copper concentrations in the shoots of cereals usually ranged from 1.0 to 12 ppm depending upon the plant species, its age and the copper status of the soil (Gupta and MacLeod, 1970; Chaudhry *et al.*, 1973; King and Alston, 1975a; Gladstones *et al.*, 1975). Copper concentrations in plant tops declined with age in all species, but more slowly in cereals and grasses than in legumes at comparable times in the season (Gladstones *et al.*, 1975). In the grain, copper concentrations usually ranged between 0.8 and 6 ppm (King and Alston, 1975a; Gladstones *et al.*, 1975; Nambiar, 1976a). King and Alston (1975a, b) found that a concentration of copper of 2.0 to 2.5 ppm in the grain was critical for copper deficiency; however, Nambiar (1976a) recorded concentrations of 0.88 to 1.58 ppm in grain of plants with adequate copper supply. A copper concentration of 1 ppm in the grain was considered by Riceman *et al.* (1940) to be the critical concentration below which deficiency occurred.

2.3.2 Zinc Deficiency

Zinc deficiency is observed in a range of plants including fruit trees, vegetable crops, cotton, legumes and various cereals (Thorne, 1957; Tisdale and Nelson, 1975), and is characterized by distinctive visual symptoms (Millikan, 1942; Australian Zinc Development Association, 1978). Leaves are affected by zinc deficiency, although symptoms may appear in the fruit or branches or be evident in the overall plant development. Some field crops do not exhibit specific deficiency symptoms, unlike corn and other grain crops.

Symptoms common to a number of crops include:

(1) Chlorosis - the appearance of light green, yellow and white areas between the veins of leaves.

(2) Necrosis - death of tissue in these discoloured, chlorotic leaf areas.

(3) Shortening of the stem or stalk internodes, resulting in a bushy 'rosetted' appearance of the leaves.

(4) Small, narrow, thickened leaves.

(5) Early loss of foliage.

(6) Stunted growth.

(7) Malformation of the fruit, often with little or no yield at all.

When deficiency occurs in wheat, the following symptoms are observed: chlorotic and necrotic stripes on each side of the midrib; however if the deficiency is severe, the leaves tend to be totally chlorotic and short. As necrosis proceeds, the leaves collapse across the middle and die (Millikan, 1942; Australian Zinc Development Association, 1978). Growth of the plant may be restricted, depending on the degree of zinc deficiency, and the plant may fail to develop beyond the seedling stage if the zinc deficiency is very severe (Millikan, 1942).

2.3.2.1 Sensitivity to Zinc Deficiency

Considerable variation among genotypes of wheat in the severity of zinc deficiency symptoms, growth depression, zinc concentrations and P/Zn concentration ratio under stress conditions was observed by Shukla and Raj (1974). Zinc concentrations of wheat varieties with zinc deficiency symptoms ranged from 4.2 to 28.3 ppm (Shukla and Raj, 1974), and this differential response to zinc was primarily dependent on the capacity of different wheat varieties to absorb soil zinc (Gladstones and Loneragan, 1967; Shukla and Raj, 1974), and differences among species are probably maintained over a wide range of soil types and nutritional levels.

Viets, Boawn and Crawford (1954) classified plants into three classes on degree of sensitivity to zinc deficiency, based on severity of symptoms and response to zinc when grown on soils low in available zinc, as follows:

very sensitive	mildly sensitive	insensitive
Corn	Alfalfa (Lucerne)	Carrots
Flax	Clovers	Peas
Citrus	Cotton	Small grains
Grapes		

Toms (1958) working in Western Australia, concluded, as a result of field observations, that oats was much more sensitive to zinc deficiency than was wheat or barley. Rye and triticale have not been examined at all under conditions of zinc deficiency to determine their sensitivities to zinc deficiency.

2.3.2.2 Zinc Requirement of Crops

A zinc level of 15 ppm or less in the leaves on a dry weight basis appears to be associated with deficiency symptoms in the majority of crops, although the critical level varies from crop to crop, and depends on the tissue and its age (Thorne, 1957; Gladstones and Loneragan, 1967). Zinc concentrations in the tops of wheat plants decreased as the plant aged, and as severity of deficiency symptoms increased (Gladstones and Loneragan, 1967). Lower values of zinc in deficient plants were associated with higher amounts of iron, copper, manganese and nitrogen.

2.4 GENOTYPIC DIFFERENCES: TRITICALE, WHEAT, RYE

The idea of producing a hybrid between wheat (Triticum) and rye (Secale) was conceived as early as the 19th century (Larter, 1974a), this hybrid being known as triticale (Triticosecale). Hexaploid and octoploid triticales are common. Triticale morphologically resembles wheat in plant and kernel characteristics, the main differences being the greater vigour, larger spike, and larger kernel size of triticale relative to wheat (Larter, 1974b). It has been shown to have superior nutritional qualities over wheat and baking qualities over rye, and combines the high protein content of wheat with the high lysine content of rye (Hulse and Spurgeon, 1974).

In the early stages of triticale breeding, it was envisaged that the synthesis of a hybrid between wheat and rye would combine the desirable agronomic and commercial properties of wheat with the winter hardiness of rye (Larter, 1974b). A major objective in triticale development was to introduce a well adapted crop on to marginal lands such as light, sandy and acid soils, to which rye is well adapted but wheat and other traditional cereals are ill adapted (Hulse, 1974). Muntzing (1961) established that triticale was best suited to conditions of soil and climate that were intermediate between those optimum for wheat and rye. Under some environmental conditions, however, triticale outyields either of its parent types.

Triticale is now sown throughout the world and shows promise of high yield, high lysine content and like rye, good performance on sandy soils (Kiss, 1974; Zillinsky, 1974). However, many of the nutritional needs of triticale have not been established because of the relatively short history of the crop (Mugwira, 1980). Mugwira *et al.* (1976) have shown that triticale is intermediate between wheat (sensitive) and rye (tolerant) in tolerance to aluminium toxicity. Mugwira and Patel

(1977) further examined aluminium tolerance and concluded that differential increases in root zone pH seemed to account for differences in aluminium tolerance among wheats and accounted for the high aluminium tolerance of rye. Triticale induced intermediate pH changes, between the high pH changes of rye and the low pH changes caused by aluminium-sensitive wheats.

The high degree of tolerance to soil acidity of triticale, as determined by Slootmaker (1974) was attributed to the addition of the rye genome in that genotype, creating a new species which can be cultivated in areas too acid for cultivation of bread wheat. Rye was tolerant of high soil acidity, whilst in wheat when tolerance was observed, it was based on a few genes of the D-genome. The lime requirement of triticale was examined by Mugwira (1980) and found to be similar to that of wheat and more than that of rye. He also observed that triticales varied considerably in their responses to lime in different soils and concluded that the response was correlated with the amounts of aluminium and manganese.

Rye has long been used as the cereal for the most impoverished soils especially sands (Herriot, 1948; Blencowe, 1957; Nuttonson, 1958), and has been used in South Australia as a crop to stabilize dune sand in agricultural areas. Rye has the ability to grow satisfactorily in soils either too deficient in copper (Mulder, 1938; Riceman and Donald, 1938) or too acid (Herriot, 1948) for wheat and other cereals. Graham and Pearce (1979) have shown rye to be 'copper-efficient' relative to other 'copper-inefficient' cereals including wheat, oats and barley. Evidence of genetic control of copper efficiency in plants was obtained from studies of wheat-rye hybrids when compared to their parent types (Graham, 1978a, b; Graham and Pearce, 1979).

Triticale was shown to have inherited the copper efficiency of its rye parentage, absorbing amounts of copper from the soil which were intermediate between those of wheat and rye (Graham and Pearce, 1979). The copper efficiency of rye appears to be associated with its greater ability to accumulate copper in its tissues (Riceman *et al.*, 1940; Piper and Walkley, 1943; Smilde and Henkens, 1967; Gladstones *et al.*, 1975; Graham and Pearce, 1979).

Gladstones and Loneragan (1967) examined concentrations of zinc in twenty five annual crop and pasture plants and observed that cereal rye (*Secale cereale*) had the highest zinc content of the cereals. They concluded from their results that a high zinc uptake could be one of the mechanisms which enable certain species to grow better than others on sandy soils of low fertility. In all nothing is known about triticale and zinc deficiency and little about rye in this regard.

2.5 ROLE OF COPPER AND ZINC IN PLANTS

2.5.1 Role of Copper in Plants

2.5.1.1 Enzymatic

Copper is a metal activator of copper proteins in plants including the following:

Copper Proteins in Plants (Vallee and Wacker, 1970)

Protein	Origin
abscorbic acid oxidase	many plants
laccase	*Rhus, Polyporus* spp.
plastocyanin	spinach, *Chlorella, Chenopodium*
stellacyanin	*Rhus vernicifera*
diamine oxidase	pea seedlings
cytochrome oxidase	various
blue protein	mung bean
polyphenol oxidase (tyrosinase)	various

Copper deficiency depressed the activities of all enzymes in shoot tips and those of the oxidases (cytochrome oxidase, ascorbate oxidase, diamine oxidase and σ-diphenol oxidase) in young leaves by 70 to 95% but had little or no effect in older parts (Walker and Loneragan, 1981). They also showed that enzyme activities of young leaves from copper-deficient plants doubled after incubation in copper solution, while copper treated plants did not respond.

Phenol oxidase

Judel (1972) studied phenol oxidase activity in plants and found that a decrease in copper content always led to a disproportionate decrease in the activity of the enzyme. In normal plants, activity was greatest in the cotyledons and decreased with height of leaves on the plant and was intense when growth was at its maximum level. Phenol oxidase activity could be completely suppressed when visual symptoms were only slight. Judel postulated that the role of phenol oxidase could be partially taken over by other enzymes, and found that the stronger the suppression of the phenol oxidase activity, the higher the orthodiphenol content in fully expanded leaves.

2.5.1.2 Photosynthesis

Copper deficiency has been reported to inhibit photosynthetic activity and induce chlorosis in leaves (Bussler, 1981). Chlorosis involves the breakdown of chloroplasts, the organelles for photosynthesis, and as a result symptoms of chlorosis can be expected to lead to a decrease in the rate of photosynthetic activity. Soloveva and Makarova (1960) showed that the amount of chlorophyll in leaves increased upon addition of copper, and postulated that copper is a catalyst for respiration and an enzyme constituent involved in the regulation of chlorophyll synthesis, carbohydrate and protein metabolism. In support of this, Baszynski *et al.*

(1978) found that the synthesis of thylakoid prenyl lipids as well as of chlorophyll a and b was lower during copper deficiency. However, Agrawal and Pandey (1972) believe that copper affects chlorophyll synthesis indirectly because the plants in their study ceased to grow as a result of copper deficiency, without showing any signs of chlorosis.

2.5.1.3 Pollen

Copper deficiency affects the reproductive phase of higher plants by its effect on pollen (Graham, 1975; Graham, 1976b). The yield of grain in copper-deficient plants may be markedly reduced, whilst the vegetative yield is not severely affected (Graham, 1975). The failure to set seed was hypothesised to be due to either:

(1) lack of sufficient photosynthate production or translocation,

(2) absence of fertilised embryos.

Evidence gained by Graham (1975, 1980) supported the latter cause that the pollen of copper-deficient plants is non-viable and fails to fertilize the ovule. This study also revealed that copper-deficient plants developed small anthers with pollen grains considerably smaller in size and number than normal. These pollen grains failed to stain with iodine, indicating non-viability.

2.5.1.4 Cytological

Schutte and Mathews (1969) reported that copper-deficient plants showed a marked deterioration in the strength of stems due to change in cells or tissues. Copper-deficient wheat was considerably less lignified than the normal plants. The epidermal and hypodermal cell walls were significantly decreased in thickness, but the area of the hypodermis was unchanged. The copper-deficient stems were also less rigid than normal stems.

These changes of structure may cause weakened stems, twisted leaves and bent ears in wheat (Schutte and Mathews, 1969; Bussler, 1981). Further characteristics of copper deficiency were the absence or defective formation of reticulate and pitted vessels, the almost exclusive formation of xylem and spiral elements, thin walled collenchyma and epidermal cells. The retarded formation of the phloem, shorter palisade cells in the leaves, and smaller and fewer chloroplasts were apparent.

2.5.2 Role of Zinc in Plants

2.5.2.1 Enzymatic

Zinc functions in plants as a metal activator of enzymes, including enolase, oxaloacetic decarboxylase, lecithinase, cysteine desulphydrase, histidine diaminase, dihydropeptidase and glycylglycine dipeptidase (Tisdale and Nelson, 1975). Some other zinc metalloenzymes existing in plants are listed below:

Zinc Metalloenzymes in Plants (Vallee and Wacker, 1970)

Protein	Origin
carbonic anhydrase	various
alcohol dehydrogenase	various
glutamic dehydrogenase	various
D-glyceraldehyde	various
L-lactic dehydrogenase	various
D-lactic dehydrogenase	yeast, *Euglena*
D-lactic cytochrome c reductase	yeast
malic dehydrogenase	various
aldolase	yeast, *Aspergillus niger*

The activities of malic dehydrogenase have been demonstrated in many plants, but no direct evidence concerning zinc content has been ascertained (Vallee and Wacker, 1970). A number of the dehydrogenases

have shown sensitivity to zinc deficiency, and metabolism can be strongly and specifically affected (Price *et al.*, 1972).

Aldolase

A relationship between zinc and aldolase activity was recognized in 1943 (O'Sullivan, 1970). It was later shown in zinc-deficient plants that aldolase activity was reduced, thus restricting protein formation by limiting hexose diphosphate metabolism. The view of many workers was that low activity found in zinc deficient plants was caused by a reduction of aldolase synthesis (O'Sullivan, 1970). O'Sullivan (1970) showed the level of aldolase activity in the plant to be a good indicator of zinc deficiency.

Carbonic anhydrase

In zinc-deficient plants carbonic anhydrase activity was less than in normal plants. Wood and Sibly (1952) believed that this behaviour was associated with a lower zinc content in the leaves, and with the blocking of metabolic reactions leading to formation of protein.

2.5.2.2 RNA and Ribosomes

There is evidence that the earliest, and possibly the causal event in the course of zinc deficiency is a sharp decrease in the levels of RNA (ribonucleic acid) and the ribosome content of cells (Price *et al.*, 1972). Some workers have suggested that protein synthesis, which is initiated through ribonucleic acid, is regulated by zinc concentration, and have postulated that zinc is a component essential to the stability of cytoplasmic ribosomes, since in cases of zinc deficiency, they have been found to be unstable (Price *et al.*, 1972; Sachdev and Deb, 1977).

2.5.2.3 Auxin

Skoog (1940) recognised that zinc deficiency affected auxin synthesis, and thus plant growth. He observed that zinc-deficient plants behaved as if they were also deficient in auxin, and that the amount of indoleacetic acid was lower in zinc-deficient tissue, even before the appearance of visible deficiency symptoms.

Activity of tryptophan synthetase, which is involved in auxin synthesis, was found to be increased in the presence of zinc. Takaki and Kushizaki (1970) concluded from their work that zinc plays a role in the metabolic pathway from tryptophan to auxin via tryptamine.

2.5.2.4 Pollen

Zinc is essential for the production of the inflorescence in subclover, being mostly accumulated in this part of the plant. Zinc deficiency caused severe flower abortion and a drastic decrease in seed-setting in the remaining flowers (Riceman and Jones, 1956). Polar (1975) observed in *Vicia faba* and *Nicotiana tabacum* L. that the highest zinc activity occurred in the pollen and that the pollen grains themselves must have been responsible since the content in the anthers alone was small. He envisaged several functions for zinc in the tip of the pollen tube:

(1) maintenance of the integrity of RNA, since RNA is synthesized during the initial phase of pollen tube elongation and is also reported as accumulating in the tips,

(2) IAA (indole-acetic acid) is supplied to the ovary by the pollen tubes and is essential for the initiation of tube development; it is synthesized by the interaction of the tubes with the style and, as zinc is essential for auxin synthesis, it plays an important role during this process.

Polar (1975) proposed that zinc was present as a zinc-organic complex of low stability since only a proportion of the zinc present in the pollen was incorporated into seeds.

2.5.2.5 Cytological

In tomato, walnut and apricot plants, abnormal enlargement of decreased number of leaf palisade cells have been observed and found to be associated with delayed or incomplete differentiation (Hewitt and Smith, 1975). In leaves of numerous species, the plastids become agglutinated, vacuolated and filled with tannin-lipid complexes or under lysis. In clover, the palisade cells divide in the plane of the lamina and irregular protrusions appear from epidermal cells; and cell membranes lose their semi-permeable properties when calcium oxalate crystals appear (Hewitt and Smith, 1975).

Electron micrograph studies of zinc deficiency in bean chloroplasts have revealed that there is a progressive loss of the grana relative to the stroma (Hewitt and Smith, 1975). Grana of younger leaves became disorganised, the frets disappeared and the compartments of the grana appeared to become isolated or split open. The plastids became vacuolated and electron transparent.

2.6 INTERACTIONS

The nutrition of the plant is changed by interactions which commonly occur among trace elements. These interactions are defined as:

(1) an influence, a mutual or reciprocal action, of one element upon another in relation to plant growth,

(2) the differential response of one element in combination with varying levels of a second element applied simultaneously (Olsen, 1972).

The effects are not additive and interactions may be positive or negative. A number of interactions occur with copper or zinc and other nutrients in soils and plants and the important ones are discussed.

2.6.1 Copper-phosphorus

High levels of soil phosphorus can accentuate deficiency of copper and it is common to find copper-phosphorus interactions in areas where large quantities of phosphatic fertilizers have been applied (Bingham and Garber, 1960). Bingham and Garber (1960) observed significant decreases in the concentration of copper in sour orange seedlings as the rate of phosphorus increased from 50 to 450 ppm P. Similarly, increasing phosphate fertiliser rates added to a high P-fixing soil of central Georgia, U.S.A. decreased the copper concentration in wheat plants from acceptable to marginal levels (Touchton, Johnson and Cunfer, 1980). The formation of phosphate salts of copper is believed to be the primary cause of reduced availability of this element however growth dilution may also be important. Dolar and Keeney (1971a) concluded that the availability of copper was greatly diminished as the quantity of available soil-phosphorus was increased.

2.6.2 Zinc-phosphorus

Zinc deficiency can be induced by application of high rates of phosphatic fertilizers (Boawn *et al.*, 1957; Thorne, 1957). Some workers have attributed this effect to a chemical reaction in the soil, whilst others have suggested that antagonism occurs within the plant between the two elements (Singh, 1976). Adriano *et al.* (1971) implicated high levels of available soil-phosphorus as causing zinc deficiency by interfering with the uptake, translocation and utilization of zinc; phosphate decreased tissue-zinc concentration and zinc flux through roots.

Plants which are zinc deficient have higher concentrations of phosphorus in their tissues which can not be solely attributed to reduced shoot growth (Safaya, 1976).

On soils low in available phosphorus, applications of zinc may accentuate phosphorus deficiency. Normally, zinc regulates phosphorus uptake, however, an excess of phosphorus inhibits zinc uptake, firstly, by curtailing its translocation into the root xylem from the endodermis, and secondly, by lowering its rate of absorption through the epidermal or surface cell layer of the root (Safaya, 1976).

The effect of phosphorus on zinc remains controversial, although it is accepted that phosphorus and zinc interact in the plant itself (Olsen, 1972). Nauru and Ocean Island rock phosphate produce superphosphate fertilizer which is high in zinc. The above effects are less in this case.

2.6.3 Copper-nitrogen

Nitrogen fertilizers depress the copper concentrations in the tops of plants and may induce copper deficiency symptoms. Where copper deficiency exists, an increase in the nitrogen level intensifies the severity of the deficiency symptoms (Sauchelli, 1969). Chaudhry and Loneragan (1970) and Nambiar (1976a) have shown that application of nitrogen to the soil severely depressed the copper concentration of plant tops and roots at all stages of plant growth by diluting the absorbed copper. This effect may sometimes be accompanied by an increase in the apparent copper "requirements" of whole plant tops (Thiel and Finck, 1973). Two effects of nitrogen on growth contributed to dilution of copper:

(1) a large increase in total growth, and

(2) a marked increase in top relative to root growth.

The movement of copper from the oldest leaves of wheat plants has been shown to correlate strongly with senescence and nitrogen loss (Hill, Robson and Loneragan, 1978a, b, 1979; Loneragan, Snowball and Robson, 1980). This explains many of the reported relationships between copper and nitrogen nutrition in plants. The effect of copper deficiency in delaying the loss of copper from old leaves resulted from the influence of copper on the adequacy of the nitrogen supply (Loneragan, Snowball and Robson, 1980).

2.6.4 Zinc-nitrogen

Nitrogen induced symptoms of zinc deficiency in wheat (Chaudhry and Loneragan, 1970), and it was concluded that nitrogen depressed the concentrations of zinc in plant tops and roots by diluting the absorbing zinc in the same way as for copper.

In contrast, Ozanne (1955) reported that increased severity of zinc deficiency occurred in subterranean clover as the nitrogen supply was increased and that it could not be attributed entirely to increased growth. It was suggested that increased nitrogen resulted in greater protein-nitrogen which retained more zinc in the roots as a zinc-protein complex (Olsen, 1972).

2.6.5 Copper-iron

The addition of iron to soil results in reduced uptake and concentration of copper in plants. Cheshire, DeKock and Inkson (1967) showed that interactions involving iron and copper explained the frequent occurrence of copper deficiency on soils of high organic matter content rather than chemical fixation of copper. Applied iron reduced the uptake and concentration of copper in oats where copper had been added to the soil.

2.6.6 Zinc-iron

The metabolic functioning of zinc in plants plays an important role in regulating the supply of iron. Rosell and Ulrich (1964) reported that plants of low zinc status have extremely high concentrations of iron in their leaves, and that the addition of zinc substantially lowers the iron concentration in these plants. The relative mobility of iron was found to be inversely related to the mobility of zinc by Warnock (1970), when examining the relationship between phosphorus-induced zinc deficiency in corn and the concentrations and mobility of iron and manganese within the plant. Lingle *et al.* (1963) found that zinc interfered with the absorption of iron from Fe EDDHA solutions and also translocation to the tops of Hawkeye soybean plants. It appeared that zinc and iron inhibited the absorption of one another since concentrations of iron were high in situations when zinc deficiency was observed, and iron concentrations were lower when zinc was plentiful.

2.6.7 Copper-molybdenum

The antagonism of copper and molybdenum is believed to be the consequence of an interaction within the plants (Giordano *et al.*, 1966). They obtained evidence indicating that copper interfered with the role of molybdenum in the enzymatic reduction of nitrate in tomato plants. It has also been observed in carrots, spinach and lettuce that application of molybdenum induced copper deficiency (MacKay *et al.*, 1966; Mortvedt *et al.*, 1972).

2.6.8 Copper-zinc

The effect of zinc on the uptake of copper has been described as competitive in nature and zinc-induced copper deficiency occurs when zinc is present in excess amounts. Millikan (1953) observed that the

zinc concentration of lucerne and subterranean clover was lowered and the copper concentration increased markedly by zinc deficiency, whilst copper deficiency in the same plants caused a reduction in the copper concentration, but the zinc content was unaffected. Absorption of copper and zinc by sugar cane leaf tissue was studied by Bowen (1969), who found that the absorption of these ions was mutually competitive and concluded that they were absorbed through the same carrier sites.

Chaudhry and Loneragan (1970) found that addition of zinc fertilizer depressed copper concentrations in roots and attributed this to a decrease in the amount of copper absorbed and in the rate of copper absorption per unit of roots in early growth. Similar responses were observed when copper fertilizers were added: zinc concentrations were decreased in roots as a result of increased growth, but primarily by reduction in the amount of zinc absorbed and the rate of zinc absorption per unit of roots in early growth.

The findings of Chaudhry and Loneragan (1970) were supported by the observations that application of zinc fertilizers may induce or accentuate copper deficiency symptoms (Gilbert, 1951) resulting in yield reductions in cereals (Mulder, 1950; Dunne, 1956; Hooper and Davies, 1968). Similarly, addition of copper fertilizers can induce or accentuate the zinc deficiency (Anderson, 1946; Riceman, 1948) by promoting plant growth. The physiological nature of the Cu-Zn interaction over a range of soil acidities has not been the subject of any studies, although work has been done on the effect of soil acidity for Cu and Zn separately.

2.7 COPPER AND ZINC FERTILIZERS

Copper and zinc deficiencies are relatively easy to correct with application of copper and zinc fertilizers. The effectiveness of various fertilizer sources, in supplying copper and zinc, depends on the

chemical reactions and solubility relationships of these materials in soils (Lindsay, 1972b).

Commercial grade copper sulphate (bluestone) is an efficient and cheap source of copper for field application to soils (Younts, 1964; Pizer *et al.*, 1966; Caldwell, 1971; Barnes and Cox, 1973), however, a number of other copper compounds are equally effective and can be used to alleviate copper deficiency. These include: cuprous oxide, copper carbonates, copper oxychloride, copper chlorides and a number of chelated copper compounds.

Inorganic compounds such as ZnO, $ZnCO_3$, and $Zn_3(PO_4)_2$ are sufficiently soluble to supply available zinc to plants (Boawn *et al.*, 1957; Brown and Krantz, 1966). Zinc sulphate, which is highly water soluble, is the most commonly used inorganic zinc fertilizer. The released zinc can precipitate as the oxides, hydroxides, carbonates or silicates, or it can be adsorbed onto the soil material (Lindsay, 1972b). Zinc chelates are also effective sources of zinc and are more available than inorganic sources per unit of zinc although exceptions have been encountered (Boawn *et al.*, 1957; Brown and Krantz, 1966).

Superphosphate and NPK fertilizers in which copper salts have been added are also effective sources of copper (Younts, 1964; Pizer *et al.*, 1966). Zinc fertilizers may be combined with various nitrogen carriers (Boawn *et al.*, 1960; Mortvedt and Giordano, 1967). However, in Australia zinc fertilizers are always combined with superphosphate. Superphosphate contains some zinc (Anderson, 1946; Ozanne, Shaw and Kirton, 1965), and when zinc fertilizers are combined with phosphate fertilizers numerous reaction products are formed (Lehr, 1972). Anderson (1946) found the greatest responses to zinc where intermediate levels of superphosphate had been applied.

In view of the number of responses observed as a result of copper and zinc application, the use of macronutrient fertilizers containing copper and zinc salts is now widespread throughout the world (Gilkes, Young and Quirk, 1975). They have shown that copper and zinc applied to the soil in this form is relatively immobile and not leached through the soil, and remains adjacent to the point of application. Plant roots may require a high contact area with the fertilizer in order to achieve an adequate supply (Boawn *et al.*, 1957) and consequently high levels of copper and zinc may need to be added. Long term residual availability of copper and zinc has been recognised (Toms, 1958; Boawn *et al.*, 1960; Pizer *et al.*, 1966; Reith, 1968; Gartrell, 1980); however, these elements may in time become less available to plants if poorly soluble compounds are formed by reactions with other fertilizer components (Lehr, 1972) or by fixation by soil minerals and organic matter (Ellis and Knezek, 1972; Brennan *et al.*, 1980).

Since the additional cost of superphosphate containing copper and zinc is considerable, the most efficient utilization by plants of these elements is required (Gilkes, Young and Quirk, 1975).

It is well established that cereal rye is tolerant of soil deficiencies of copper, whilst wheats are generally sensitive to most trace elements and to high soil acidity. However, little is known about cereal rye under conditions of zinc deficiency and extremes of pH. Triticale, the hybrid of wheat and rye, has been shown to have inherited the tolerance to copper deficiency of its rye parentage in one environment, absorbing amounts of copper from the soil which were intermediate between those of wheat and rye (Graham and Pearce, 1979). Nothing is known about triticale in regard to zinc deficiency and extremes of pH. It is of importance then to know whether triticale behaves like wheat or rye in

tolerance of copper and zinc deficiency in a range of soils of varying degree of deficiency and pH.

It is the intention of this thesis study to examine these aspects, and increase the knowledge available on the nutrition of triticale and rye under conditions of copper and zinc deficiency, which are common in many soils of the cereal growing regions of South Australia.

3.0 EXPERIMENTAL MATERIALS AND METHODS

3.1 PROGRAM OF INVESTIGATION

POT EXPERIMENT 1 TOLERANCE OF TRITICALE, WHEAT AND RYE TO COPPER DEFICIENCY

This experiment was designed to study the effect of soil pH on the availability of copper to triticale and its parent species, wheat and rye in a copper-deficient soil, and to compare their performance and degree of sensitivity to copper-deficiency in pots.

POT EXPERIMENT 2 TOLERANCE OF TRITICALE, WHEAT AND RYE TO ZINC DEFICIENCY

This experiment was designed to examine the effect of soil pH on the availability of zinc to triticale and its parent species, wheat and rye in a zinc-deficient soil, and to compare their performance and degree of sensitivity to zinc-deficiency in pots. Another objective of this experiment was to compare the response to zinc in this experiment with that of copper in Experiment 1.

POT EXPERIMENT 3 TOLERANCE OF TRITICALE, WHEAT AND RYE IN THREE TRACE ELEMENT-DEFICIENT SOILS DIFFERING IN pH TO COPPER AND ZINC DEFICIENCY

This experiment was designed to examine the performance of triticale and its parent species, wheat and rye, and to compare their sensitivity to the trace elements, copper and zinc, when grown in pots on trace element deficient soils of various pH with different levels of copper and zinc deficiency.

3.2 POT EXPERIMENTS

3.2.1 Pot Experiment 1

3.2.1.1 Soil Treatment

A copper-deficient siliceous sand from heath country at Woods Well, County of Cardwell, South Australia (Prescott, 1944) was selected for this experiment. Woods Well is situated near the coast, at the western border of an extensive area of heath in the Upper South East of South Australia.

The collection site was midway down the slope in virgin scrub, its Australian grid reference being - Northing 6015920 and Easting 376660. The top 8 cm of grey sand with considerable organic matter accumulation was discarded, and the next 15 cm of light grey sand collected. The sand was air-dried and sieved to remove as much coarse organic matter as possible. Details of the sand used in this experiment appear in Appendix 1. The sand, at its natural pH of 7.0 constituted one environment and an additional two were obtained by treating the sand in the following ways:

(1) the addition of 35 ml of 0.1N H_2SO_4 per kg sand, producing an acidic environment of pH 5.0.

(2) the addition of 10 g of $CaCO_3$ per kg sand, producing an alkaline environment of pH 8.4.

The amounts of chemical required to obtain the desired pH were determined from the results of a soil incubation test of one week duration in which various rates of addition of acid and lime were compared.

The environments required were made up by mixing the air-dried sand for one hour, with either the acid or the carbonate, in 20 kg batches, using a cement mixer specially adapted to prevent contamination of the sand. It was not possible to control the pH levels rigidly owing to the

heterogeneity of the sand, the timelag in reaching equilibrium and the discriminatory nutrient absorbing behaviour of the plants.

3.2.1.2 Sand Culture Technique

Plants were grown in an evaporatively cooled glasshouse in undrained plastic pots (16 cm diameter x 15 cm high) which were lined with polythene bags containing 3 kg of soil. Ten seeds were sown 2 cm deep and equidistant on a circle of 8 cm diameter on 17th May, 1977. The plants emerged within five days and on day 14 (from sowing) were thinned to three evenly spaced plants per pot.

3.2.1.3 Genotypes

The hexaploid Armadillo-type triticale, T22 from CIMMYT, Mexico, is effectively a hybrid of tetraploid wheat and diploid rye. T22 contains only 6 rye chromosomes (2R is missing). *Triticum aestivum* cv. Halberd, a locally adapted wheat and *Secale cereale* cv. South Australian Commercial rye were chosen to represent the parent species in this study, but are unrelated genetically to the triticale.

3.2.1.4 Treatments and Experimental Design

Treatments comprised the three soil (pH) environments, as indicated earlier, the three genotypes mentioned above, and two levels of copper supply (0 and 4.0 mg Cu per pot as $CuSO_4$) all combined factorially within three replicates. A randomized block design was used to locate the pots in the glasshouse in two North-South rows, nine pots in each row, for each of the three randomized blocks (Figure 3.2.1).

Basal nutrients were added in solution to each pot as follows:

Solution 1A : 750 mg NH_4NO_3; 260 mg K_2SO_4; 150 mg $MgSO_4.7H_2O$

Solution 1B : 130 mg $CaSO_4.2H_2O$ (suspension)

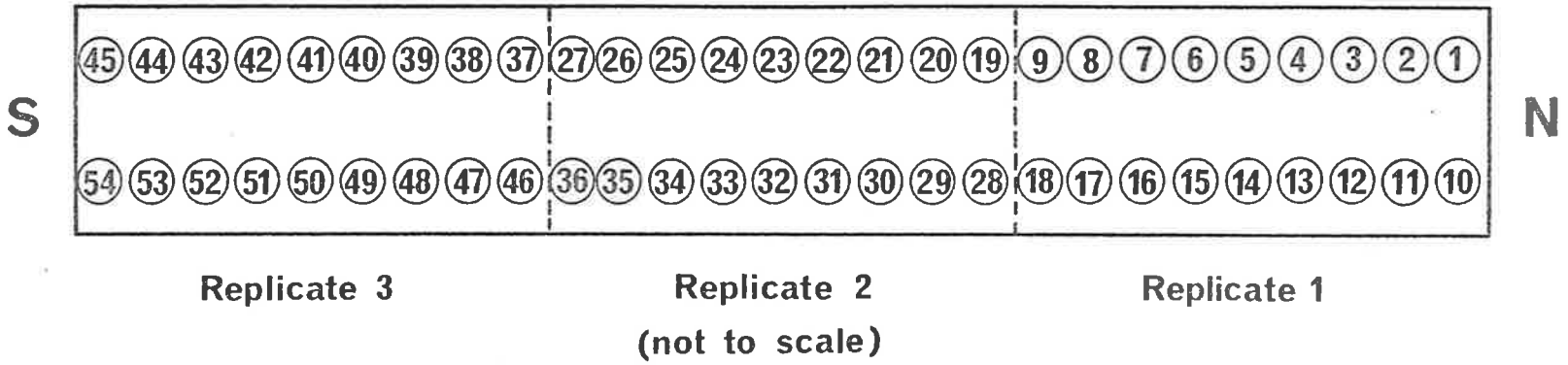


FIGURE 3.2.1. Diagram showing the arrangement of pots in the glasshouse for Pot Experiment 1. Treatments were allocated to these pots at random.

Solution 2 : 330 mg KH_2PO_4

Solution 3 : 25 mg $FeSO_4.7H_2O$; 25 mg $MnSO_4.4H_2O$; 17.7 mg $ZnSO_4.7H_2O$; 2 mg $H_2MoO_4.H_2O$; 10 mg H_3BO_3

Solution 4, Treatment nutrient: 15.8 mg $CuSO_4.5H_2O$ (i.e. 4 mg Cu per pot as required)

Solutions 1 to 3 were applied just prior to sowing and distilled-deionized water was added between solutions to aid nutrient dispersal and minimise nutrient interaction. Solution 4 was applied to the pots where appropriate 14 days after sowing.

At this stage a mulch of 120 g of black polythene beads was placed on the soil surface to reduce the evaporative water loss from the soil. Ten days later cylinders of black polythene shading material (50% transmission) were placed around the plants to a height of about 17 cm to support the plants and control excessive tillering.

Disease, commonly powdery mildew (*Erysiphe graminis*) was controlled by spraying all pots three times with 0.045 percent benomyl solution and sulphur-dusting the plants where required, and the glasshouse was fumigated once with nicotine sulphate to control aphids.

3.2.1.5 Water Use

Water usage was calculated weekly by weighing each pot and then watering the pots to Field Capacity (12%) with distilled-deionized water, thus replacing the water lost in the interval before weighing. In periods of high water use late in the season pots were given mid-week waterings. Water usage was used as a non-destructive index of growth, and to show the affect of treatments on growth.

3.2.1.6 Plant Measurements

Prior to harvest the following data were recorded for main culms and tillers separately:

number of days from sowing to ear emergence

number of days from sowing to anthesis

number of days from sowing to maturity

3.2.1.7 Harvesting and Measurements

The plants were harvested at maturity and yield components measured. At harvest on 28th November, 1977, the following measurements were taken:

plant height to top of the ear for main culms (mean for three plants in pot)

number of tillers per pot

number of ears per pot

At the conclusion of the experiment, the soil pH was measured in each pot to see how much it had changed over the duration of the experiment. The three plants within a pot were examined as a single entity, although the results are expressed on a single plant basis. The following measurements were made:

weight of ears per pot

weight of grain per pot

weight of straw per pot

number of spikelets per pot

number of grains per pot

The roots were recovered by washing away the sand using deionized water, then root weight and crown weight were measured on a pot basis.

3.2.1.8 Plant Copper Determinations

The grain and straw + chaff were analysed for copper, and the copper content (μg) of each plant part was calculated by the product of concentration (μg g^{-1}) and dry weight (g). The method of analysis appears in section 3.3.1.

3.2.2 Pot Experiment 2

The design of this experiment, and the soil used were the same as for Pot Experiment 1, although the soil collection site was slightly different, and there were some experimental differences.

3.2.2.1 Sand Culture Technique

This experiment was sown on 27th June, 1978. Most triticale and rye plants had emerged six days after sowing, however, the wheat showed poor germination and on day 9 the wheat pots were replanted with pre-germinated seed which had emerged by day 13. The seedlings were later (day 17) thinned to three evenly spaced plants per pot.

3.2.2.2 Treatments and Experimental Design

Treatments comprised the soil (pH) environments and genotypes as in Pot Experiment 1, and two levels of zinc supply (0 and 4.0 mg Zn per pot as $ZnSO_4$) all combined factorially within three replicates. The design and layout were identical to Pot Experiment 1, although the randomization was different.

Basal nutrients and their schedule of application were as for Pot Experiment 1 with the following minor changes:

Solution 3 : 17.7 mg $ZnSO_4.7H_2O$ was omitted from this solution and 1 mg $CoSO_4.7H_2O$ and 15.8 mg $CuSO_4.5H_2O$ were included.

Solution 4 : 15.8 mg $CuSO_4.5H_2O$ was replaced by 17.7 mg $ZnSO_4.7H_2O$ (ie. 4 mg Zn per pot).

The pots in Experiment 2 were mulched, the plants shaded and disease controlled in an identical manner to Pot Experiment 1. In addition, when plants became infested with aphid they were sprayed with 1.5 ml per litre pyrethrum solution as necessary.

3.2.2.3 Water Use

Water usage was determined on a weekly basis using the technique employed in Pot Experiment 1; however, late in the season adjustments were made in the addition of water to compensate for the weights of the plants.

3.2.2.4 Plant Measurements

Plant measurements made prior to harvest were essentially the same as the previous experiment, although the tillers were divided into three categories for this experiment, these being:

main culm

primary tillers

secondary tillers

3.2.2.5 Harvesting and Measurements

When the plants were harvested between 22nd and 24th November 1978, measurements made on the plants and the harvest technique employed were identical to those of the previous experiment as was the analysis of data.

3.2.2.6 Plant Zinc and Manganese Determinations

The grain and straw + chaff were analysed for zinc and manganese. The zinc and manganese contents (µg) of each plant were calculated by the product of concentration (µg g^{-1}) and dry weight (g).

3.2.3 Pot Experiment 3

3.2.3.1 Soil Preparation

Three trace element-deficient soils were selected for this experiment on the basis of their pH. It was recognised that these soils would also differ in their degree of deficiency in copper and zinc, and in the nature of their deficiencies.

The soils were:

Young Sand (pH 5.05) - a dark grey humus podsolized sand, developed on the aeolian sand of the ranges, from sclerophyll country on the Mount Burr sand complex, Hundred of Riddoch, County Grey, South Australia (Stephens, Crocker, Butler and Smith, 1941). The collection site was midway down an embankment 15 m from a pine plantation, on soil which has never been fertilized. The Australian grid reference of this location is - Northing 5835970 and Easting 458250. The top 20 cm of grey sand darkened by large amounts of organic matter was discarded, and the next 40 cm of grey sand collected.

Woods Well Sand (pH 7.10) - a solonized light grey siliceous sand, from heath country at Woods Well, Hundred of Glyde, County Cardwell, South Australia (Prescott, 1944; Anderson and Neal-Smith, 1951). This soil was the same as for the two previous experiments, and was collected at the site used in Pot Experiment 1.

Robe Sand (pH 8.80) - a yellow calcareous sand, of coastal sand dune type from Robe, Hundred of Waterhouse, County Robe, South Australia (Thomas, 1937). It was a yellow calcareous sand, composed essentially of fine marine shell fragments, containing about 70% calcium carbonate. The collection site was midway down the east face of a coastal sand dune in virgin scrub. The Australian grid reference of this location is - Northing 5881800 and Easting 391200. The top 8 cm of sand containing organic matter was discarded and the next 20 cm of yellow sand collected.

These soils were air-dried and sieved to remove as much coarse organic matter as possible, and at their natural pHs constituted the three environments to be examined. Details of the soils appear in Appendix 1.

3.2.3.2 Sand Culture Technique

On 17th June 1979, this experiment was sown following the sand culture technique used in Pot Experiment 1. A fourth genotype, wheat cv. Gatcher was also sown; however, only five seeds were sown per pot. Most seedlings had emerged 4 days after sowing, and on day 10 were thinned to three evenly spaced plants per pot.

3.2.3.3 Genotypes

The additional genotype, *Triticum aestivum* cv. Gatcher is another locally adapted wheat variety which is unrelated genetically to the triticale, but which had a reputation for sensitivity to zinc deficiency.

3.2.3.4 Treatments and Experimental Design

Treatments comprised the three soil (pH) environments, as indicated earlier, the four genotypes previously mentioned, and two levels of copper supply (0 and 4.0 mg Cu per pot as $CuSO_4$) and two

levels of zinc supply (0 and 4.0 mg Zn per pot as $ZnSO_4$), all combined factorially within two replicates. The pots were located in the glasshouse in three North-South rows, sixteen pots in each row, for each of the two randomized blocks (Figure 3.2.2).

Basal nutrients and their schedule of application were as for Pot Experiment 1 with the following minor alterations:

Solution 3 : 17.7 mg $ZnSO_4.7H_2O$ was omitted from this solution and 1 mg $CoSO_4.7H_2O$ was included

Solution 5 : an additional solution containing 17.7 mg $ZnSO_4.7H_2O$ (ie. 4 mg Zn per pot)

Solution 6 : an additional solution containing 2.5 mg $MnSO_4.4H_2O$

Solution 5 was applied to the pots where appropriate 14 days after sowing. Solution 6 was added to the pots of the calcareous soil at weekly intervals for a period of 10 weeks, commencing at week 4 after sowing. This was to overcome any risk of deficiency of manganese which could occur in that soil.

The pots in this experiment were mulched, the plants shaded and disease controlled in an identical manner to the previous experiment.

3.2.3.5 Water Use

Water usage was determined on a weekly basis using the method employed in Pot Experiment 1, although the value of Field Capacity was different for the three soils (Young Sand, 16%; Woods Well Sand, 14%; Robe Sand, 18.5%). Late in the season, adjustments were made in the addition of water to compensate for the weights of the plants.

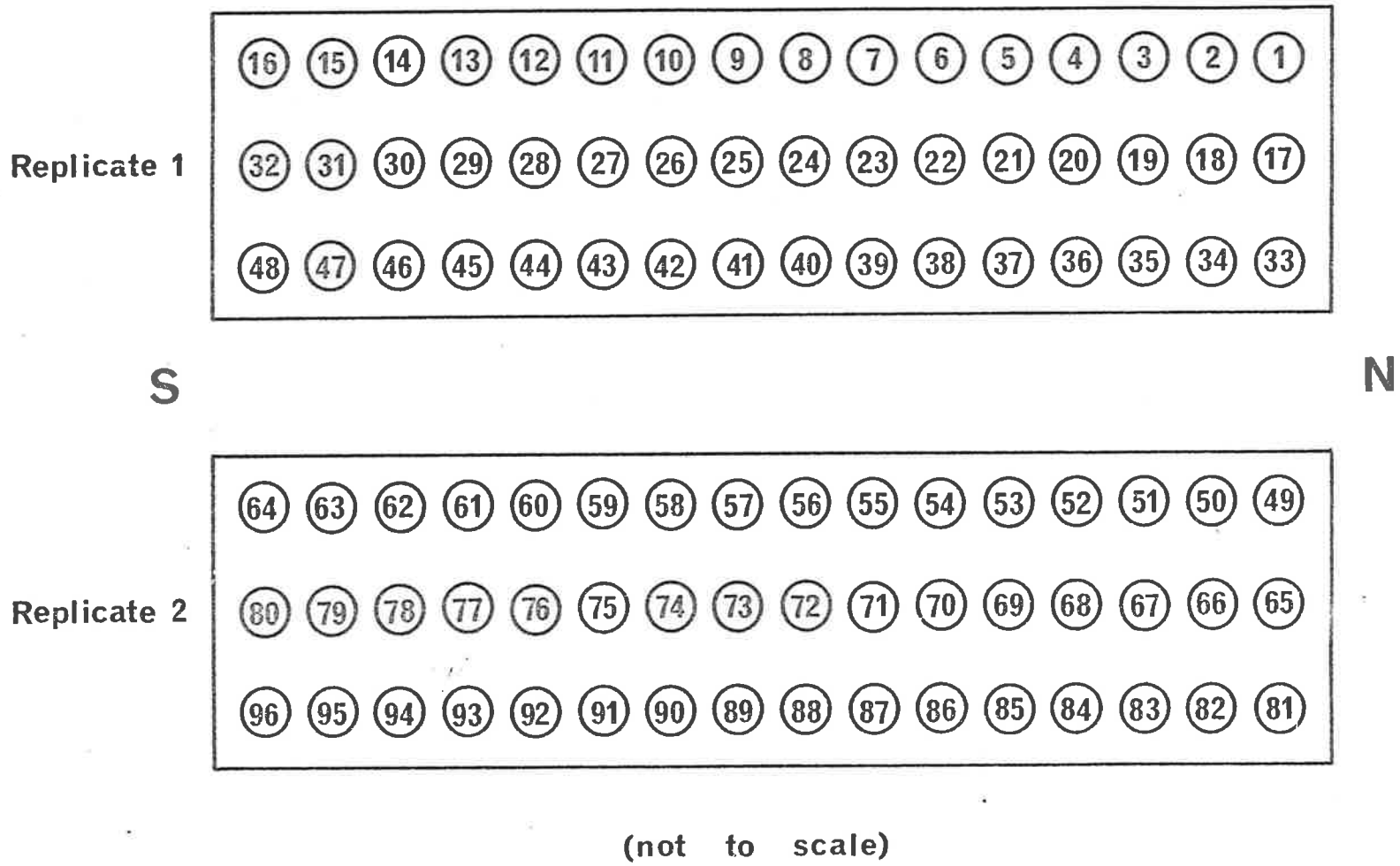


FIGURE 3.2.2. Diagram showing the arrangement of pots in the glasshouse for Pot Experiment 3. Treatments were allocated to these pots at random.

3.2.3.6 Plant Measurements

In addition to the plant measurements made prior to harvest in Pot Experiment 1, pollen viability counts were made on the plants in this experiment. Again, the measurements were made on the three categories of tillers used in Pot Experiment 2.

3.2.3.7 Harvesting and Measurements

The majority of plants were harvested at maturity (26th to 27th November, 1979), however both replicates of wheat cv. Gatcher and Halberd at pH 5.0, with treatments (Omg Cu, O mg Zn) and (Omg Cu, 4 mg Zn) were harvested on 19th October, 1979 as they had died off prematurely. Both the harvest technique and the yield components measured were identical to those of the first experiment and data were treated in the same manner.

3.2.3.8 Plant Copper, Zinc and Manganese Determination

The grain and straw + chaff of a selection of samples were analysed for copper and manganese, and the copper and manganese uptakes determined by multiplying the relevant concentrations ($\mu g\ g^{-1}$) by the dry weights (g).

3.3 ANALYTICAL METHODS

3.3.1 Copper Analysis

Whole grain samples and ground straw + chaff samples were oven-dried at 80°C overnight and then 0.5 g weighed into calibrated digestion tubes. Five ml of tri-acid mixture[1] was added and samples were left to stand overnight. A 1 mm glass bead was added to prevent bumping and the tubes were heated on Maloney burners, slowly at first, for 20 minutes while the major part of the oxidation proceeded. After all the nitric acid had distilled off the tubes were heated strongly to complete the oxidation and boil off excess perchloric acid ($HClO_4$). When only sulphuric acid was left, the digest was complete, and after cooling, the digests were diluted with distilled-deionized water and 4 ml of 0.25% APDC[2] solution added. The digest was made up to 25 ml using distilled-deionized water, 4 ml of MIBK[3] was added, the tubes capped and then mixed for 30 seconds on a Vortex mixer. This mixing was necessary to that the APDC could react with the copper in the digest to form an organic complex, soluble in MIBK, which is read and gives the amount of copper in the sample. The tubes were read on an atomic absorption spectrophotometer with an air-acetylene flame and set at a wavelength of 324.7 nm.

A Standard series was prepared from a known solution of $CuSO_4$, to which 3 ml of 1N H_2SO_4 was added before the addition of APDC to bring the acidity of the standards to that of the samples.

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1 Tri-acid mixture is made up of 40 volumes Univar nitric acid (HNO_3), 4 volumes Analar perchloric acid ($HClO_4$) and 1 volume Analar sulphuric acid (H_2SO_4).

2 APDC is ammonium pyrrolidine dithiocarbamate.

3 MIBK is iso-butylmethylketone.

3.3.2 Zinc and Manganese Analysis

The digestion procedure used for samples to be analysed for zinc and manganese was the same as that used for copper; however, the samples were read directly in aqueous solution without organic extraction. Following tri-acid digestion, the samples were diluted to 25 ml with distilled-deionized water, capped, mixed on a Vortex mixer and then read on an atomic absorption spectrophotometer with an air-acetylene flame at wavelengths of 213.8 nm (zinc) or 279.5 nm (manganese).

Standards were prepared as for Cu, using 3 ml of 1N H_2SO_4 to bring the acidity of the standards to that of the samples.

3.3.3 Soil pH Measurement

Core samples of sand of 1 cm diameter to the full depth of the pots were taken. Soil pH was then determined with a pH meter in a 1:5 sand: water suspension after equilibrating for 24 hours.

4.0 RESULTS

4.1 POT EXPERIMENT 1

4.1.1 Growth and Visual Symptoms

All plants germinated and grew normally until mid-tillering (60 days after sowing) when wheat plants without added copper showed the "wilting" symptom (Graham, 1976a) at all soil pHs (Plate 1). In wheat, the usual progression of symptoms appeared in the copper-deficient plants: withered leaf tips, reduced growth and stem elongation, delayed development of ears and delayed senescence. The triticale at the alkaline pH, showed signs of copper deficiency, but these appeared just prior to heading (80 days after sowing): stem elongation was reduced, later tillers showed signs of "wilting" and grain was not produced in those tillers with ears. Rye showed no symptoms in any treatment.

4.1.2 Water Use

4.1.2.1 Weekly Water Use

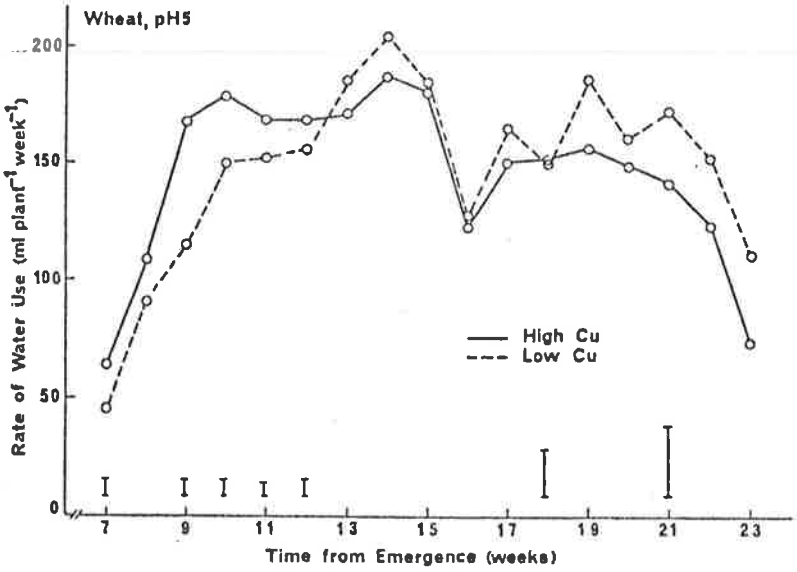
Early in the season (to heading) the rate of water use of copper-deficient wheat plants was significantly lower than that of the healthy plants, but at this stage a "crossover" occurred and thereafter the copper-deficient plants used more water (Figure 4.1.1 to 4.1.3), in the same way as observed by Graham (1976a). In all soil (pH) environments, the "crossover" of the water use curves was similar, but the magnitude of the differences became smaller as pH increased and was not significant at high soil pH. As grain development began there was little difference in water use between treatments until towards maturity, when the rate of water use began to decline in the healthy plants owing to senescence of leaves. Copper-deficient wheat plants in the acid and neutral environments maintained a high water consumption owing to delayed maturity. However, the deficiency of copper in the alkaline environment had a larger effect

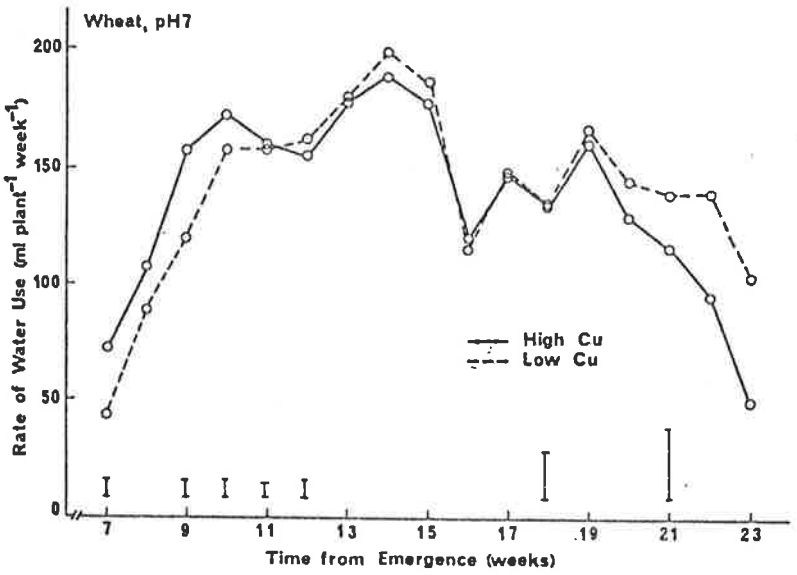
PLATE 1. Close-up of a copper-deficient wheat plant showing the typical "wither-tip" symptom associated with copper deficiency.

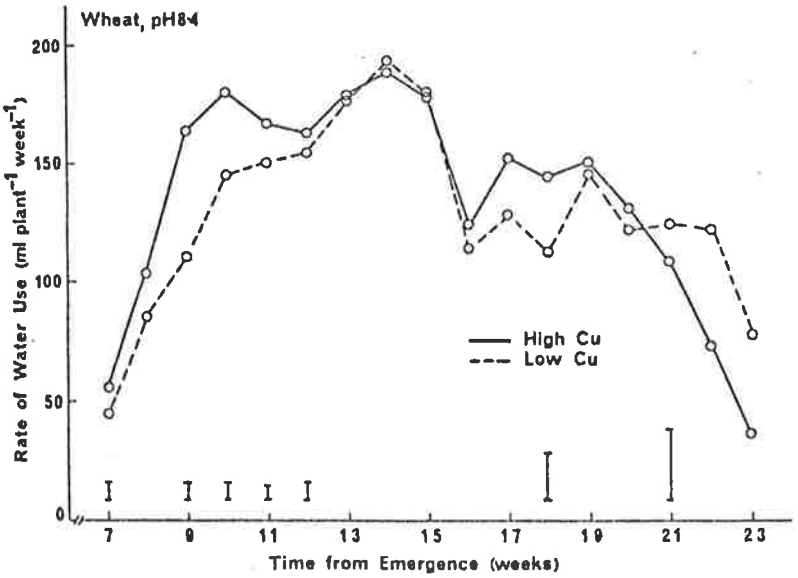
FIGURE 4.1.1. Effect of level of copper supply on the weekly water use (ml $plant^{-1}$) throughout the season of wheat at pH 5.0. Data are the means of 9 plants (3 plants per pot for each of 3 replicates). Vertical bars indicate LSD values for $P < 0.05$.

FIGURE 4.1.2. Effect of level of copper supply on the weekly water use (ml $plant^{-1}$) throughout the season of wheat at pH 7.0. Data are the means of 9 plants (3 plants per pot for each of 3 replicates). Vertical bars indicate LSD values for $P < 0.05$.

FIGURE 4.1.3. Effect of level of copper supply on the weekly water use (ml $plant^{-1}$) throughout the season of wheat at pH 8.4. Data are the means of 9 plants (3 plants per pot for each of 3 replicates). Vertical bars indicate LSD values for $P < 0.05$.


Wheat, pH5
Rate of Water Use (ml plant^{-1} week^{-1})
200
150
100
50
0
High Cu
Low Cu
7
9
11
13
15
17
19
21
23
Time from Emergence (weeks)


Wheat, pH7
Rate of Water Use (ml plant^{-1} week^{-1})
200
150
100
50
0
High Cu
Low Cu
7
9
11
13
15
17
19
21
23
Time from Emergence (weeks)


Wheat, pH8·4
Rate of Water Use (ml plant^{-1} week^{-1})
200
150
100
50
0
High Cu
Low Cu
7
9
11
13
15
17
19
21
23
Time from Emergence (weeks)

on vegetative growth which counteracted the effect of delayed maturity so that the water requirements of these plants were not much different from their control plants with an adequate supply of copper.

Both copper treatment and soil pH influenced the water use of triticale but to a lesser degree than for wheat (Appendix 2, Figures 1 to 3), but neither soil pH nor level of copper affected the water use of rye (Appendix 2, Figures 4 to 6). Copper supply affected the water requirements of triticale only after anthesis, and only at pH 5.0 and 8.4; low copper plants needed more water probably because of the development of late secondary tillers.

4.1.2.2 Total Water Use

The total amount of water used over the whole season was neither affected by genotype nor copper treatment; and soil pH had only a slight, if significant, effect (Table 4.1.1). The effect of soil pH depended on genotype. Water use increased with increasing soil pH in triticale and decreased in wheat. There was no effect on rye. Although copper treatment had statistically significant effects on total water use of triticale, the effect at pH 5.0 was the reverse of that at pH 8.4 and since these effects were not reflected in the other genotypes or at pH 7.0, they are probably of no biological significance.

4.1.3 Plant Height

Application of copper generally increased height of plants, but again the direction of its effect depended on genotype, with the soil pH becoming more important above neutrality (Table 4.1.2). Growth of copper-deficient wheat plants was depressed in all soil (pH) environments and as a consequence plant height was reduced. Height of triticale responded positively to copper in the neutral and alkaline environments,

TABLE 4.1.1. Effect of level of copper, soil pH and genotype on the total water use (ml plant^{-1}) over the whole season. Data are the means of 3 replicates.

Treatment	Cu added per pot (mg)	Soil pH 5.0	7.0	8.4
Genotype				
Wheat	0	2500	2380	2190
	4	2450	2310	2300
Triticale	0	2200	2220	2430
	4	2020	2210	2130
Rye	0	2300	2290	2370
	4	2310	2350	2410

LSD (P = 0.05) for the genotype - soil pH - Cu interaction : 144

Statistical analyses appear in Appendix 3.

TABLE 4.1.2. Effect of copper supply, soil pH and genotype on plant height (cm). Data are main culm heights at maturity and the means of 9 plants (3 plants per pot for each of 3 replicates).

Treatment	Cu added per pot (mg)	Soil pH 5.0	7.0	8.4
Genotype				
Wheat	0	36	43	32
	4	86	92	96
Triticale	0	93	86	73
	4	99	95	96
Rye	0	113	122	107
	4	115	115	115

LSD (P = 0.05) for the genotype - Cu and soil pH - Cu interactions : 7.6

Statistical analyses appear in Appendix 4.

especially the latter. Rye showed small responses in opposite directions to copper at the neutral and alkaline pH.

There was a significant genotype-copper interaction ($P < 0.001$) and a significant soil pH-copper interaction ($P < 0.01$) for plant height which could be attributed largely to the increased response to copper at the alkaline soil pH of the wheat and triticale, relative to rye.

4.1.4 Tillering

Copper-deficient plants tillered profusely, but most wheat tillers failed to produce fertile ears or grain. Rye was relatively unaffected and again triticale was intermediate, with plants in soil at pH 8.4 most severely affected (Table 4.1.3). There was a significant genotype-soil pH interaction ($P < 0.001$), a significant genotype-copper interaction ($P < 0.001$) and a significant genotype-soil pH-copper interaction ($P < 0.05$) which accounted for pronounced, but differing responses by the three genotypes in tiller production to copper deficiency especially at the alkaline soil pH. Copper-deficient wheat plants produced very few ears compared to the healthy plants in all the soil (pH) environments, whilst the opposite trend was observed for triticale. When the soil pH was increased to an alkaline extreme, the sensitivity of triticale to copper-deficiency increased and the number of ears produced in the absence of copper rose substantially.

4.1.5 Delay in Maturity

Soil pH had little effect on the time of ear emergence, anthesis or maturity, whilst the application of copper promoted early maturity in all genotypes (Table 4.1.4). Copper-deficient wheat plants produced ears very late in the season in all of the soil environments, but none of these ears developed beyond anthesis. Copper-deficient triticale plants at the

TABLE 4.1.3. Tiller production and ear production per plant at maturity. Data are means of 3 replicates of 3 plants per pot.

Treatment	Cu added per pot (mg)	Soil pH 5.0	Soil pH 7.0	Soil pH 8.4	Soil pH 5.0	Soil pH 7.0	Soil pH 8.4
		A. Number of culms per plant			B. Number of ears per plant		
Genotype							
Wheat	0	7.3	5.6	4.7	0.7#	1.1#	0.6#
	4	3.6	2.7	2.6	3.0	2.6	2.2
Triticale	0	1.6	3.4	5.2	1.4	3.2	4.7#
	4	1.2	2.0	1.9	1.2	1.8	1.7
Rye	0	3.0	2.6	4.1	2.7	2.6	3.7
	4	2.6	3.2	3.0	2.6	2.9	2.8
LSD (P = 0.05) for the genotype-soil pH - Cu interaction:			1.28			0.78	

these ears failed to produce grain and were still green at harvest

Statistical analyses appear in Appendices 5 and 6.

TABLE 4.1.4. Number of days to ear emergence, anthesis and maturity of the genotypes as affected by soil pH and level of applied copper. Data are the means of 9 plants (3 plants per pot and 3 replicates).

Treatment	Cu added per pot (mg)	Soil pH 5.0	Soil pH 7.0	Soil pH 8.4	Soil pH 5.0	Soil pH 7.0	Soil pH 8.4	Soil pH 5.0	Soil pH 7.0	Soil pH 8.4
		Ear emergence			Anthesis			Maturity		
A. Main culms										
Genotype										
Wheat	0	164	164	164	-*	-*	-*	-*	-*	-*
	4	91	86	92	101	95	99	154	151	151
Triticale	0	84	88	93	94	96	101	142	151	163
	4	85	82	85	94	92	94	141	140	139
Rye	0	95	94	96	105	104	108	159	159	163
	4	93	93	97	102	103	106	158	155	158
LSD (P = 0.05) for the genotype - soil pH - Cu interaction:			3.2			2.3			4.0	
B. Other tillers										
Genotype										
Wheat	0	-*	169	-*	-*	-*	-*	-*	-*	-*
	4	104	103	97	117	110	102	167	164	162
Triticale	0	98**	104	105	98	114	125	148	164	171
	4	104**	97	97	113	108	102	152	159	154
Rye	0	101	99	108	115	112	123	169	165	168
	4	102	97	105	114	115	110	167	163	163

* = not reached by harvest date, but for purposes of statistical analysis, high values were substituted for missing values.

** = 2 pots for Omg Cu, 1 pot for 4 mg Cu.

Statistical analyses appear in Appendices 7, 8 and 9.

alkaline pH were later than the copper-sufficient treatments in ear emergence, anthesis and maturity, and although no grain was produced the ears did dry off. Rye was unaffected.

Copper deficiency was more severe at the high soil pH and so ear emergence, anthesis and maturity became progressively later with increasing soil pH for the triticale, resulting in a significant genotype-soil pH-copper interaction. The same trend applied both to the main culm ears and later ears, and so only main culm data was statistically analysed.

4.1.6 Dry Matter Production

Total shoot dry matter is shown in Figure 4.1.4A. Wheat was sensitive to copper-deficiency in all soil (pH) environments, whilst triticale was only sensitive to copper deficiency at the neutral and alkaline pH. Rye was tolerant of copper deficiency under all soil (pH) environments. Copper-deficient plants in all soil environments had lower shoot yields than the healthy plants.

There was a significant soil pH-copper interaction ($P < 0.05$) and a significant genotype-soil pH-copper interaction ($P < 0.05$). These were attributed to the increased responses to copper of the wheat and triticale relative to the rye at the alkaline soil pH. The shoot yields of triticale were superior to wheat and rye in acid conditions and intermediate at higher pH.

Application of copper significantly increased the mean shoot weight per plant by increasing both the weight of grain and straw (Figure 4.1.4A and B). In copper-deficient plants the dry weight of straw was the major component of the total shoot weight but in the healthy plants the grain weight became important. The contribution of the grain weight to the total shoot weight per plant was a function of

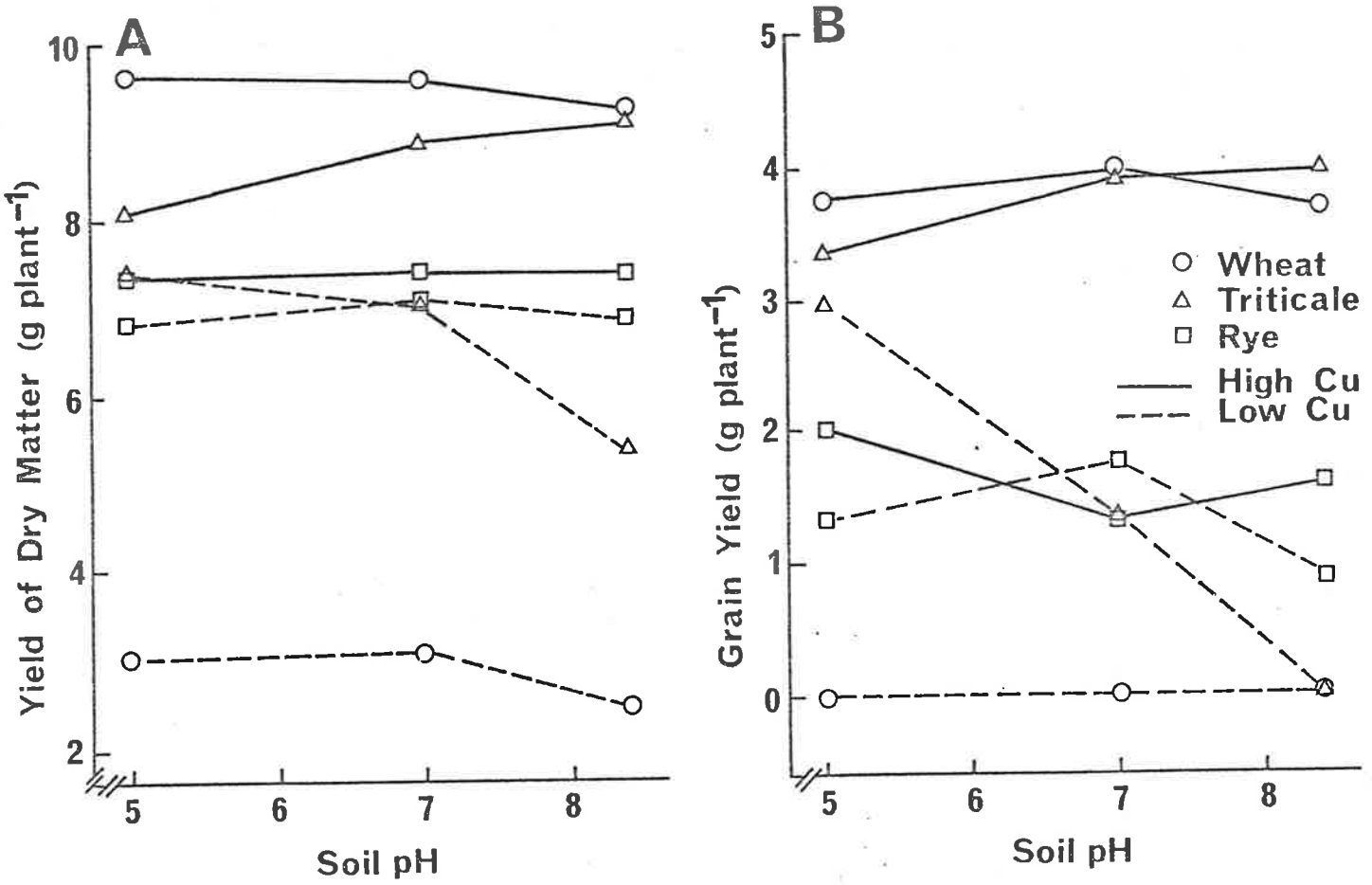


FIGURE 4.1.4. Effect of soil pH, level of copper supply and genotype on A. total shoot dry matter (g plant^{-1}) and B. total grain yield (g plant^{-1}). Means of 3 replicates. LSD (P = 0.05) of the genotype-soil pH-copper interaction is 2.95 for total shoot dry matter and 2.10 for total grain yield. Statistical analyses appear in Appendices 10 and 12.

the plant genotype which could be expressed by the harvest index (Table 4.1.5). With adequate copper supplied, rye had a considerably lower harvest index than wheat and triticale; and the harvest index of copper-deficient plants was obviously much lower than that of copper-sufficient plants.

4.1.7 Grain Yield and Its Components

The effect of copper is more pronounced on grain yield than on vegetative yield (Figure 4.1.4B). Copper-deficient wheat plants failed to produce grain under all soil (pH) conditions. Triticale was tolerant to copper-deficiency at low soil pH, but became progressively more sensitive to copper deficiency as the soil pH was increased and failed to produce grain in an alkaline environment. Rye was relatively tolerant of copper-deficiency however, in all the soil (pH) environments.

The grain yields attained in this experiment showed a highly significant genotype-soil pH-copper interaction ($P < 0.001$), attributed to the increased response of wheat and triticale, relative to the rye under alkaline conditions. Triticale was superior to wheat and rye in acid conditions but became intermediate with respect to grain yields per plant, in the alkaline environment.

An apparently anomalous result was the depressed grain production of rye plants with added copper at pH 7.0, possibly the consequence of the random spatial arrangement of plants not allowing for sufficient cross-pollination and thus resulting in poor seed set. This rye cultivar is open-pollinated. The number of ears produced per plant was influenced both by the level of copper and the soil pH (Table 4.1.3). This was not reflected, however, in any increase in grain yield.

TABLE 4.1.5. Effect of level of copper and soil pH on the harvest index. Data are means of 3 replicates.

Treatment	Cu added per pot (mg)	Soil pH 5.0	7.0	8.4
Genotype				
Wheat	0	0.000	0.000	0.000
	4	0.390	0.415	0.398
Triticale	0	0.401	0.185	0.001
	4	0.414	0.440	0.440
Rye	0	0.199	0.252	0.135
	4	0.278	0.179	0.216

LSD (P = 0.05) for the genotype - soil pH - Cu interaction : 0.088

Statistical analyses appear in Appendix 13.

All ears of copper-deficient wheat and triticale plants had substantially fewer spikelets per ear (Table 4.1.6), many of which were sterile. Under conditions of severe copper deficiency no grains were produced. In the neutral environment where the grain yield of triticale was reduced to some degree by copper deficiency, both the number of grains per ear and the weight per grain contributed to the reduction in grain yield.

The number of grains per plant (Table 4.1.6) showed the same pattern as grain yield.

4.1.8 Dry Weight of Roots

The dry weight of roots was intermediate for triticale, irrespective of the copper treatment, whilst rye had the highest dry weight of roots and wheat the least. Soil pH had no direct effect on the dry weight of roots, however all genotypes responded to the application of copper (Table 4.1.7). The dry weight of roots was generally increased by copper application, but the magnitude of the effect varied between genotypes. Reduced shoot growth by copper-deficient plants in all soil (pH) environments was associated with the development of a less extensive root system by these plants. This occurred as a direct result of the copper deficiency in the soil.

It must be noted that the roots were not ashed in this study. The dry weight of roots tabulated includes a proportion of weight attributable to sand particles clinging to the roots and it is possible that this proportion may vary according to the genotype and copper treatment.

TABLE 4.1.6. Yield and components of grain yield at maturity.

Treatment	Cu added per pot (mg)	No. of grains per plant	No. of spikelets per ear	No. of grains per ear	Weight per grain (mg)	Grain yield per plant (g)
A. pH 5.0						
Genotype						
Wheat	0	0.0	11.4	0.0	-	0.00
	4	102.8	18.8	34.3	36.6	3.76
Triticale	0	67.0	22.9	47.9	44.3	2.97
	4	70.6	24.4	58.8	47.5	3.35
Rye	0	61.7	32.5	25.7	22.4	1.38
	4	87.1	34.8	36.3	23.4	2.04
B. pH 7.0						
Genotype						
Wheat	0	0.0	11.5	0.0	-	0.00
	4	107.0	18.0	41.2	37.1	3.97
Triticale	0	38.6	19.1	14.3	36.0	1.39
	4	76.3	23.1	42.4	51.0	3.89
Rye	0	79.8	34.2	36.2	22.3	1.78
	4	52.1	33.0	19.3	25.9	1.35
C. pH 8.4						
Genotype						
Wheat	0	0.0	11.0	0.0	-	0.00
	4	96.6	20.1	43.9	38.1	3.68
Triticale	0	0.0	9.8	0.4	-	0.00*
	4	90.0	22.3	52.9	44.3	3.99
Rye	0	49.7	31.5	20.7	18.1	0.90
	4	70.8	34.6	27.2	22.9	1.62
LSD (P = 0.05) for the genotype - soil pH - Cu interaction :		23.2		15.6	12.2	0.70
and for the soil pH - Cu and genotype - Cu interactions:			2.7			

* = 0.003 (negligible)

Statistical analyses appear in Appendices 12, 14, 15, 16 and 17.

TABLE 4.1.7. Effect of level of copper and soil pH on the dry weight of roots per plant (g). Data are means of 3 replicates.

Treatment	Cu added per pot (mg)	Soil pH 5.0	7.0	8.4
Genotype				
Wheat	0	0.59	0.51	0.42
	4	0.87	1.09	1.23
Triticale	0	0.88	1.33	1.61
	4	1.21	1.13	1.39
Rye	0	2.65	3.17	2.49
	4	2.70	4.39	3.06

LSD (P = 0.05) for the genotype effect: 0.42

and for the copper effect: 0.35

Statistical analyses appear in Appendix 18.

4.1.9 Copper in the Plant

The concentration of copper in the straw (stem, leaf and chaff) and grain is shown in Table 4.1.8. All genotypes showed a response to soil pH. As the soil pH was increased, there was a decline in the concentration of copper, both for straw and all classes of grain. The response to copper was spectacular, particularly for the triticale and rye, with these genotypes retaining considerably more copper in the straw at the high level of copper supply. The copper concentration in the grain showed that the concentration of copper in triticale was intermediate between that of wheat and rye. Rye retained the highest concentrations of copper in the grain under all soil pH conditions at both low and high levels of copper supply.

The effects of soil pH and of copper on the concentration of copper in the straw, as described above are both highly significant ($P < 0.001$) as was the genotype-copper interaction. These reflected the differing responses of the three genotypes, both to the soil pH and the level of copper. The interactions were more involved for the grain. There was a significant genotype-soil pH interaction ($P < 0.05$) and a highly significant genotype-copper interaction ($P < 0.001$), in addition to a highly significant soil pH-copper interaction ($P < 0.001$) for the main culms. However, for primary tiller grain the genotype-copper interaction ($P < 0.05$) was the only significant one while for secondary tillers both the genotype-copper interaction ($P < 0.001$) and the soil pH-copper interaction ($P < 0.05$) were significant.

The copper content of the straw (Figure 4.1.5 and Appendix 23) showed a highly significant response to the level of copper supply and to soil pH, although the difference between genotypes was not that large. There were no significant interactions: the genotype and soil pH main

TABLE 4.1.8. Concentration of copper in straw, main culm grain, primary tiller grain and secondary tiller grain.

Treatment	Cu added per pot (mg)	Concentration of copper ($\mu g\ g^{-1}$) Straw	Main culm grain	Primary tiller grain	Secondary tiller grain
A. pH 5.0					
Genotype					
Wheat	0	3.14	-*	-*	-*
	4	3.24	3.39	3.02	3.16
Triticale	0	2.48	0.39	0.40	-*
	4	4.70	4.39	1.79	1.51
Rye	0	2.03	1.40	1.63	0.70
	4	4.05	6.09	5.49	6.42
B. pH 7.0					
Genotype					
Wheat	0	2.73	-*	-*	-*
	4	2.98	2.97	2.96	2.60
Triticale	0	2.07	0.29	0.17	-*
	4	3.53	3.48	3.10	-**
Rye	0	2.21	1.34	1.39	0.68
	4	3.81	6.66	5.39	5.59
C. pH 8.4					
Genotype					
Wheat	0	2.66	-*	-*	-*
	4	2.92	1.90	1.67	1.02
Triticale	0	2.16	-*	-*	-*
	4	2.95	2.58	2.14	0.53
Rye	0	1.49	0.83	0.57	0.40
	4	2.99	3.81	3.56	3.27
LSD (P = 0.05) for the genotype - Cu interaction:		0.46	0.43	0.77	0.84
and for the soil pH - Cu interaction:			0.43		0.84

* = no grain

** = no heads produced

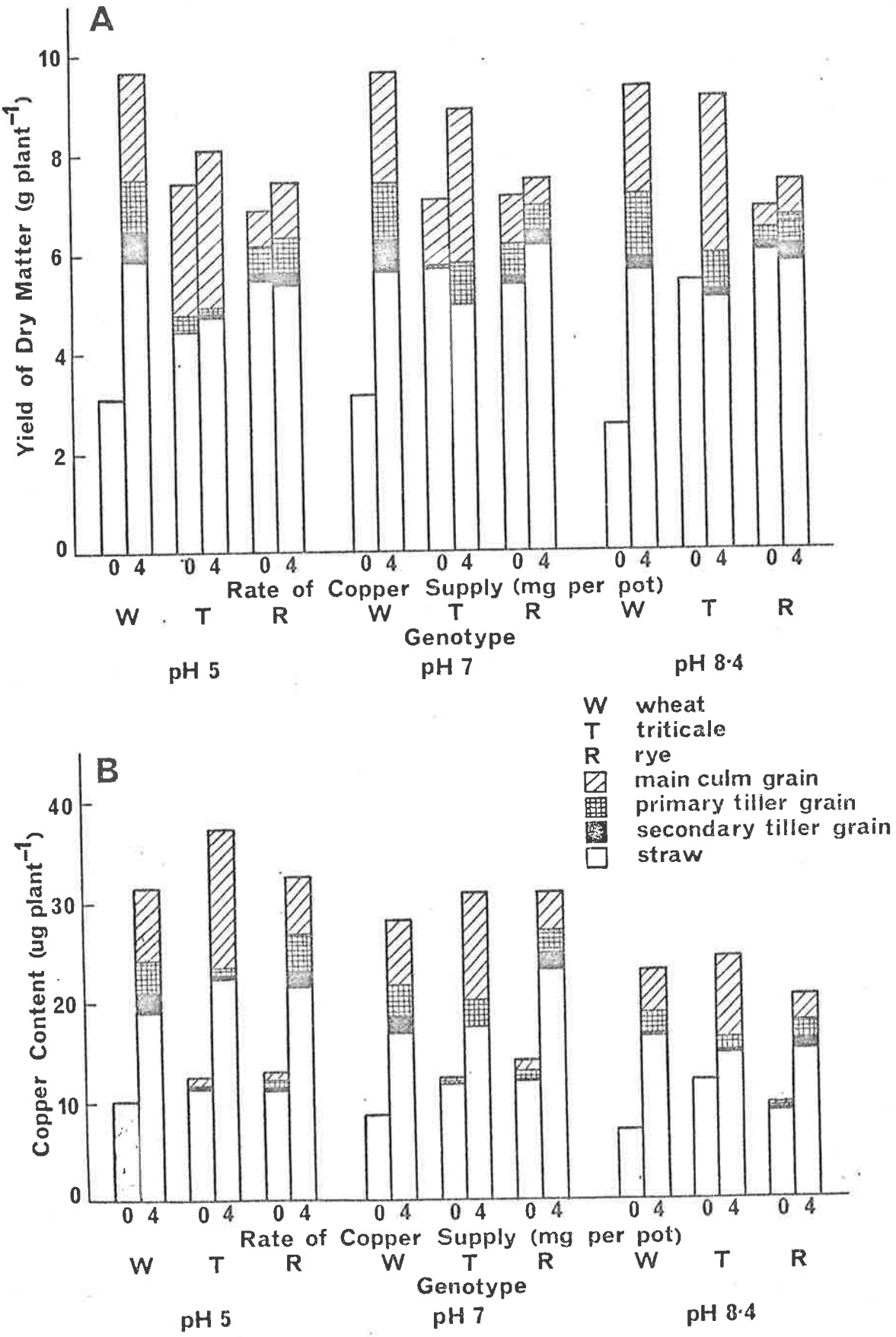
Statistical analyses appear in Appendices 19, 20, 21 and 22.

FIGURE 4.1.5. Effect of soil pH and level of copper supply on

A. total shoot dry matter (g plant^{-1}) and

B. copper content (µg plant^{-1}) for plant components of wheat, triticale and rye.

Statistical analyses appear in Appendices 11, 23, 26, 27, 28, 29, 30, 31.


A
Yield of Dry Matter (g plant^{-1})
0
2
4
6
8
10
0 4 0 4 0 4 0 4 0 4 0 4 0 4 0 4 0 4
Rate of Copper Supply (mg per pot)
W T R W T R W T R
Genotype
pH 5
pH 7
pH 8·4
W wheat
T triticale
R rye
main culm grain
primary tiller grain
secondary tiller grain
straw
B
Copper Content (ug plant^{-1})
0
10
20
30
40
0 4 0 4 0 4 0 4 0 4 0 4 0 4 0 4 0 4
Rate of Copper Supply (mg per pot)
W T R W T R W T R
Genotype
pH 5
pH 7
pH 8·4

effects were significant at $P < 0.01$, whilst the copper main effect was significant at $P < 0.001$.

Figure 4.1.5 and Appendices 24 and 25 showed the amount of copper translocated to the grain (µg per plant). The copper content of the grain showed highly significant responses to the level of copper supply, soil pH and to genotypes. At the high level of copper supply, grain copper content was highest in the triticale owing to its high yield and moderate concentrations of copper. All genotypes responded to application of copper but had less copper translocated to the grain when the plants were grown in an alkaline environment. The genotype, soil pH and copper main effects, along with the genotype-copper interaction, were all highly significant. However, the soil pH-copper interaction was significant for the primary tiller and secondary tiller grain, and the genotype-soil pH-copper interaction ($P < 0.05$) only significant for the primary tiller grain (Appendices 26, 27 and 28).

Discussion of these results begins on page 156.

4.2 POT EXPERIMENT 2

4.2.1 Growth and Visual Symptoms

The plants germinated and showed no difference between genotypes until early-tillering (30 days after sowing) when zinc deficiency symptoms were observed in the wheat plants grown at the high pH. The leaf blades wilted 1-2 cm from the sheath, and had chlorotic stripes on each side of the midrib. This resulted in necrotic areas which caused the collapse of the leaf blade at its midlength and eventually led to death of the leaf. By mid-tillering (50 days after sowing) triticale had similar symptoms at the alkaline pH.

Plants with deficiency symptoms also showed reduction in plant growth and stem elongation, and delay in development of heads and their subsequent senescence (particularly for wheat).

Plate 2 shows a zinc-deficient wheat plant with typical deficiency symptoms.

4.2.2 Water Use

4.2.2.1 Weekly Water Use

In the acidic and neutral environments there were no significant differences in weekly water use produced by the zinc treatment for any of the genotypes. This data is summarized in Appendix 32, Figures 1 to 6. At pH 8.4, however, both wheat and triticale showed the "crossover" effect found for copper in Experiment 1. Figures 4.2.1 to 4.2.3 give the weekly water use for the wheat, triticale and rye, respectively, in the alkaline environment where differences were statistically significant.

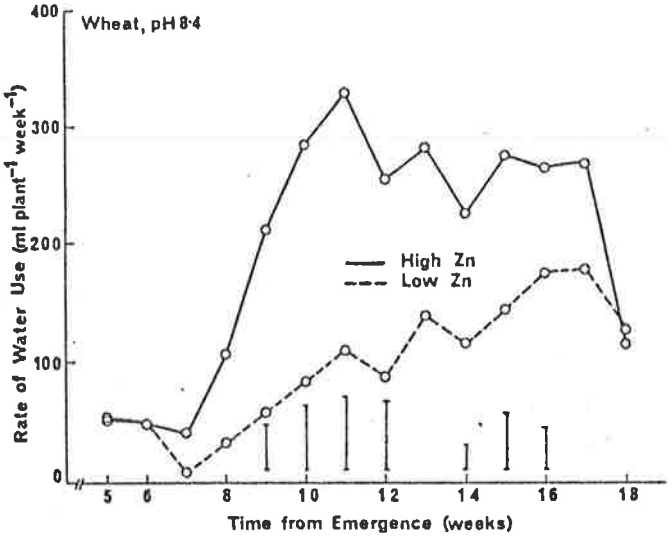
Associated with the zinc-deficient wheat plants was a lower weekly water use than usual during the period to week 17 (milk stage) after

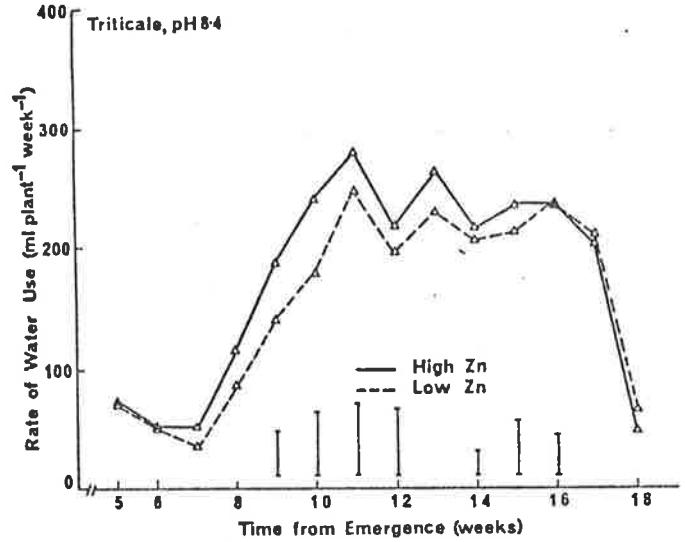
PLATE 2. Close-up of a zinc-deficient wheat plant showing typical zinc deficiency symptoms: chlorotic and necrotic areas on the leaves.

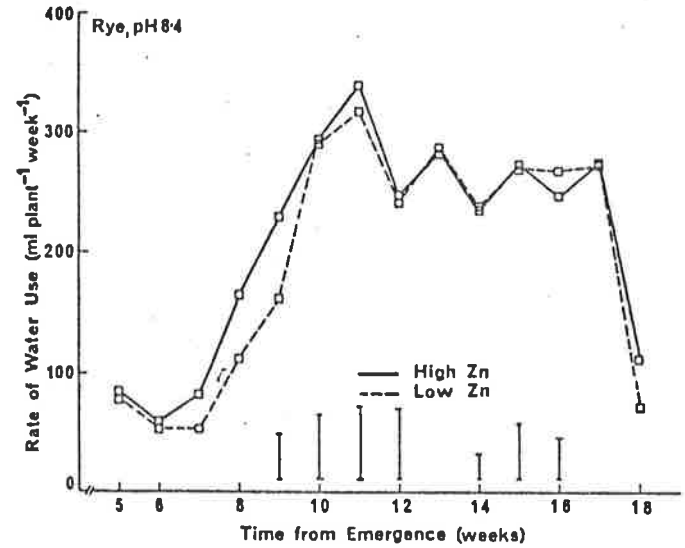
FIGURE 4.2.1. Effect of level of zinc supply on the weekly water use (ml plant^{-1}) throughout the season of wheat at pH 8.4. Data are means of 9 plants (3 plants per pot for each of 3 replicates). Vertical bars indicate LSD values for $P < 0.05$.

FIGURE 4.2.2. Effect of level of zinc supply on the weekly water use (ml plant^{-1}) throughout the season of triticale at pH 8.4. Data are the means of 9 plants (3 plants per pot for each of 3 replicates). Vertical bars indicate LSD values for $P < 0.05$.

FIGURE 4.2.3. Effect of level of zinc supply on the weekly water use (ml plant^{-1}) throughout the season of rye at pH 8.4. Data are the means of 9 plants (3 plants per pot for each of 3 replicates). Vertical bars indicate LSD values for $P < 0.05$.


Wheat, pH 8·4
Rate of Water Use (ml plant⁻¹ week⁻¹)
400
300
200
100
0
High Zn
Low Zn
5
6
8
10
12
14
16
18
Time from Emergence (weeks)


Triticale, pH 8·4
Rate of Water Use (ml plant⁻¹ week⁻¹)
400
300
200
100
0
High Zn
Low Zn
5
6
8
10
12
14
16
18
Time from Emergence (weeks)


Rye, pH 8·4
Rate of Water Use (ml plant⁻¹ week⁻¹)
400
300
200
100
0
High Zn
Low Zn
5
6
8
10
12
14
16
18
Time from Emergence (weeks)

which time the plants used more water. A similar pattern existed for zinc-deficient triticale plants. Until week 15 (anthesis) zinc-deficient triticale plants used considerably less water than the healthy plants, but after the "crossover" there was no significant difference in the weekly water use between zinc treatments. Rye was tolerant to both level of zinc and soil pH and did not show any differences between zinc treatments in weekly water use at any soil pH.

4.2.2.2 Total Water Use

The differences in water use between zinc treatments were largest for wheat, which was the most sensitive to zinc deficiency (Table 4.2.1). Rye, which was relatively tolerant to a deficiency of zinc, showed no significant differences in water use between zinc treatments. This caused the genotype-zinc interaction which was significant ($P < 0.05$).

There was in fact a significant genotype-soil pH-zinc interaction ($P < 0.01$): water use of wheat and triticale at pH 8.4, relative to rye, showed a significant decline in the absence of added zinc. The other first order interactions were also statistically significant ($P < 0.01$).

4.2.3 Plant Height

Application of zinc to the plants favoured growth and so increased height measured at maturity (Table 4.2.2). This height difference was only observed in the alkaline environment where the severity of the zinc deficiency was greatest and the differing sensitivities of the genotypes could be seen.

These findings were supported by the appropriate significant interactions as outlined in Appendix 34.

TABLE 4.2.1. Effect of level of zinc, soil pH and genotype on the total water use (ml plant^{-1}) over the whole season. Data are the means of 3 replicates.

Treatment	Zn added per pot (mg)	Soil pH 5.0	7.0	8.4
Genotype				
Wheat	0	2800	2850	1370
	4	2770	2910	2740
Triticale	0	2690	2730	2160
	4	2690	2790	2400
Rye	0	2930	2900	2720
	4	2920	2950	2920

LSD (P = 0.05) for the genotype-soil pH-Zn interaction : 355

Statistical analyses appear in Appendix 33.

TABLE 4.2.2. Effect of zinc supply, soil pH and genotype on plant height (cm). Data are main culm heights at maturity and the mean of 9 plants (3 plants per pot for each of 3 replicates).

Treatment	Zn added per pot (mg)	Soil pH 5.0	7.0	8.4
Genotype				
Wheat	0	106	101	36
	4	100	98	98
Triticale	0	102	103	86
	4	104	100	104
Rye	0	144	136	130
	4	131	136	138

LSD (P = 0.05) for the genotype-soil pH-Zn interaction : 13.6

Statistical analyses appear in Appendix 34.

4.2.4 Tillering

Although zinc-deficient wheat and triticale plants tillered profusely, the number of ears was changed only slightly by application of zinc (Table 4.2.3); the ears of zinc deficient plants, however, had considerably fewer grains. Soil pH and level of zinc significantly influenced the number of tillers produced by the genotypes ($P < 0.05$), but the three genotypes showed different responses. This was indicated by the genotype-soil pH-zinc interaction ($P < 0.001$).

Zinc-deficient wheat and triticale plants at pH 8.4 produced fewer ears per plant than their healthy counterparts, although triticale was still intermediate. This again was demonstrated by nature of the significant soil pH-zinc interaction ($P < 0.05$).

4.2.5 Delay in Maturity

Zinc-deficient wheat and triticale plants in the alkaline environment were late in maturing and at harvest were still somewhat green (Table 4.2.4). The ears on the zinc-deficient triticale plants emerged at the usual time but were slow in developing to anthesis and maturity. On zinc-deficient wheat plants the ears were late in emerging and then slow in subsequent development. The number of days to ear emergence, anthesis and maturity for the other plant treatments were unaffected by either soil pH or level of zinc.

4.2.6 Dry Matter Production

Application of zinc caused significant differences in the shoot dry matter of all genotypes but only at high pH (Figure 4.2.4A and Appendix 41). The response to zinc under these conditions was largest for wheat and least for rye. Plate 3 illustrates this well. Triticale was intermeidate in all soil (pH) environments, while wheat was superior

TABLE 4.2.3. Tiller production and ear production per plant at maturity. Data are means of 3 replicates of 3 plants per pot.

Treatment	Zn added per pot (mg)	Soil pH 5.0	Soil pH 7.0	Soil pH 8.4	Soil pH 5.0	Soil pH 7.0	Soil pH 8.4
		A. Number of culms per plant			B. Number of ears per plant		
Genotype							
Wheat	0	3.3	3.6	7.2	2.4	2.8	1.2#
	4	2.8	3.3	3.0	2.2	2.7	2.3
Triticale	0	2.1	2.0	1.6	1.9	1.8	1.3#
	4	2.2	2.3	2.1	1.7	1.7	1.7
Rye	0	3.1	3.0	3.0	2.8	2.7	2.3
	4	3.2	3.2	3.4	2.6	2.4	2.6

LSD (P = 0.05) for the

genotype-soil pH-Zn interaction: 0.98

soil pH-Zn interaction: 0.81

these ears failed to mature by harvest.

Statistical analyses appear in Appendices 35 and 36.

TABLE 4.2.4. Number of days to ear emergence, anthesis and maturity of the genotypes as affected by soil pH and level of applied zinc. Data are the means of 9 plants (3 plants per pot and 3 replicates).

Treatment	Zn added per pot (mg)	Soil pH 5.0	Soil pH 7.0	Soil pH 8.4	Soil pH 5.0	Soil pH 7.0	Soil pH 8.4	Soil pH 5.0	Soil pH 7.0	Soil pH 8.4
		Ear emergence			Anthesis			Maturity		
A. Main culms										
Genotype										
Wheat	0	84	88	100	96	96	106	130	131	-*
	4	85	85	88	96	95	99	130	130	131
Triticale	0	75	75	78	86	87	91	122	121	-*
	4	74	75	78	85	88	89	121	121	122
Rye	0	79	81	85	92	95	95	128	130	134
	4	80	80	82	95	93	95	131	129	128
LSD (P = 0.05) for the genotype-zinc interaction and for the soil pH-Zn interaction:		2.6			genotype effect and the soil pH effect:	1.9		genotype-soil pH-Zn interaction:	4.0	
B. Primary Tillers										
Genotype										
Wheat	0	89	95	-*	101	101	-*	135	134	-*
	4	90	92	94	100	100	104	135	135	135
Triticale	0	79	82	84	91	93	100	125	125	-*
	4	78	83	85	90	94	94	124	125	126
Rye	0	82	84	91	98	99	102	133	135	139
	4	82	83	83	98	101	101	135	134	135
C. Secondary Tillers										
Genotype										
Wheat	0	94	102	-*	105	110	-*	139	139	-*
	4	93	97	100	106	104	107	141	139	139
Triticale	0	-*	85	-*	-*	94	-*	-*	-*	-*
	4	-*	90	-*	-*	100	-*	-*	134	-*
Rye	0	87	89	94	104	103	105	138	140	143
	4	87	88	84	101	102	103	140	137	137

* = not reached by harvest date, but for purposes of statistical analysis high values were substituted for missing values.

Statistical analyses appear in Appendices 37, 38, 39.

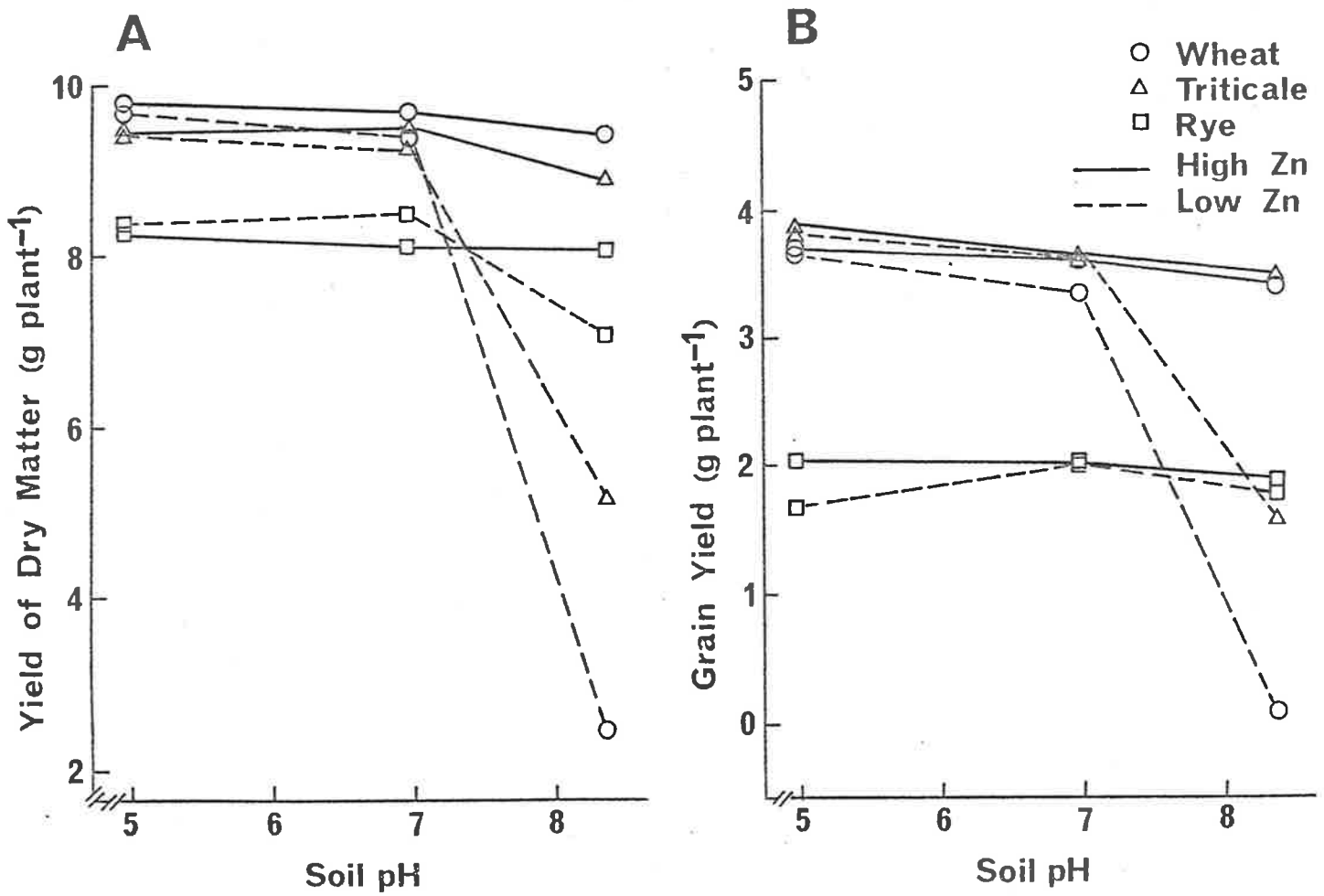


FIGURE 4.2.4. Effect of soil pH, level of zinc supply and genotype on A. total shoot dry matter (g plant^{-1}) and B. total grain yield (g plant^{-1}). Means of 3 replicates. LSD (P = 0.05) of the genotype-soil pH-zinc interaction is 0.92 for total shoot dry matter and 0.48 for total grain yield. Statistical analyses appear in Appendices 41 and 43.

PLATE 3. The difference between genotypes in sensitivity to a deficiency of zinc at pH 8.4. Wheat, triticale and rye, from left to right in pairs (without zinc added, with zinc added).

at pH 5.0 and failed badly at pH 8.4. These differential responses are expressed in statistical terms as a significant genotype-soil pH-zinc interaction. Triticale was less sensitive to zinc deficiency than wheat, but not as tolerant as rye.

The contribution of the grain to the shoot weight of the plants (defined as 'harvest index') did not vary until the pH was increased to 8.4 when the grain production was markedly reduced in the absence of zinc. Under all soil (pH) conditions, both the shoot yield and harvest index of rye were lower than those of triticale and wheat.

The degree of zinc deficiency in the soil was marginal in that the effect of the soil pH on the availability of that element was not marked until the pH became alkaline. A soil pH-zinc interaction existed by virtue of these effects.

4.2.7 Grain Yield and Its Components

The level of copper supply affected the reproductive phase more than the vegetative (Figure 4.1.4), while the level of zinc (and of pH) affected both in a similar way (Figure 4.2.4). Rye was relatively tolerant of the zinc deficient soil in which wheat produced very little grain and triticale showed some reduction in grain yield (a high soil pH). Triticale was less sensitive to zinc deficiency than wheat, but not tolerant like rye.

Grain yield was similar to shoot dry matter in that it showed a highly significant genotype-soil pH-zinc interaction ($P < 0.001$). At pH 5.0 and 7.0, irrespective of zinc treatment, triticale outyielded both wheat and rye in grain production, at pH 8.4, however, triticale without added zinc was intermediate between wheat and rye whilst with added zinc it was still superior to its parent types.

The number of grains per plant (Table 4.2.5 and Appendix 44) showed the same pattern as grain yield, although the genotype-soil pH-zinc interaction was not as strong. Reduction in grain yield which occurred at high soil pH resulting from zinc deficiency was caused both by a decrease in the number of grains per ear and lower weight per grain. The biggest effect was felt in the number of grains produced per ear. Wheat showed the greatest reductions in the number of grains per ear and the size of the grain, whilst rye was unaffected.

4.2.8 Dry Weight of Roots

The dry weight of roots (Table 4.2.6 and Appendix 48) was not significantly affected by either the level of zinc supply or the soil pH, although the application of zinc generally increased the dry weight of roots. The genotype markedly affected the dry weight of roots and consequently a significant difference existed between them. In all soil (pH) environments, irrespective of the zinc treatment, the dry weight of roots was largest for rye and smallest for wheat.

The roots were not ashed in this study and so the dry weight of roots tabulated includes a proportion of weight attributable to sand particles clinging to the roots. It is possible that this proportion may vary according to the genotype and zinc treatment.

4.2.9 Zinc and Manganese in the Plant

The concentrations of zinc in the straw (stem, leaf and chaff) and grain are shown in Table 4.2.7. There was a response to soil pH by all genotypes, but it was more prominent in the components of grain than in the straw. As the soil pH was increased, the concentration of zinc in all plant parts declined, irrespective of the zinc treatment. A strong response to the application of zinc was obvious in all soil (pH)

TABLE 4.2.5. Yield and components of grain yield at maturity.

Treatment	Zn added per pot (mg)	No. of grains per plant	No. of spikelets per ear	No. of grains per ear	Weight per grain (mg)	Grain yield per plant (g)
A. pH 5.0						
Genotype						
Wheat	0	110.6	19.3	46.1	32.8	3.63
	4	105.8	19.1	48.1	34.7	3.67
Triticale	0	97.3	21.3	51.2	38.7	3.76
	4	92.7	20.1	54.5	41.1	3.81
Rye	0	108.8	35.0	38.8	13.4	1.67
	4	97.4	36.9	37.5	20.8	2.03
B. pH 7.0						
Genotype						
Wheat	0	103.9	18.8	37.1	31.9	3.32
	4	108.7	18.9	40.2	33.0	3.59
Triticale	0	87.9	20.4	48.8	40.7	3.57
	4	91.2	21.0	53.7	39.6	3.61
Rye	0	117.1	36.2	43.4	17.0	1.99
	4	100.9	39.1	42.0	19.8	1.99
C. pH 8.4						
Genotype						
Wheat	0	6.6	16.7	5.5	11.6	0.08
	4	114.8	20.3	49.9	29.5	3.38
Triticale	0	42.1	18.3	31.7	37.8	1.56
	4	97.6	21.7	57.4	35.6	3.48
Rye	0	85.8	35.5	37.3	20.7	1.77
	4	103.0	34.8	39.6	18.3	1.88
LSD (P = 0.05) for the genotype-soil pH-Zn interaction:		24.9		13.5	4.3	0.48
and for the genotype effect:		1.2				
and for the zinc effect:		1.0				

Statistical analyses appear in Appendices 43, 44, 45, 46 and 47.

TABLE 4.2.6. Effect of level of zinc and soil pH on the dry weight of roots per plant (g). Data are means of 3 replicates.

Treatment	Zn added per pot (mg)	Soil pH 5.0	7.0	8.4
Genotype				
Wheat	0	1.52	2.17	1.48
	4	1.95	2.00	1.85
Triticale	0	2.44	2.01	1.96
	4	3.12	2.06	2.20
Rye	0	5.19	3.72	4.77
	4	5.95	4.51	7.03

LSD (P = 0.05) for the genotype effect: 0.90

Statistical analyses appear in Appendix 48.

TABLE 4.2.7. Concentration of zinc in straw, main culm grain, primary tiller grain and secondary tiller grain.

Treatment	Zn added per pot (mg)	Concentration of zinc ($\mu g\ g^{-1}$) Straw	Main culm grain	Primary tiller grain	Secondary tiller grain
A. pH 5.0					
Genotype					
Wheat	0	12.4	20.1	18.4	13.2
	4	34.6	39.2	37.5	40.8
Triticale	0	17.6	23.7	23.1	-*
	4	60.3	51.9	45.3	-*
Rye	0	16.9	30.4	27.8	27.7
	4	56.2	50.3	47.2	48.6
B. pH 7.0					
Genotype					
Wheat	0	9.3	9.9	10.0	6.3
	4	23.9	27.9	29.1	30.8
Triticale	0	16.4	13.0	10.4	2.8
	4	30.7	45.9	35.7	9.8
Rye	0	12.3	17.5	14.7	17.3
	4	33.3	40.8	38.4	37.9
C. pH 8.4					
Genotype					
Wheat	0	8.0	4.4	3.2	-*
	4	9.4	9.8	9.3	9.1
Triticale	0	12.2	9.9	11.0	-*
	4	15.0	12.5	11.4	-*
Rye	0	13.4	11.6	12.6	11.7
	4	16.6	26.2	24.1	16.5
LSD (P = 0.05) for the					
genotype-soil pH-Zn interaction:		7.61	7.35	soil pH-Zn interaction: 3.85	6.77

* = no grain.

Statistical analyses appear in Appendices 49, 50, 51, 52.

environments, and it was equally as important for the straw as for the different grain components.

The effects of soil pH and application of zinc on the concentration of zinc in straw and grain components were both highly significant ($P < 0.001$) as was the genotype-soil pH interaction for all but secondary tiller grain ($P < 0.05$). There was also a highly significant difference ($P < 0.001$) in the zinc concentration of the straw and grain components as a function of the genotype. At all soil pHs triticale and rye retained higher concentrations of zinc in the straw than did wheat, but the differences became less pronounced with increasing soil pH. The general pattern was similar for the grain, although at high pH the differences between wheat and triticale were less as a result of the increased severity of zinc deficiency in that environment.

For the straw and main culm grain there was also a significant genotype-soil pH-zinc interaction ($P < 0.05$) as a result of the above factors.

Wheat, triticale and rye showed no difference in manganese concentration of the straw (Table 4.2.8), although manganese concentration was strongly influenced by the acidity of the soil independently of the zinc treatment. The concentration of manganese in the straw declined when zinc was added to the plants, particularly at higher pH where zinc deficiency occurred.

The concentration of manganese in the grain components showed the same response to soil pH as did the manganese concentration in the straw; however, the genotypes differed in their manganese concentrations in the grain. At pH 8.4, in the presence of added zinc, manganese levels were extremely low.

TABLE 4.2.8. Concentration of manganese in straw, main culm grain, primary tiller grain and secondary tiller grain.

Treatment	Zn added per pot (mg)	Concentration of manganese ($\mu g\ g^{-1}$) Straw	Main culm grain	Primary tiller grain	Secondary tiller grain
A. pH 5.0					
Genotype					
Wheat	0	158	78	85	57
	4	170	81	85	81
Triticale	0	169	63	58	*
	4	197	66	61	*
Rye	0	166	73	76	73
	4	220	86	82	85
B. pH 7.0					
Genotype					
Wheat	0	79	47	49	41
	4	69	45	51	50
Triticale	0	106	50	48	20
	4	96	53	48	16
Rye	0	75	54	53	52
	4	91	53	51	55
C. pH 8.4					
Genotype					
Wheat	0	41	11	7	*
	4	9	12	12	10
Triticale	0	21	33	26	*
	4	10	14	13	*
Rye	0	21	27	31	29
	4	20	26	27	16
LSD (P = 0.05) for the soil pH-Zn interaction:		21.18	genotype-soil pH interaction: 9.94	9.72	21.81

* = no grain

Statistical analyses appear in Appendices 53, 54, 55, 56.

The zinc content of the straw (Figure 4.2.5 and Appendix 60) showed the same pattern as the concentration of zinc in the straw. The amount of zinc translocated to the grain (Figure 4.2.5 and Appendices 61 and 62) showed highly significant responses to the level of zinc supply, soil pH and to genotypes (Appendices 63, 64 and 65). There were also significant interactions which could be attributed to the differing responses of the genotypes to zinc deficiency at the alkaline pH. Under acid and neutral pH conditions, for both zinc treatments, the zinc contents of the grain and straw were highest in triticale resulting from the high yield and high concentrations of zinc. In the alkaline environment, however, triticale was intermediate to wheat and rye, owing to the decline in yields and zinc concentrations which occurred for all plant parts. Rye was highest.

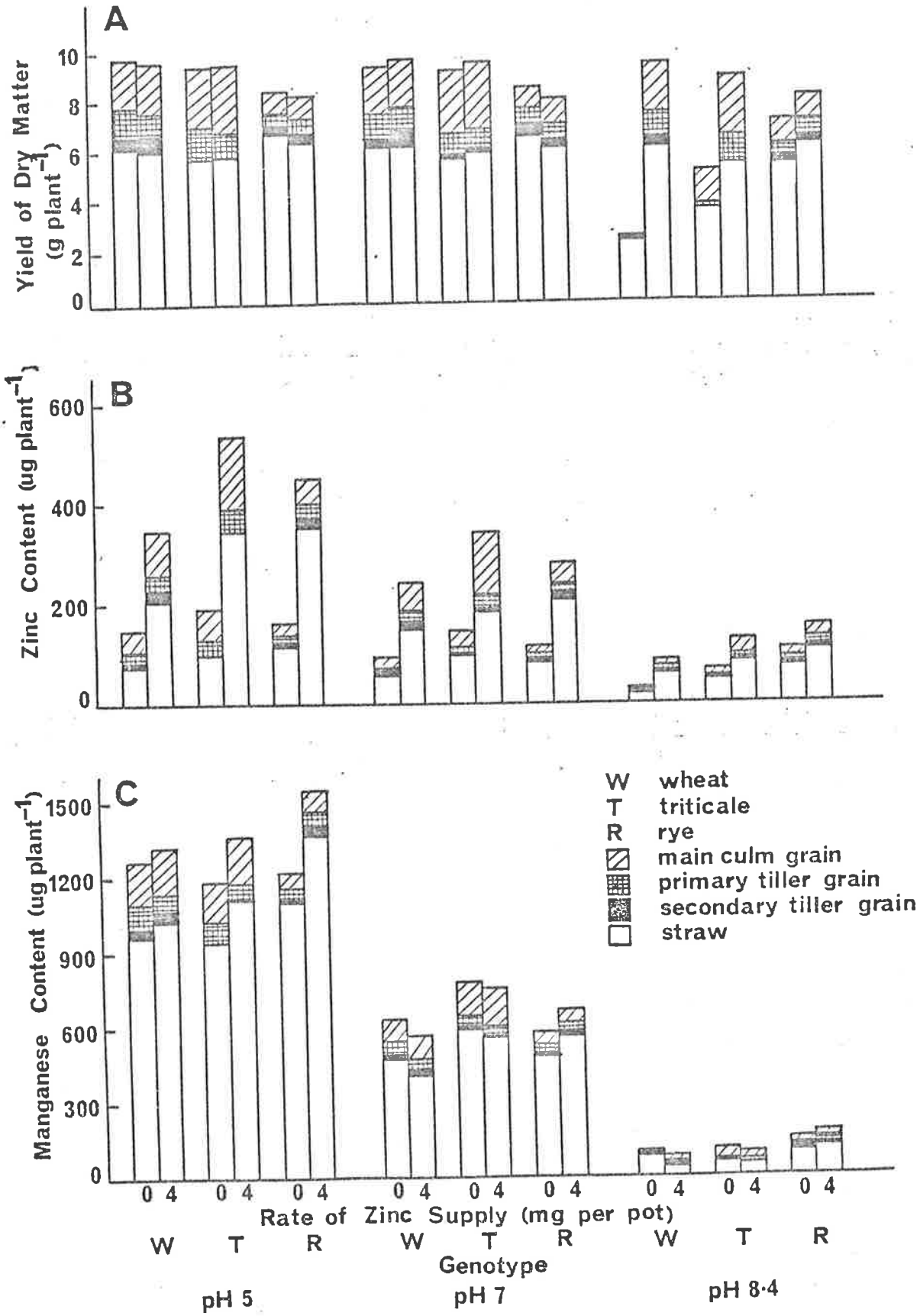
The manganese content of the straw (Figure 4.2.5 and Appendix 66) was largely independent of the zinc treatment, slightly influenced by genotype ($P < 0.05$), but markedly affected by the soil pH ($P < 0.001$). Manganese retained in the straw showed the same pattern towards pH as the concentration of manganese in the straw. The genotype effect was the result of the differing sensitivities of wheat, triticale and rye to zinc deficiency.

The manganese contents of the various components of grain (Figure 4.2.5 and Appendices 67, 68, 69 and 70) showed responses to genotype and soil pH, similar to those observed for the manganese concentrations. Zinc application only had a marked influence on the manganese content of the main culm grain. The effect of zinc on the manganese content of the primary tiller grain was only slight whilst manganese content of the secondary tiller grain was completely independent of the level of zinc supply and only reflected the other main effects.

Discussion of these results begins on page 160.

FIGURE 4.2.5. Effect of soil pH and level of zinc supply on A. total shoot dry matter (g plant^{-1}), B. zinc content (µg plant^{-1}) and C. manganese content (µg plant^{-1}) for plant components of wheat, triticale and rye.

Statistical analyses appear in Appendices 42, 57, 58, 59, 60, 63, 64, 65, 66, 68, 69, 70.


A
Yield of Dry Matter (g plant^{-1})
0
2
4
6
8
10
B
Zinc Content (ug plant^{-1})
0
200
400
600
C
Manganese Content (ug plant^{-1})
0
300
600
900
1200
1500
W wheat
T triticale
R rye
main culm grain
primary tiller grain
secondary tiller grain
straw
0 4 0 4 0 4 0 4 0 4 0 4 0 4 0 4 0 4
Rate of Zinc Supply (mg per pot)
W T R W T R W T R
Genotype
pH 5
pH 7
pH 8·4

4.3 POT EXPERIMENT 3

4.3.1 Growth and Visual Symptoms

All plants germinated and appeared to have normal growth until early-tillering (25-30 days after sowing) when wheat cv. Halberd in the Mt. Burr soil (pH 5.0)+ and Woods Well soil (pH 7.1)+ showed symptoms of copper and zinc deficiency. Curiously, plants supplied with neither copper nor zinc showed symptoms of both these deficiencies at once. On some plants the symptoms appeared separately on different leaves, whilst in others they appeared to develop together on the same leaves (Plate 4).

By mid-tillering (50 days after sowing) wheat cv. Halberd in the Robe soil (pH 8.8)+, wheat cv. Gatcher and triticale in all the soil environments, and rye at pH 5.0 showed various symptoms of copper and zinc deficiency. Wheat cv. Halberd at pH 8.8 responded to both the application of copper and zinc. Wheat cv. Gatcher was severely retarded by copper and zinc deficiency at pH 5.0 and also responded to application of copper and zinc at pH 7.1 and 8.8, although the severity of the deficiency was not as marked. Triticale was also affected by deficiency of copper and zinc in all the soil environments.

For all genotypes, plants without either copper or zinc added exhibited symptoms of both deficiencies, separately and together on the leaves. The copper and zinc treatments also showed their respective deficiency symptoms and these symptoms were most severe at pH 5.0 and least at pH 7.1 for all genotypes.

The pH 5.0 soil was so deficient in copper that even rye responded to application of copper and zinc. Rye without either copper or zinc showed symptoms of copper deficiency and slight symptoms of zinc

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+ in this section soil types will be designated by their pH for simplicity.

deficiency. Similarly, the plants without copper only showed symptoms of copper deficiency; and those without zinc only gave a slight response to the application of zinc. So severe was the deficiency of copper in this soil that the control plants (with both added copper and zinc) at pH 5.0 showed "stripes" of light and dark green which indicated that the plants may have been deficient in copper, or possibly another element (Plate 5). The copper and zinc deficiency symptoms were associated with retardation of plant growth and stem elongation, and delayed development of heads and senescence.

4.3.2 Water Use

4.3.2.1 Weekly Water Use

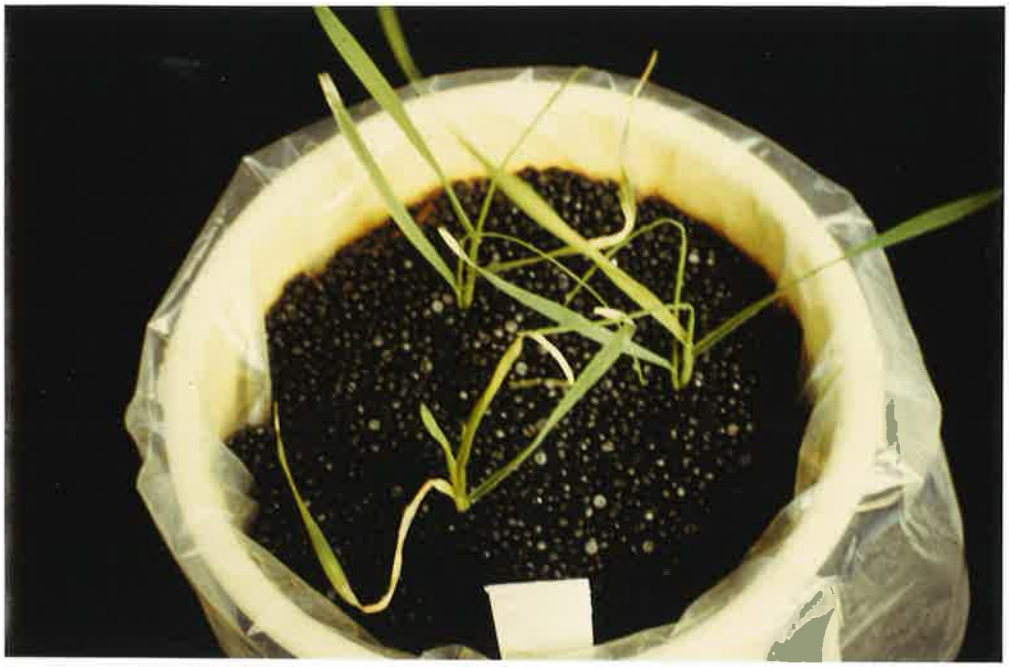
The influence of copper, zinc and soil type (chosen on the basis of soil pH) on weekly water use of the four genotypes is summarised in Figures 4.3.1 to 4.3.4 and Appendix 71. Copper- and zinc-deficient plants at pH 5.0 had a lower rate of water use than the healthy plants (Figures 4.3.1 to 4.3.4), however, in the other soil environments the situation was more complex.

At pH 5.0, copper deficiency was the most important factor influencing the rate of water use. Plants with neither copper nor zinc, and those with only zinc added had similar, low weekly rates of water use. Those plants with only copper added, however, had higher weekly rates of water use, in some cases nearing that of the plants with both added copper and zinc.

At pH 7.1, there was little difference in weekly water use among treatments for the triticale and rye except during the early stages of growth. For both wheat cultivars, however, the weekly water use was complex in this soil: there was a "crossover" in the water use curves

PLATE 4. Close-up of a wheat plant showing symptoms of both copper and zinc deficiency: "wither-tip" of copper deficiency, and chlorotic and necrotic areas characteristic of zinc deficiency.

PLATE 5. Close-up of a wheat plant with added copper and added zinc (complete treatment) at pH 5.0 showing "stripes" of light and dark green.



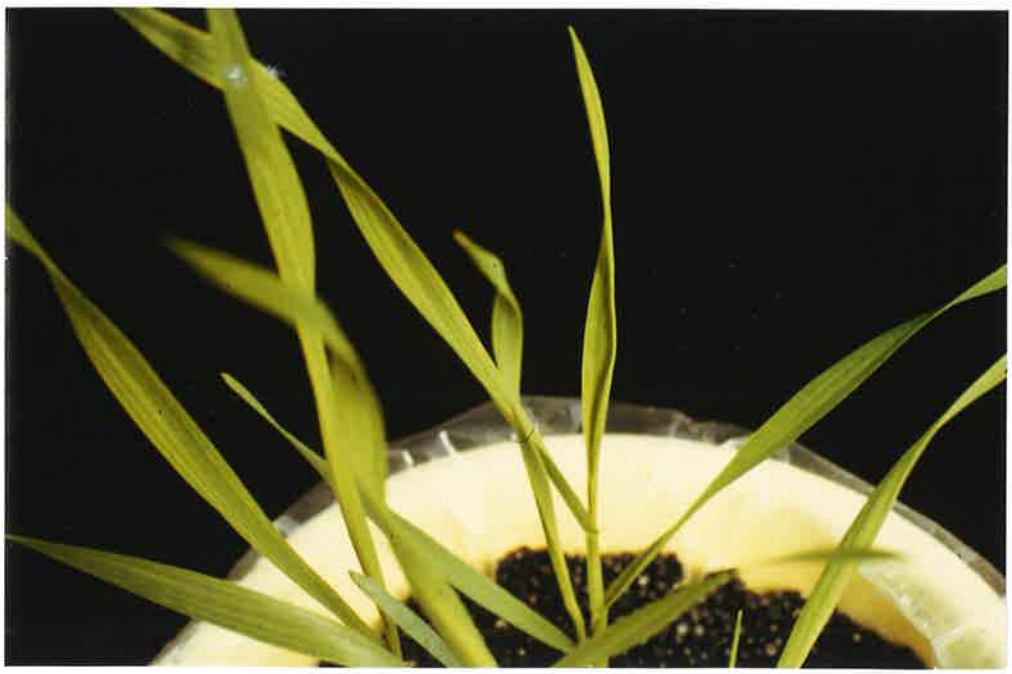
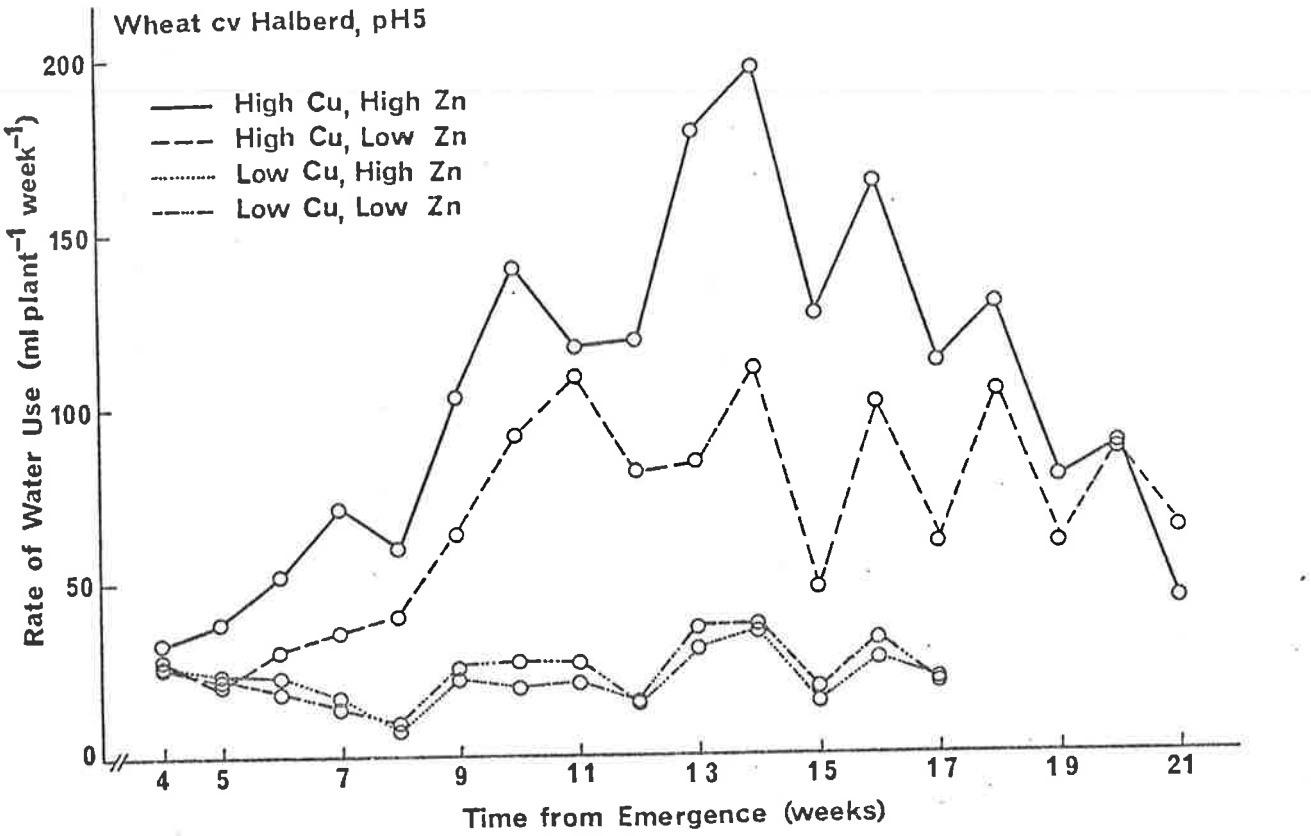


FIGURE 4.3.1. Effect of level of copper and zinc supply on the weekly water use (ml plant^{-1}) throughout the season of wheat cv. Halberd at pH 5.0. Data are means of 6 plants (3 plants per pot for each of 2 replicates).

FIGURE 4.3.2. Effect of level of copper and zinc supply on the weekly water use (ml plant^{-1}) throughout the season of wheat cv. Gatcher at pH 5.0. Data are means of 6 plants (3 plants per pot for each of 2 replicates).


Wheat cv Halberd, pH5
High Cu, High Zn
High Cu, Low Zn
Low Cu, High Zn
Low Cu, Low Zn
Rate of Water Use (ml plant^{-1} week^{-1})
200
150
100
50
0
4
5
7
9
11
13
15
17
19
21
Time from Emergence (weeks)

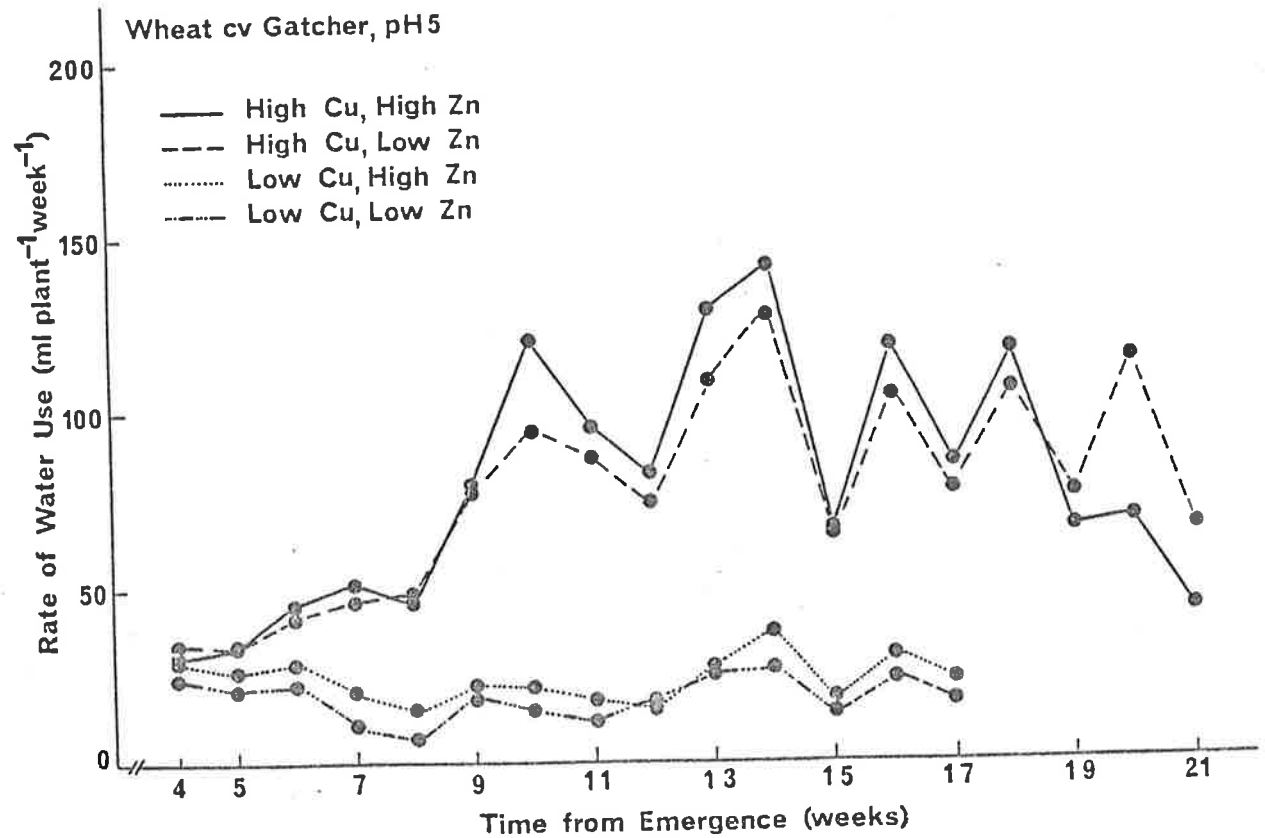
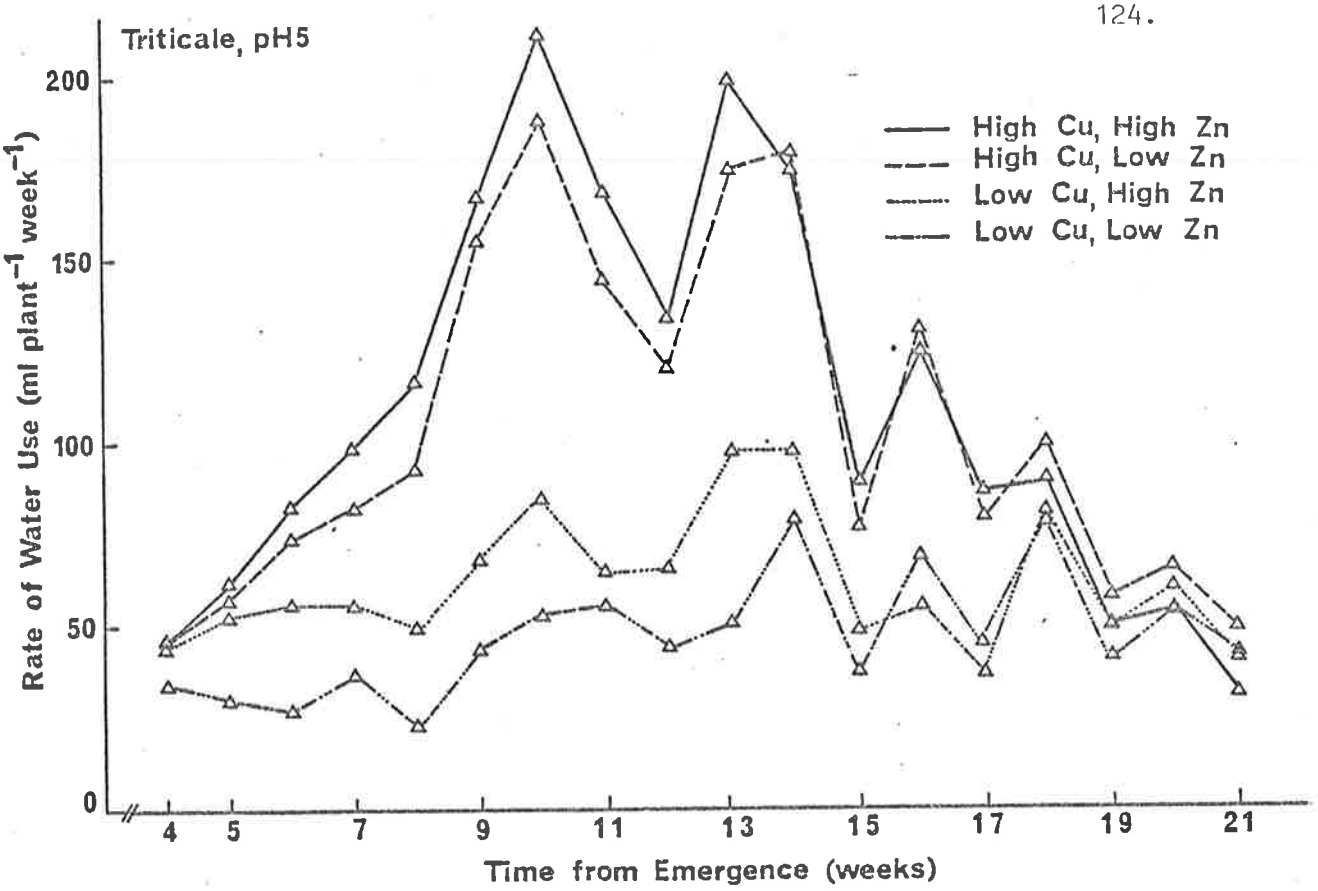
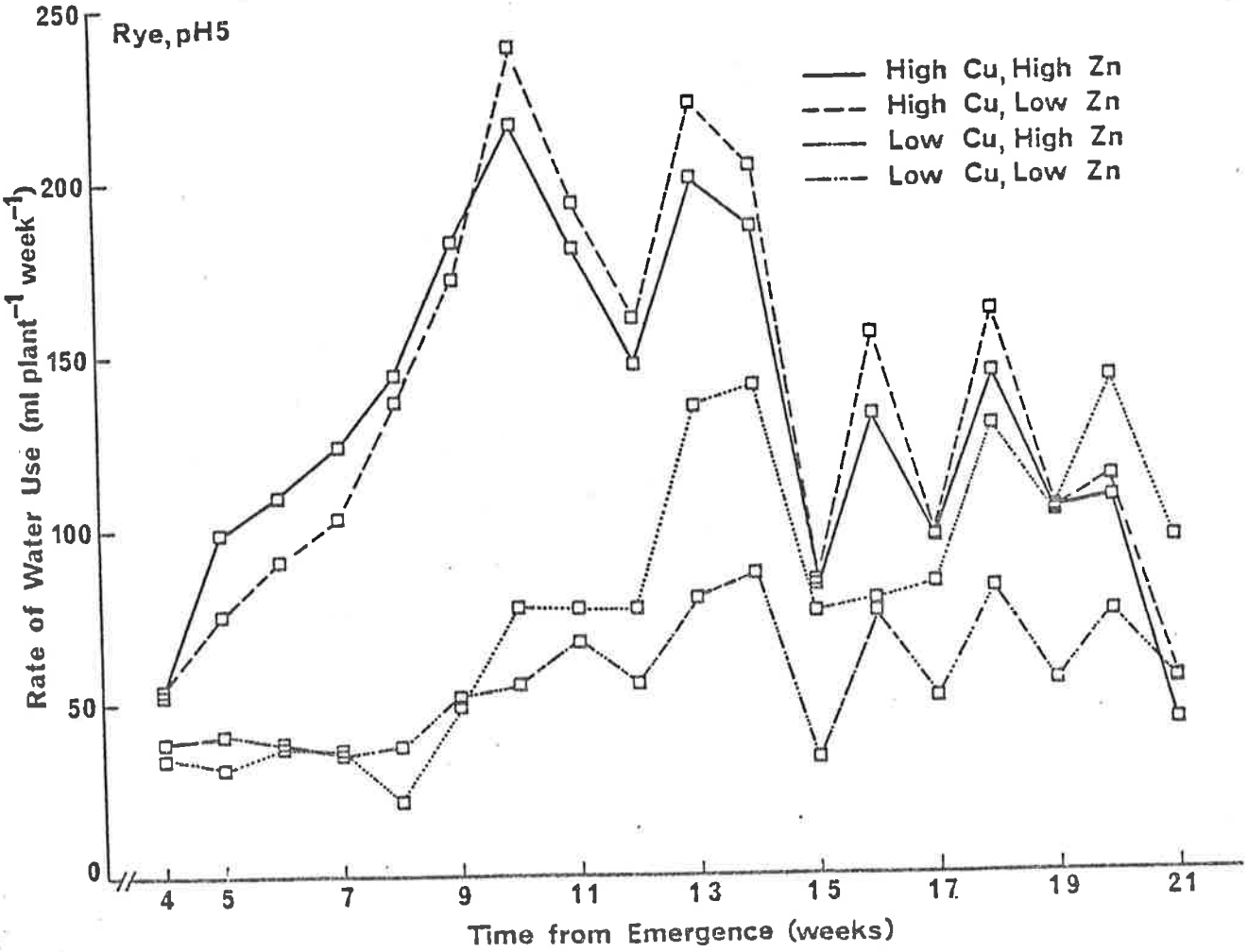

Wheat cv Gatcher, pH5
High Cu, High Zn
High Cu, Low Zn
Low Cu, High Zn
Low Cu, Low Zn
Rate of Water Use (ml plant^{-1}week^{-1})
200
150
100
50
0
4
5
7
9
11
13
15
17
19
21
Time from Emergence (weeks)

FIGURE 4.3.3. Effect of level of copper and zinc supply on the weekly water use (ml plant^{-1}) throughout the season of triticale at pH 5.0. Data are means of 6 plants (3 plants per pot for each of 2 replicates).

FIGURE 4.3.4. Effect of level of copper and zinc supply on the weekly water use (ml plant^{-1}) throughout the season of rye at pH 5.0. Data are means of 6 plants (3 plants per pot for each of 2 replicates).


Triticale, pH5
High Cu, High Zn
High Cu, Low Zn
Low Cu, High Zn
Low Cu, Low Zn
Rate of Water Use (ml plant^{-1} week^{-1})
0
50
100
150
200
4
5
7
9
11
13
15
17
19
21
Time from Emergence (weeks)


Rye, pH5
High Cu, High Zn
High Cu, Low Zn
Low Cu, High Zn
Low Cu, Low Zn
Rate of Water Use (ml plant^{-1} week^{-1})
0
50
100
150
200
250
4
5
7
9
11
13
15
17
19
21
Time from Emergence (weeks)

for the different treatments and whilst the healthy plants used more water early in the season, they later used less (Appendix 71, Figures 1 to 4).

At pH 8.8, the weekly water use curves for both wheat cultivars were similar to those at pH 7.1, but the difference in the rate of weekly water use among treatments was considerably larger at pH 8.8. Weekly water use of triticale showed similar trends to the wheats in this soil, although the differences among treatments were smaller. Rye, however, showed little or no differences in weekly water use among treatments (Appendix 71, Figures 5 to 8).

4.3.2.2 Total Water Use

Total water use over the whole season differed among the genotypes with triticale intermediate between the wheats and rye. All genotypes showed strong responses to soil type and level of copper supply, but responded only slightly to the level of zinc supply (Table 4.3.1). The total water use of all genotypes was lowest in the acidic environment for all treatments, whilst total water use in the alkaline environment was highest for all treatments with the exception of wheat cv. Gatcher (-Cu-Zn and -Cu+Zn) where it was intermediate.

A significant genotype-soil pH-copper interaction ($P < 0.05$) occurred as a result of the differing severity of copper deficiency in the three soils and the differential effects this had on the responses of the four genotypes. There was also a significant genotype-copper-zinc interaction ($P < 0.01$) attributed to the differing responses of the wheat cultivars compared to triticale and rye on the addition of zinc to the plants in the presence or absence of copper.

TABLE 4.3.1. Effect of copper and zinc supply, soil pH and genotype on the total water usage (ml plant^{-1}) over the whole season. Data are means of 2 replicates.

Treatment	Cu added per pot (mg)	Zn added per pot (mg)	Soil pH 5.0	7.1	8.8
Genotype					
Wheat cv. Halberd	0	0	326	2189	2623
	0	4	300	2125	1983
	4	0	1209	2362	2737
	4	4	1843	2433	2992
Wheat cv. Gatcher	0	0	250	2272	1702
	0	4	324	1870	1492
	4	0	1374	2090	2120
	4	4	1405	2261	2546
Triticale	0	0	829	2187	2524
	0	4	1091	2335	2865
	4	0	1856	2213	2237
	4	4	1969	2373	2726
Rye	0	0	1006	2579	2962
	0	4	1078	2638	3107
	4	0	2414	2585	2887
	4	4	2347	2503	3091

LSD (P = 0.05) for the genotype-Cu-Zn interaction: 223
and for the genotype-soil pH-Cu interaction: 273

Statistical analyses appear in Appendix 72.

4.3.3 Plant Height

The neutral soil was the most favourable environment for plant growth, the alkaline soil intermediate, and the acid soil the least conducive to plant growth (Table 4.3.2). Rye was tallest under all conditions, triticale generally intermediate in height and the wheats shortest of the genotypes. In the absence of copper, the application of zinc accentuated the copper deficiency resulting in shorter plants in the majority of cases than those plants with neither copper nor zinc. In the acid soil the copper deficiency was so severe that even plants which had both added copper and zinc were reduced in height.

A significant genotype-soil pH-copper interaction ($P < 0.001$) existed as a result of differing responses among the genotypes to copper deficiency in the acid soil relative to their responses in the other soils. The antagonistic actions of zinc in the absence of copper in accentuating copper deficiency resulted in a significant genotype-copper-zinc interaction ($P < 0.001$).

4.3.4 Tillering

Application of copper decreased the number of tillers produced per plant, whereas zinc application had no direct influence on the number of tillers produced (Table 4.3.3). At pH 5.0, however, the copper deficiency was so severe that the wheat plants with added copper were still deficient in copper or, possibly another element and produced more tillers per plant.

In the absence of copper, application of zinc accentuated the copper deficiency resulting in increased tiller production. This accounted for the copper-zinc interaction ($P < 0.001$) observed.

TABLE 4.3.2. Effect of copper and zinc supply, soil pH and genotype on plant height (cm). Data are main culm heights at maturity and the mean of 6 plants (3 plants per pot for each of 2 replicates).

Treatment	Cu added per pot (mg)	Zn added per pot (mg)	Soil pH 5.0	7.1	8.8
Genotype					
Wheat cv. Halberd	0	0	19	63	58
	0	4	19	44	34
	4	0	43	85	80
	4	4	65	105	96
Wheat cv. Gatcher	0	0	21	57	40
	0	4	25	37	37
	4	0	41	80	66
	4	4	66	104	112
Triticale	0	0	32	100	88
	0	4	24	93	78
	4	0	73	100	102
	4	4	87	107	107
Rye	0	0	40	144	126
	0	4	64	141	140
	4	0	124	133	142
	4	4	116	135	146

LSD (P = 0.05) for the genotype-soil pH-Cu interaction: 14.8
and for the genotype-Cu-Zn interaction: 12.1

Statistical analyses appear in Appendix 73.

TABLE 4.3.3. Tiller production and ear production per plant at maturity.

Data are means of 2 replicates of 3 plants per pot.

Treatment	Cu added per pot (mg)	Zn added per pot (mg)	Soil pH 5.0	Soil pH 7.1	Soil pH 8.8	Soil pH 5.0	Soil pH 7.1	Soil pH 8.8
			A. Number of culms per plant			B. Number of ears per plant		
Genotype								
Wheat cv. Halberd	0	0	2.2	4.8	3.5	0.0	1.2	1.5
	0	4	2.0	6.2	4.5	0.0	0.5	0.0
	4	0	5.8	4.5	3.8	0.3	3.0	2.8
	4	4	2.3	3.5	3.7	2.0	2.8	2.7
Wheat cv. Gatcher	0	0	1.5	4.3	3.2	0.0	0.8	1.2
	0	4	1.8	5.7	5.0	0.0	0.8	1.3
	4	0	5.2	4.3	3.0	2.5	3.0	3.0
	4	4	2.0	3.0	3.2	1.5	3.0	2.7
Triticale	0	0	5.3	2.8	3.3	0.0	1.8	2.8
	0	4	4.8	4.8	6.0	0.0	3.5	4.5
	4	0	3.8	2.8	2.2	2.0	1.8	1.3
	4	4	2.7	3.0	2.5	1.8	2.0	2.0
Rye	0	0	4.5	4.0	4.0	0.2	2.3	2.7
	0	4	3.7	4.0	4.8	1.3	3.2	3.2
	4	0	4.0	4.7	3.8	2.2	2.5	2.3
	4	4	3.2	3.7	4.3	2.2	2.2	2.7

LSD (P = 0.05) for the Cu-Zn interaction: 2.09

and for the genotype-Cu-Zn interaction: 1.81

Statistical analyses appear in Appendices 74 and 75.

Copper deficiency also resulted in a marked reduction in the number of tillers producing ears (Table 4.3.3). This occurred both in the absence and presence of zinc, and responses to copper were more pronounced at pH 5.0 than in the other soils. Concurrently, the responses by the genotypes to application of copper and zinc differed; the wheats were similar, and triticale and rye behaved in the same way, although oppositely to wheat.

The observed differences between genotypes in the three soils together with the antagonistic action between the copper and zinc, resulted in the genotype-copper-zinc interaction ($P < 0.001$).

4.3.5 Pollen Viability

Pollen was non-viable in copper-deficient wheat plants in all soils and in copper-deficient triticale and rye plants at pH 5.0 (Table 4.3.4). In the absence of copper, the application of zinc accentuated the copper deficiency resulting in a decline in the pollen viability, as observed for the triticale and rye (exception: replicate 1 of rye at pH 5.0).

Examination of the pollen viability data revealed that the copper deficiency was most severe at pH 5.0, intermediate at pH 8.8 and least severe at pH 7.1. No such conclusion could be drawn from the data on the nature or severity of the zinc deficiency in the different soils.

The wheats were more sensitive to copper deficiency than triticale which was more sensitive than rye under all conditions. Zinc deficiency alone had little direct effect on the pollen viability of any of the genotypes. The pollen viability of the +Cu-Zn treatment for wheat cv. Halberd at pH 5.0 was the result of acute copper deficiency.

TABLE 4.3.4. Effect of level of copper and zinc on the pollen viability of four genotypes grown in three soils of different pH. Pollen viability expressed as percentage of grains staining with iodine. Pollen was taken from main culms. Data are means of 2 replicates.

Treatment	Cu added per pot (mg)	Zn added per pot (mg)	Soil pH 5.0	7.1	8.8
Genotype					
Wheat cv. Halberd	0	0	0	0*	0
	0	4	0	0	0
	4	0	0	86	85
	4	4	94	91	85
Wheat cv. Gatcher	0	0	0	0*	0*
	0	4	0	0	0
	4	0	96+	88	92
	4	4	89	96	98
Triticale	0	0	0	84	76
	0	4	0	48	83+
	4	0	67	82	77
	4	4	89	91	80
Rye	0	0	0	93	81
	0	4	75+	74	69
	4	0	85	94	95
	4	4	89	87	86

LSD (P = 0.05) for the genotype-soil pH-Cu-Zn interaction: 16.7

* = anther undeveloped + = data for only 1 replicate

Statistical analyses appear in Appendix 76.

4.3.6 Delay in Maturity

Both copper and zinc deficiency delayed the emergence of ears and their subsequent development (Table 4.3.5), however deficiency of copper delayed ear emergence, anthesis and maturity to a greater extent.

At pH 5.0, rye was the only genotype that produced ears in the treatments without added copper, and these were very late in emerging. In the other soils, all treatments produced ears although the ears of copper-deficient wheat and triticale plants emerged somewhat later than their healthy counterparts. Zinc-deficient wheat and triticale plants produced ears later than their healthy counterparts, but the delay was not as large as that for the copper-deficient plants. Ear emergence, anthesis and maturity for the ears of rye plants, however, were unaffected by either the level of copper or zinc except at pH 5.0.

The same trend applied to the main culm ears and later ears.

4.3.7 Dry Matter Production

Application of either copper or zinc produced significant differences in the shoot dry matter of ~~all genotypes~~ wheat and triticale under all conditions and rye under conditions of copper deficiency (Figure 4.3.5). Wheat was extremely sensitive to copper deficiency in all the soils and responded significantly to copper application. In the absence of copper, application of zinc accentuated the copper deficiency and reduced dry matter production even further in several cases.

Wheat cv. Gatcher yielded less dry matter than wheat cv. Halberd, for all treatments in the three soils, which probably reflected a lower yield potential for that cultivar rather than a greater sensitivity to the copper deficiency. Triticale was intermediate in dry matter production in all the soils, while rye was tolerant of copper deficiency at pH 7.1 and 8.8, but gave a significant response at pH 5.0.

TABLE 4.3.5. Mean number of days to emergence, anthesis and maturity of the four genotypes as affected by soil pH and level of applied copper and zinc. Data are the means of 2 replicates.

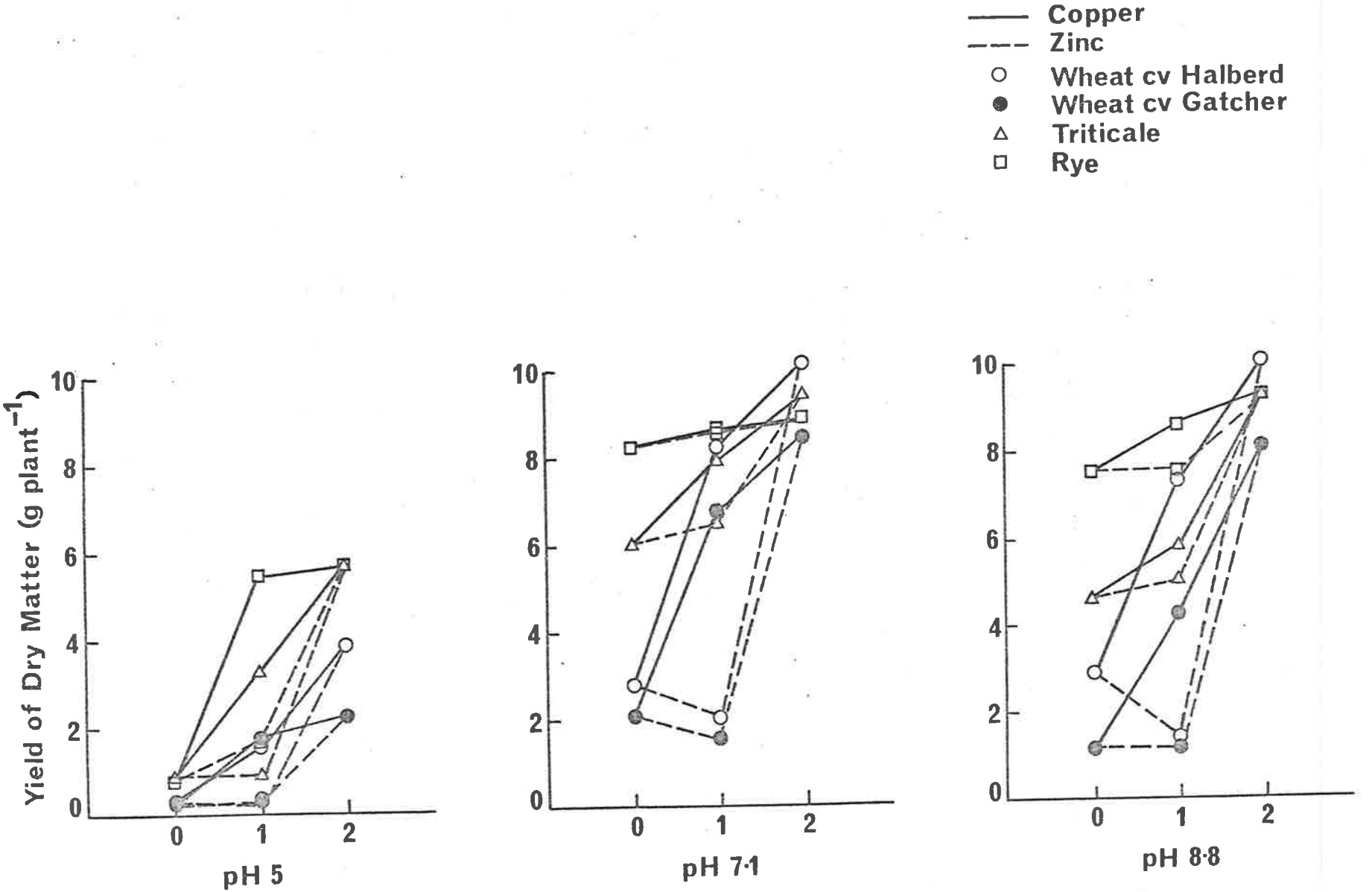
Treatment	Cu added per pot(mg)	Zn added per pot(mg)	Soil pH 5.0	Soil pH 7.1	Soil pH 8.8	Soil pH 5.0	Soil pH 7.1	Soil pH 8.8	Soil pH 5.0	Soil pH 7.1	Soil pH 8.8
			Emergence			Anthesis			Maturity		
A. Main culms											
Genotype											
Wheat cv.	0	0	-*	108	110*	-*	114*	117*	-*	-*	-*
Halberd	0	4	-	152	-	-	-	-	-*	-	-
	4	0	145	99	105	154	106	112	-	148	143
	4	4	98	83	91	105	91	98	138	127	132
Wheat cv.	0	0	-*	107	100	-*	115	110*	-*	151	142*
Gatcher	0	4	-	122	124	-	127	-	-	154	-
	4	0	100	86	93	111	94	98	143	129	136
	4	4	84	69	74	92	78	84	138	124	124
Triticale	0	0	-*	78	81	-*	89	90	-*	133	139
	0	4	-	78	87	-	88	97	-	137	146
	4	0	81	76	75	92	89	89	137	130	132
	4	4	77	75	80	89	86	89	128	127	130
Rye	0	0	137	84	83	140	96	96	154*	139	148
	0	4	110	78	84	147	93	98	-	137	142
	4	0	85	84	84	100	97	96	145	144	142
	4	4	82	81	82	96	96	97	141	137	137
LSD (P = 0.05) for the genotype-Cu-Zn interaction: 6.9 and soil pH-Cu-Zn interaction: 6.0						soil pH-Cu-Zn interaction: 4.4			genotype-soil pH-Cu interaction: 5.9		
B. Primary tillers											
Genotype											
Wheat cv.	0	0	-*	114*	117*	-*	119*	124*	-*	-*	-*
Halberd	0	4	-*	-	-	-*	-	-	-*	-	-
	4	0	-	102	108	-	110	117	-	151	146
	4	4	107	85	95	111	95	103	152	138	141
Wheat cv.	0	0	-*	112	115	-*	117	123*	-*	154	146*
Gatcher	0	4	-	133	127	-	133	-	-	157	-
	4	0	107	88	96	118	98	103	147	132	141
	4	4	90	70	76	111	82	86	143	127	127
Triticale	0	0	-*	80	84	-*	92	95	-*	136	143*
	0	4	-	83	92	-	92	102	-	140	-
	4	0	83	79	79	97	94	94	141	132	134
	4	4	82	77	83	95	90	94	131	129	134
Rye	0	0	-*	87	86	-*	99	100	-*	148	151
	0	4	118	80	87	-	97	100	-	142	144
	4	0	89	87	88	107	100	98	146	148	145
	4	4	83	84	85	98	98	99	143	140	141
C. Secondary tillers											
Genotype											
Wheat cv.	0	0	-*	120*	-*	-*	124*	-*	-*	-*	-*
Halberd	0	4	-*	-	-	-*	-	-	-*	-	-
	4	0	-*	107	111	-*	113	120	-*	154	150
	4	4	-	88	97	-	99	106	-	140	144
Wheat cv.	0	0	-*	-*	-*	-*	-*	-*	-*	-*	-*
Gatcher	0	4	-	-	-	-	-	-	-	-	-
	4	0	116*	90	98	125*	100	109	151*	135	144
	4	4	-	72	78	-	84	90	-	128	129
Triticale	0	0	-*	-*	-*	-*	-*	-*	-*	-*	-*
	0	4	-*	-	105*	-*	-	112*	-*	-	150*
	4	0	-*	85	-	-*	99	-	-*	137	-
	4	4	-	82	87	-	91	99	-	130	137
Rye	0	0	-*	94	95	-*	105	106	-*	151	154
	0	4	-*	85	89	-*	102	103	-*	147	146
	4	0	-	89	94	-	105	105	-	152	148
	4	4	86	88	88	100	101	100	147	144	147

* = not reached by harvest date, but for purposes of statistical analysis (main culms), high values were substituted for missing values.

Statistical analyses appear in Appendices 77, 78 and 79.

FIGURE 4.3.5. Effect of level of copper and zinc supply, soil pH and genotype on total shoot dry matter (g plant^{-1}). Means of 2 replicates. LSD (P = 0.05) for the genotype-Cu-Zn interaction is 0.63 and for the soil pH-Cu-Zn interaction is 0.55. Statistical analyses appear in Appendix 80.

0, 1 and 2 on the abscissa refer to no added nutrient, 1 and 2 added elements respectively.


Copper
Zinc
Wheat cv Halberd
Wheat cv Gatcher
Triticale
Rye
Yield of Dry Matter (g plant^{-1})
0
2
4
6
8
10
0
1
2
pH 5
pH 7·1
pH 8·8

Plates 6 to 14 illustrate the effects of copper and zinc on the growth of each of the genotypes in the three soils.

After the addition of 4.0 mg Cu per pot in the presence of an adequate zinc supply, the plants grown at pH 5.0 still yielded considerably less than plants grown in the other two soils. These plants were considered to be still deficient in copper despite the fact that 4.0 mg Cu per pot is generally a luxury amount (Graham, 1976a; Graham and Pearce, 1979).

Wheat and triticale responded significantly to the application of zinc in all soils but the response was considerably less than that for copper. Rye did not respond to application of zinc under any conditions. Responses to application of zinc were largest in the acid soil, intermediate in the calcareous soil, and least in the neutral soil.

There was a highly significant genotype-soil pH-copper interaction ($P < 0.01$) which was the result of differential genotype responses to the varying degrees of copper deficiency in the three soils. A highly significant genotype-copper-zinc interaction ($P < 0.001$) existed caused by the differing sensitivities of the genotypes to either copper or zinc deficiency relative to the antagonistic action between them. There was also a significant soil pH-copper-zinc interaction ($P < 0.01$) which resulted from the extent and nature of the antagonistic action between the copper and zinc in the three soils. It also depended on the degree of deficiency of these elements.

Application of either copper or zinc significantly increased the shoot dry weight per plant by increasing the weight of both grain and straw (Table 4.3.6). In copper- and zinc-deficient plants the dry weight of straw was the major component of the total shoot weight: grain weight was

PLATE 6. Four pots of wheat cv. Halberd grown in the Mt. Burr soil (pH 5.0) showing the influence of copper and zinc on growth.
From left to right:
-Cu-Zn, -Cu+Zn, +Cu-Zn, +Cu+Zn (complete).

PLATE 7. Four pots of wheat cv. Halberd grown in the Woods Well soil (pH 7.1) showing the influence of copper and zinc on growth.
From left to right:
-Cu-Zn, -Cu+Zn, +Cu-Zn, +Cu+Zn (complete).

PLATE 8. Four pots of wheat cv. Halberd grown in the Robe soil (pH 8.8) showing the influence of copper and zinc on growth.
From left to right:
-Cu-Zn, -Cu+Zn, +Cu-Zn, +Cu+Zn (complete).

PLATE 9. Four pots of triticale cv. T22 grown in the Mt. Burr soil (pH 5.0) showing the influence of copper and zinc on growth.
From left to right:
-Cu-Zn, -Cu+Zn, +Cu-Zn, +Cu+Zn (complete).

PLATE 10. Four pots of triticale cv. T22 grown in the Woods Well soil (pH 7.1) showing the influence of copper and zinc on growth.
From left to right:
-Cu-Zn, -Cu+Zn, +Cu-Zn, +Cu+Zn (complete).

PLATE 11. Four pots of triticale cv. T22 grown in the Robe soil (pH 8.8) showing the influence of copper and zinc on growth.
From left to right:
-Cu-Zn, -Cu+Zn, +Cu-Zn, +Cu+Zn (complete).

PLATE 12. Four pots of rye cv. S.A. Commercial grown in the Mt. Burr soil (pH 5.0) showing the influence of copper and zinc on growth.
From left to right:
-Cu-Zn, -Cu+Zn, +Cu-Zn, +Cu+Zn (complete).

PLATE 13. Four pots of rye cv. S.A. Commercial grown in the Woods Well soil (pH 7.1) showing the influence of copper and zinc on growth.
From left to right:
-Cu-Zn, -Cu+Zn, +Cu-Zn, +Cu+Zn (complete).

PLATE 14. Four pots of rye cv. S.A. Commercial grown in the Robe soil (pH 8.8) showing the influence of copper and zinc on growth.
From left to right:
-Cu-Zn, -Cu+Zn, +Cu-Zn, +Cu+Zn (complete).

TABLE 4.3.6. Dry weight of straw (stem, leaf and chaff), grain and total dry weight at maturity. Data are means of 2 replicates.

Treatment	Cu added per pot (mg)	Zn added per pot (mg)	Soil pH 5.0	Soil pH 7.1	Soil pH 8.8	Soil pH 5.0	Soil pH 7.1	Soil pH 8.8	Soil pH 5.0	Soil pH 7.1	Soil pH 8.8
			Straw (g plant^{-1})			Grain (g plant^{-1})			Total (g plant^{-1})		
Genotype											
Wheat cv. Halberd	0	0	0.25	2.78	2.87	0.00	0.00	0.03	0.25	2.78	2.90
	0	4	0.18	2.00	1.42	0.00	0.00	0.00	0.18	2.00	1.42
	4	0	1.53	5.20	4.93	0.03	3.05	2.38	1.56	8.25	7.31
	4	4	2.49	6.04	6.00	1.37	4.10	4.04	3.86	10.14	10.04
Wheat cv. Gatcher	0	0	0.17	2.09	1.12	0.00	0.00	0.00	0.17	2.09	1.12
	0	4	0.24	1.51	1.13	0.00	0.00	0.00	0.24	1.51	1.13
	4	0	1.50	4.40	2.98	0.20	2.32	1.23	1.70	6.72	4.21
	4	4	1.49	4.91	4.73	0.64	3.54	3.33	2.13	8.45	8.06
Triticale	0	0	0.81	4.53	4.38	0.00	1.43	0.22	0.81	5.96	4.56
	0	4	0.89	6.46	5.02	0.00	0.07	0.00	0.89	6.53	5.02
	4	0	2.80	4.91	3.63	0.44	3.02	2.15	3.24	7.93	5.78
	4	4	3.45	5.55	5.98	2.27	3.87	3.23	5.72	9.43	9.21
Rye	0	0	0.80	6.08	6.27	0.00	2.12	1.31	0.80	8.20	7.58
	0	4	1.69	7.08	6.71	0.00	1.47	0.83	1.69	8.55	7.54
	4	0	4.03	5.95	6.38	1.41	2.70	2.18	5.44	8.65	8.57
	4	4	3.83	6.15	7.10	1.77	2.77	2.21	5.70	8.92	9.29
LSD (P = 0.05) for the genotype-Cu-Zn interaction:			0.55							0.63	
and the soil pH-Cu-Zn interaction:			0.48							0.55	
genotype-soil pH-Cu-Zn interaction:						0.49					

Statistical analyses appear in Appendixes 80, 81 and 82.

low or nil. The contribution of grain weight to total shoot weight per plant was greatest for healthy plants, and progressively decreased according to the degree of copper- and zinc-deficiency in the plants. There were also differences which were a function of the plant genotype: rye had a considerably lower proportion of grain than wheat or triticale.

4.3.8 Grain Yield and Its Components

Copper-deficient wheat plants failed to produce grain in any soil (Table 4.3.6 and Figure 4.3.6), while triticale only produced a small amount of grain at pH 7.1. Grain production of rye was reduced at pH 7.1 and 8.8, whilst no grain was produced at pH 5.0.

Rye was tolerant of zinc-deficiency at pH 7.1 and 8.8, but at pH 5.0 zinc-deficiency reduced the grain production. Wheat and triticale were very sensitive to the degree of zinc-deficiency in the soil at pH 5.0: grain production was reduced to extremely low levels. In the other soils, zinc-deficiency caused a significant reduction in the grain yields of wheat and triticale, but not as marked as that at pH 5.0. At pH 7.1 and 8.8, wheat cv. Gatcher was most sensitive to a deficiency of zinc, while triticale was least sensitive at pH 7.1 and intermediate between rye and wheat at pH 8.8.

The level of both copper and zinc supply influenced the number of ears produced per plant by each of the genotypes in all of the soils (Table 4.3.7), but an increase in the number of ears per plant did not necessarily result in increased grain yield.

At pH 5.0, copper-deficient plants did not produce ears (with the exception of rye) while zinc-deficient plants produced ears but grain production was very low. The number of spikelets per ear and the number of grains per ear were both reduced considerably, although with the

FIGURE 4.3.6. Effect of level of copper and zinc supply, soil pH and genotype on total grain yield (g plant^{-1}). Means of 2 replicates. LSD (P = 0.05) for the genotype-soil pH-Cu-Zn interaction is 0.49. Statistical analyses appear in Appendix 82.

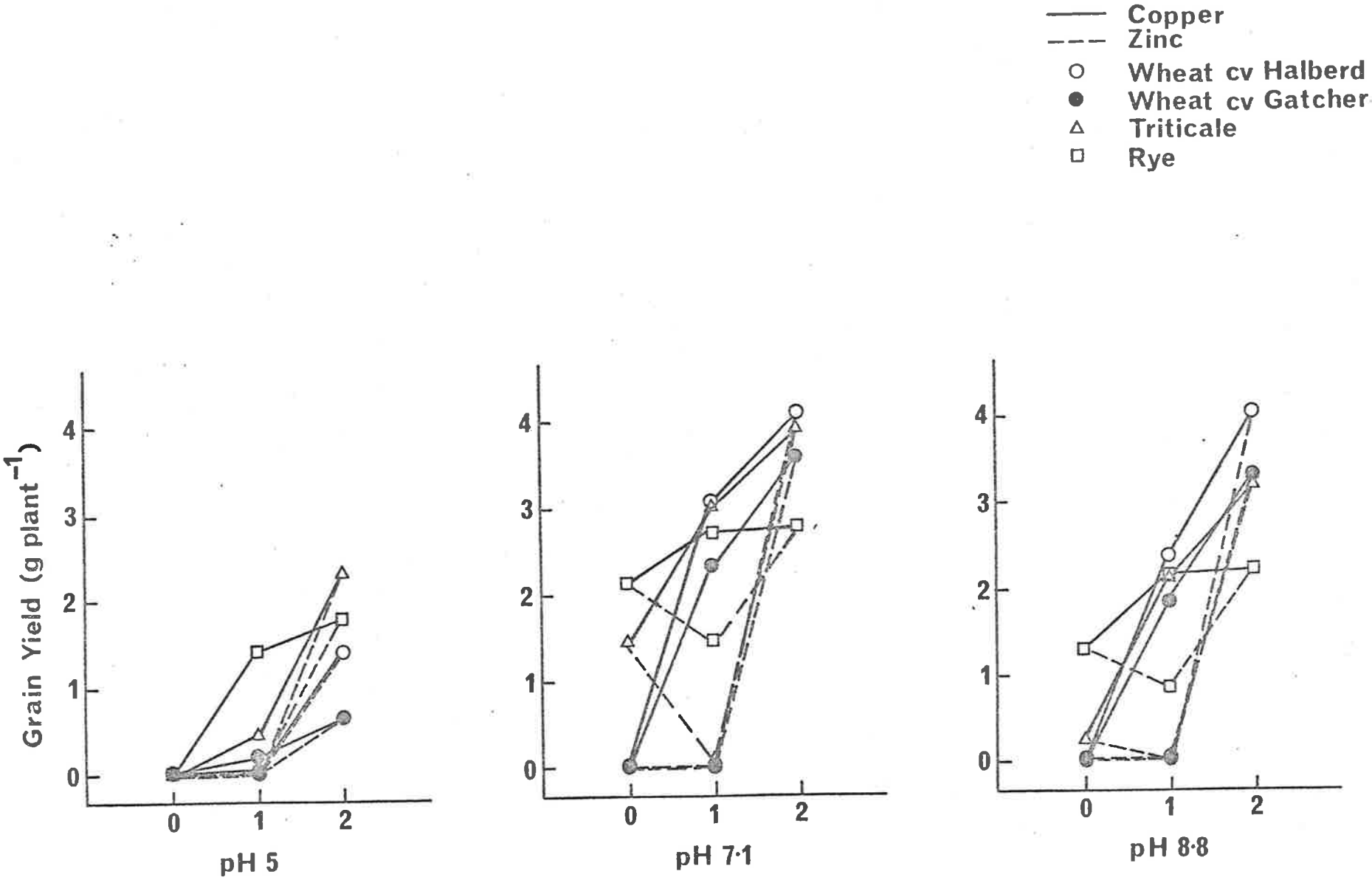

Copper
Zinc
Wheat cv Halberd
Wheat cv Gatcher
Triticale
Rye
Grain Yield (g plant^{-1})
0
1
2
3
4
pH 5
pH 7·1
pH 8·8

TABLE 4.3.7. Yield and components of grain yield at maturity.

Treatment	Cu added per pot (mg)	Zn added per pot (mg)	No. of ears per plant	No. of grains per plant	No. of spikelets per ear+	No. of grains per ear+	Weight per grain (mg)+	Grain yield per plant (g)
A. pH 5.0								
Genotype								
Wheat cv. Halberd	0	0	0.0	0.0	0.0	0.0	0.0	0.00
	0	4	0.0	0.0	0.0	0.0	0.0	0.00
	4	0	0.3	2.3	20.0	7.8	12.8	0.03
	4	4	2.0	43.2	18.7	21.6	31.7	1.37
Wheat cv. Gatcher	0	0	0.0	0.0	0.0	0.0	0.0	0.00
	0	4	0.0	0.0	0.0	0.0	0.0	0.00
	4	0	2.5	5.5	9.1	2.2	36.3	0.20
	4	4	1.5	15.3	14.1	10.2	41.8	0.64
Triticale	0	0	0.0	0.0	0.0	0.0	0.0	0.00
	0	4	0.0	0.0	0.0	0.0	0.0	0.00
	4	0	2.0	12.4	17.4	6.2	35.5	0.44
	4	4	1.8	65.5	21.3	36.4	34.6	2.27
Rye	0	0	0.2	0.0	27.5	0.0	0.0	0.00
	0	4	1.3	0.0	27.1	0.0	0.0	0.00
	4	0	2.2	54.1	37.2	24.6	26.1	1.41
	4	4	1.7	75.6	48.0	44.5	23.4	1.77
B. pH 7.1								
Genotype								
Wheat cv. Halberd	0	0	1.2	0.0	18.1	0.0	0.0	0.00
	0	4	0.5	0.0	18.3	0.0	0.0	0.00
	4	0	3.0	89.4	19.7	29.8	34.1	3.05
	4	4	2.8	116.8	18.9	41.7	35.1	4.10
Wheat cv. Gatcher	0	0	0.8	0.0	16.9	0.0	0.0	0.00
	0	4	0.8	0.0	13.1	0.0	0.0	0.00
	4	0	3.0	60.6	17.1	20.2	38.3	2.32
	4	4	3.0	96.6	16.7	32.2	36.6	3.54
Triticale	0	0	1.8	55.6	20.5	30.9	25.7	1.54
	0	4	3.5	11.2	17.2	3.2	6.2	0.07
	4	0	1.8	67.1	21.8	37.3	45.0	3.02
	4	4	2.0	89.4	21.2	44.7	43.3	3.87
Rye	0	0	2.3	87.9	37.5	38.2	24.1	2.12
	0	4	3.2	72.3	36.9	22.6	20.3	1.47
	4	0	2.5	111.0	38.9	44.4	24.3	2.70
	4	4	2.2	105.2	39.5	47.8	26.3	2.77
C. pH 8.8								
Genotype								
Wheat cv. Halberd	0	0	1.5	2.2	18.6	1.5	13.3	0.03
	0	4	0.0	0.0	0.0	0.0	0.0	0.00
	4	0	2.8	73.9	19.2	26.4	32.2	2.38
	4	4	2.7	91.5	19.3	33.9	44.1	4.04
Wheat cv. Gatcher	0	0	1.2	0.0	14.3	0.0	0.0	0.00
	0	4	1.3	0.0	9.5	0.0	0.0	0.00
	4	0	3.0	34.8	16.0	11.6	35.3	1.23
	4	4	2.7	95.0	16.4	35.2	35.0	3.33
Triticale	0	0	2.8	13.7	15.7	4.9	16.0	0.22
	0	4	4.5	0.0	14.9	0.0	0.0	0.00
	4	0	1.3	46.1	21.0	35.5	46.6	2.15
	4	4	2.0	85.6	24.3	42.8	37.7	3.23
Rye	0	0	2.7	75.6	38.1	28.0	17.3	1.31
	0	4	3.2	75.2	35.7	23.5	11.0	0.83
	4	0	2.3	79.8	39.8	34.7	27.3	2.18
	4	4	2.7	88.3	38.3	32.7	25.0	2.21
LSD (P = 0.05) for the soil pH-Cu-Zn interaction:			0.5					
genotype-Cu-Zn interaction:			0.6	10.7				
genotype-soil pH-Cu-Zn interaction:								0.49

+ = derived values. These values have been derived from data which has been statistically analysed, however, they have not been statistically analysed. No statistical significance could be attached to them due to the extent of missing values in the original sets of data.

Statistical analyses appear in Appendices 75, 82 and 83.

exception of wheat, the weight per grain was not very different from that of the healthy plants.

All plants produced ears at pH 7.1 but copper-deficient wheat plants did not produce grain. Neither copper nor zinc treatment had any influence on the number of spikelets per ear, but the number of grains produced per ear was influenced quite strongly by the copper treatment and to a lesser degree by the zinc treatment. Only copper treatment, however, affected the weight per grain. The number of grains per plant showed the same pattern as grain yield.

The genotypes followed the same trends at pH 8.8 as for pH 7.1 but the magnitude of the copper and zinc effects were greater.

4.3.9 Dry Weight of Roots

In all soils, and for all genotypes (with the exception of rye), the plants without copper had the least extensive root systems. Application of copper significantly increased the dry weight of roots while application of zinc had little effect (Table 4.3.8).

For the majority of treatments and for genotypes other than wheat cv. Halberd, the dry weight of roots was highest in the neutral soil. This reflected the vigour of the plants indicating that the degree of copper and zinc deficiency was least severe in that soil. Again, the dry weight of roots was largest for rye and least for wheat: triticale maintained an intermediate position. However, the magnitude of the dry weight of roots was influenced by the soil type, as demonstrated by virtue of the highly significant genotype-soil pH interaction.

It must be remembered that the roots were not ashed in this study and so the dry weight of roots would most certainly contain a proportion of sand which may vary between genotypes and soils.

TABLE 4.3.8. Effect of level of copper and zinc on the dry weight of roots per plant (g) of four genotypes grown in three soils of different pH. Data are means of 2 replicates of 3 plants.

Treatment			Soil pH		
	Cu added per pot (mg)	Zn added per pot (mg)	5.0	7.1	8.8
Genotype					
Wheat cv. Halberd	0	0	0.04	0.55	0.66
	0	4	0.04	0.20	0.13
	4	0	0.94	2.12	2.60
	4	4	0.92	1.86	2.09
Wheat cv. Gatcher	0	0	0.03	0.80	0.16
	0	4	0.05	0.12	0.18
	4	0	0.48	3.03	1.23
	4	4	0.40	1.72	1.45
Triticale	0	0	0.17	1.68	1.54
	0	4	0.16	2.06	1.29
	4	0	0.99	2.27	2.15
	4	4	0.95	5.18	2.82
Rye	0	0	0.12	6.52	5.17
	0	4	0.33	7.01	5.99
	4	0	1.49	5.18	5.39
	4	4	1.14	5.42	5.79

LSD (P = 0.05) for the genotype-soil pH interaction: 1.04
and for the genotype-Cu interaction: 0.85

Statistical analyses appear in Appendix 84.

4.3.10 Copper and Manganese in the Plant

In the acid and calcareous soils, bulked grain and straw from the -Cu-Zn and +Cu+Zn (complete) treatments for three genotypes were analysed for copper and manganese to determine whether or not the plants were still deficient in copper in the complete treatment or possibly suffering from manganese deficiency. The three genotypes analysed were wheat cv. Halberd, triticale and rye. Only one wheat cultivar was selected for copper and manganese analysis as both wheat cultivars behaved in a similar manner in all aspects of the study already considered.

The concentrations of copper in the straw (stem, leaf and chaff) and grain are shown in Table 4.3.9. In the acid soil, all genotypes failed to produce grain in the -Cu-Zn treatment. Both straw and grain responded strongly to application of copper and zinc in this soil, however, from the concentrations in grain it would appear that the wheat was still copper-deficient in the complete treatment (1 $\mu g\ g^{-1}$ is the critical level, Gartrell *et al.*, 1979a, b). In the calcareous soil, the concentration of copper in the straw and grain increased when copper and zinc was added to the plants, although the largest responses occurred in the grain. Triticale was intermediate between wheat and rye with respect to copper concentration in the grain in both soils. Rye maintained the highest copper concentration. Concentrations in straw of triticale at pH 5.0 and wheat at pH 8.8 suggest Piper-Steenbjerg effects (Steenbjerg, 1951).

There was insufficient material for a set of zinc analyses. It was considered important to establish that manganese was adequate. The concentration of manganese in the straw and grain (Table 4.3.10 and Appendices 87 and 88) decreased with the application of copper and zinc in every case despite genotypic differences. Despite the extreme difference in pH of these soils and the dominant role of pH on manganese

TABLE 4.3.9. Concentration of copper in straw and grain of plants grown in the acid and calcareous soils. Data are means of 2 replicates.

Treatment	Cu added per pot (mg)	Zn added per pot (mg)	Concentration of copper ($\mu g\ g^{-1}$) Straw	Grain
A. pH 5.0				
Genotype				
Wheat cv.	0	0	1.15	-*
Halberd	4	4	2.49	0.71
Triticale	0	0	4.19	-*
	4	4	2.36	1.13
Rye	0	0	1.51	-*
	4	4	3.12	1.87
B. pH 8.8				
Genotype				
Wheat cv.	0	0	3.39	0.38+
Halberd	4	4	2.00	1.17
Triticale	0	0	1.78	0.52
	4	4	2.69	1.90
Rye	0	0	1.54	0.58
	4	4	1.78	3.67
LSD (P = 0.05) for the genotype-soil pH-CuZn interaction:			1.88	
and for the genotype-CuZn interaction:				0.70

* = no grain

\+ = data for only 1 replicate

Statistical analyses appear in Appendices 85 and 86.

TABLE 4.3.10. Concentration of manganese in straw and grain of plants grown in the acid and calcareous soils. Data are means of 2 replicates.

Treatment	Cu added per pot (mg)	Zn added per pot (mg)	Concentration of manganese ($\mu g\ g^{-1}$) Straw	Grain
A. pH 5.0				
Genotype				
Wheat cv.	0	0	166.34	-*
Halberd	4	4	28.30	21.67
Triticale	0	0	53.25	-*
	4	4	16.65	12.84
Rye	0	0	75.15	-*
	4	4	16.55	24.23
B. pH 8.8				
Genotype				
Wheat cv.	0	0	69.00	67.18+
Halberd	4	4	23.50	12.08
Triticale	0	0	73.10	63.68
	4	4	15.65	16.69
Rye	0	0	126.65	48.49+
	4	4	34.75	37.14
LSD (P = 0.05) for the genotype-soil pH-CuZn interaction:			45.01	
and for the genotype-CuZn interaction:				9.54

* = no grain

\+ = data for only 1 replicate

Statistical analyses appear in Appendices 87 and 88.

availability, the concentrations in plants in the two soils were remarkably similar. There was no suggestion of either toxicity or deficiency of manganese in either. Rye again showed its ability to absorb and translocate manganese to the shoot and grain. This triticale was not better than the wheat, something which has been observed in the field (Graham, unpubl.).

The copper content of the straw in the acid soil (Table 4.3.11 and Appendix 89) in the absence of added copper and zinc showed the same pattern as the concentration of copper in the straw, however, for the +Cu +Zn (complete) treatment, rye had the highest copper content and wheat the lowest. In the calcareous soil, in the absence of added copper and zinc wheat had the highest copper content in the straw and rye the lowest, whilst in the presence of added copper and zinc, triticale had the highest copper content in the straw and rye the lowest. For both soils, the amount of copper translocated to the grain (Table 4.3.11 and Appendix 90) showed the same genotype ranking in both the -Cu -Zn and +Cu +Zn (complete) treatments. Rye had the highest copper content in the grain and wheat the lowest.

Discussions of these results begin on page 165.

TABLE 4.3.11. Copper content in straw and grain of plants grown in the acid and calcareous soils. Data are means of 2 replicates.

Treatment	Cu added per pot (mg)	Zn added per pot (mg)	Copper content (μg plant^{-1}) Straw	Grain
A. pH 5.0				
Genotype				
Wheat cv.	0	0	0.11	-*
Halberd	4	4	5.28	0.97
Triticale	0	0	1.74	-*
	4	4	6.53	2.59
Rye	0	0	1.19	-*
	4	4	9.90	3.33
B. pH 8.8				
Genotype				
Wheat cv.	0	0	9.17	0.02+
Halberd	4	4	9.93	4.73
Triticale	0	0	6.25	0.13
	4	4	13.12	5.99
Rye	0	0	8.32	0.84
	4	4	10.99	8.13
LSD (P = 0.05) for the soil pH and CuZn effects:			2.98	0.90

* = no grain

\+ = data for only 1 replicate

Statistical analyses appear in Appendices 89 and 90.

5.0 DISCUSSION

5.1 POT EXPERIMENT 1

Copper-deficient soils in the field vary in total amounts of and availability of copper, depending on pH. Acid soils, often sandy and leached in higher rainfall areas, tend to have low total contents of copper, but high proportions available to plants, whilst in alkaline soils the total contents may be higher but availability to plants considerably lower. This is the result of decreased solubility of copper in alkaline soils (Leeper, 1952).

For this study, three different environments were created by adjusting the pH of a neutral copper-deficient sand. While there may have been other effects of adjusting the pH, the major effect was expected to be on the availability of the limiting trace element: copper. Copper was expected to be displaced from adsorbed sites by the added hydrogen ions at pH 5.0 and to be removed from the soil solution and exchangeable sites as insoluble oxides, hydroxides and organic chelates at pH 8.4. That copper was indeed still the major limiting factor after pH adjustment was demonstrated by the appearance of classical symptoms of copper deficiency in all cases where treatments led to serious yield reductions.

The performance of rye in the adverse conditions of serious copper deficiency and extremes of pH was outstanding, and although well-known, was demonstrated anew in comparison with its hybrid. The performance of triticale for which much has been claimed but little documented at this time, was also impressive especially when compared to the overall sensitivity of wheat (the cultivar, Halberd, being among the least sensitive wheats tested (Nambiar, 1976b)). Triticale outyielded both wheat and rye at pH 5.0, was the equal of rye at pH 7.0, and while failing to set grain at pH 8.4, still outyielded wheat vegetatively (Figure 4.1.4).

The effect of copper was pronounced on grain yield, while vegetative yield was reduced only slightly (Figure 4.1.4). This was consistent with the findings of Graham (1975, 1976b) that the critical effect of copper deficiency in cereals is induced pollen sterility, small anthers being developed with fewer, abnormal pollen grains while the ovules were normal.

The superior performance of triticale in comparison to wheat over all pH environments and its tolerance (like rye) to some adverse conditions was due to higher concentrations and greater total uptake of copper in shoots and grain. At the high level of copper supply, grain copper content was highest in the triticale owing to its high yield and moderate concentrations of copper. The concentration of copper in the grain of triticale was generally intermediate between that of wheat (lowest) and rye (highest). However, the copper concentrations in the grain of all genotypes were generally very low in this experiment (Table 4.1.8).

The increased content of copper in the grain of triticale occurred as the result of greater retranslocation of absorbed copper from the shoot to the developing ear and grain. In the triticale, there was considerably greater translocation, in terms of μg plant^{-1}, of absorbed copper in the shoot, to the grain than for wheat or rye, the latter presumably limited by its low yield potential (Figure 4.1.5). These results supported the conclusions of Graham (1978a) and Graham and Pearce (1979), that copper efficiency was transferable from rye to triticale, and that it was due largely to greater translocation of copper to the shoot, especially the ear and grain, rather than to a lower metabolic requirement of copper.

Copper efficiency (as defined by Graham and Pearce (1979)) was, however, not due to a lower functional requirement such as proposed by Loneragan (1968). In both rye and triticale, the concentrations ($\mu g\ g^{-1}$) and absolute amounts (μg) of copper were higher than for wheat.

Graham and Pearce (1979) compared the performance of two triticales with their wheat and rye parent types in one pH environment only, and consequently, interpretation of the results was limited. This study extended the number of pH environments in which copper efficiency was examined, and different triticale and rye genotypes were studied: triticale cv. T22 and S.A. Commercial rye. Results clearly showed that copper efficiency of triticale and rye was maintained over the whole pH range, pH 5.0 to pH 8.4, and that this triticale had also inherited tolerance of low pH from its rye parent.

This study also demonstrated conclusively, that uptake of copper was pH dependent, as a consequence of the strong influence of soil pH on the availability of copper. These results contrast with those of Piper and Beckwith (1949) who found that the effect of soil reaction on the availability of copper was small and not significant. In that study on two neutral soils adjusted to acid and alkaline extremes (similar pHs to those examined here), the three pasture species (*Medicago polymorpha, Erodium cygnorum, Hordeum leporinum*) under examination showed nearly as much copper taken up from neutral and alkaline soils as from acid soil. Earlier investigations had indicated, however, that on some soils, copper was slightly more available to plants under acid soil conditions than under neutral or alkaline conditions (Piper, 1942; Piper and Walkley, 1943; Oertel *et al.*, 1946). Results obtained in this study were more in agreement with the findings of those earlier investigations than with those of Piper and Beckwith.

The change in availability was, however, insufficient to affect the response as measured of wheat (highly sensitive) or of rye which was highly tolerant. Triticale, however, responded dramatically to pH treatment and as expected for such a hybrid was intermediate in tolerance to copper deficiency. The genotype-soil pH interaction was thus particularly strong. Since the degree of copper deficiency in the pots was severe (at all pHs), the tolerance of triticale is probably adequate for most field situations when copper deficiency is likely. Preliminary field work supports this view (Graham and Davies, pers. comm.).

New reports of copper deficiency in traditional cereals in South Australia still occur despite 40 years of research and the high residual value of copper (Reuter, Hannam, Judson and Dodson, 1977; Gartrell, 1980). This would appear to be due largely to the increased use of nitrogen which aggravates copper deficiency (Chaudhry and Loneragan, 1970). Thus in marginal situations where yield loss without symptoms or unexpected nitrogen-fertilizer induced copper deficiency may occur, triticale as a crop would appear to have an "ecological" advantage over the more traditional wheat, other things being equal.

5.2 POT EXPERIMENT 2

Genotypic differences among crop plants were discussed by Graham (1978b) in terms of nutrient efficiency, defined simply as the relative yield of a genotype on deficient soil compared to its yield at optimum nutrition. High nutrient efficiency was due to greater absorption of the nutrient or greater yield per unit of nutrient absorbed (Graham, 1978b). Graham (1978a) and Graham and Pearce (1979) showed conclusively that copper efficiency was transferable from rye to triticale: rye and triticale were termed copper-efficient and wheat copper-inefficient.

This study was the first undertaken to determine whether or not zinc efficiency was transferable from rye to triticale. Data collected showed conclusively that triticale and rye were zinc-efficient with respect to the soil used, and wheat was zinc-inefficient. Zinc-efficiency was indeed transferable from rye to triticale. Triticale was intermediate between its parent species in its tolerance to zinc deficiency. Triticale outyielded both wheat and rye in grain production for all treatments, except the most zinc-deficient (pH 8.4, Figure 4.2.4).

The conclusions were based on relative grain yield, which for wheat was 2% but for rye approached 100% (within the limits of experimental error), and the relative grain yield of triticale was approximately 45% (Table 5.2.1). The same conclusion was reached if total shoot yields were considered instead of grain yield.

Yields obtained in this study supported the findings of Gladstones and Loneragan (1967) and Shukla and Raj (1974) that differential response to zinc occur among genotypes. These workers found that species differed characteristically in their ability to utilize plant nutrients from soil.

TABLE 5.2.1. Effect of adjusted soil pH on relative yield of grain from -Zn treatments (as a percentage of that in +Zn treatments).

Genotype	Soil pH	Relative Yield (%)
Wheat	5.0	99
	7.0	92
	8.4	2
Triticale	5.0	99
	7.0	99
	8.4	45
Rye	5.0	82
	7.0	100
	8.4	94

Zinc deficiency reduced yields, both at the vegetative stage and the reproductive stage, by comparable amounts. Decreased grain production under conditions of zinc deficiency (pH 8.4) was partly due to less vigorous growth of the plant, a consequence of the role of zinc in the enzyme systems regulating plant growth (Vallee and Wacker, 1970), and partly as a result of the essential nature of zinc for the production of inflorescences (Riceman and Jones, 1956); zinc content and activity was highest in the pollen of plants: a portion was transferred to the pollen tubes as they developed during fertilization and concentrated towards their tips (Polar, 1975).

Evidence supported the view that zinc efficiency in triticale and rye was due to greater absorption of zinc and greater translocation to the ear and grain. The concentration ($\mu g\ g^{-1}$) and absolute contents (μg) of zinc in all plant parts of rye and triticale were higher than those of wheat at maturity.

Zinc efficiency was maintained over all pH environments. Concentrations and absolute amounts of zinc were higher in triticale and rye in all pH environments, irrespective of the zinc status of the soil. The performance of triticale was outstanding in all instances where ~~that~~ zinc was not ~~a~~ limiting ~~factor~~ to plant growth: the uptake of zinc was considerably higher in triticale than in wheat or rye owing to the combination of high yield (like wheat) and high concentrations ~~(like rye)~~ of zinc (like rye) in shoots and grain of triticale. However, when zinc was limiting (pH 8.4), triticale was sensitive like wheat and had very low zinc concentrations in the various plant parts. Rye was highest under these conditions.

Triticale outperformed its parent species at pH 5.0 and pH 7.0 whilst being intermediate between them at pH 8.4. This resembles heterosis, a concept used by geneticists when comparing the performance

of a hybrid (F_1) against that of its parental genotypes (Knight, 1973). In these studies, triticale was compared to its parental species, not to its parental genotypes and this is therefore, not strictly heterosis (hybrid vigour). The heterosis-like effect was demonstrated in the concentration and uptake data, but was not clear in the (grain) yield data. Rye showed superior performance at the low zinc level (pH 8.4) and the hybrid at moderate zinc level (pH 5.0 and pH 7.0).

The results further demonstrated the tolerance of triticale to low pH as observed in the copper study. Triticale had indeed inherited tolerance to both low pH and zinc deficiency as well as copper efficiency from its rye parent. Since confining plant roots to small pots usually exaggerates soil nutrient deficiencies (Stevenson, 1967), it is likely that the degree of zinc efficiency shown by triticale in this soil adjusted to pH 8.4 would be adequate for maximum yield in most field soils in South Australia.

Zinc deficiency was marginal in this soil at its natural pH. Adding acid (H_2SO_4) to the soil increased the availability of zinc and thus eliminated the deficiency. Addition of lime ($CaCO_3$), however, decreased the zinc availability to levels such that the deficiency was quite severe and produced marked effects. Wear (1956) and Brown and Jurinak (1964) showed conclusively that the effect of addition of lime (calcium carbonate) in increasing soil pH and thereby decreasing the uptake of zinc by plants was solely a pH effect, rather than an increase in adsorbing surface of calcium carbonate or other effect due to the Ca^{2+} ion or to any inhibitory effects of the competing Ca^{2+} ion. It seemed likely that a soluble form of zinc at lower pH was converted to a less soluble and less available form in the soil at higher pH values. Brown and Jurinak (1964) also observed that copper followed a similar pattern to zinc.

The level of zinc deficiency in the soil made alkaline was comparable to the level of copper deficiency in the same soil when adjusted to an acid pH (compare Figures 4.1.4B and 4.2.4B). The main effect of adjusting the pH was expected to be on the availability of zinc, the most limiting factor, although other changes could possibly have occurred. Symptoms characteristic of a zinc deficiency were observed on all occasions that a significant yield reduction occurred confirming that zinc was indeed the primary limiting factor after pH adjustment.

Manganese concentration of the various plant parts showed a strong pH dependence, declining as the pH was raised, irrespective of zinc treatment. Zinc application did not affect the manganese concentration when zinc was marginal or non-limiting (pH 5.0 and pH 7.0); however, when zinc was limiting (pH 8.4), in those genotypes sensitive to zinc deficiency, zinc application did have a depressive effect on the absorption of manganese. The levels of manganese at pH 8.4 were close to manganese deficiency, but the high yields at +Zn would indicate that perhaps manganese was just not limiting.

5.3 POT EXPERIMENT 3

For this study three sands, all deficient in copper and zinc were selected on the basis of their pH, but of course these soils differed in the degree and nature of their deficiencies as a consequence of the processes by which they were formed.

Results showed conclusively that copper and zinc deficiency were most severe in the acid sand (pH 5.0), least in the neutral sand (pH 7.1) and intermediate in the calcareous sand (pH 8.8). For all treatments in which yield reductions occurred, classic symptoms of copper and/or zinc deficiency were observed on the plants. All genotypes, including rye, responded to copper in the acid sand (Table 5.3.1). Symptoms and plant yields suggested that the addition of 4 mg pot^{-1} of copper, as copper sulphate, in the presence of an adequate zinc supply was not sufficient to overcome the extreme copper deficiency in this soil which contained considerable organic matter. The severity of the copper deficiency at pH 5.0 was indicated in Table 5.3.1 by virtue of the fact that the yield attainment of the +Cu+Zn (complete) treatment was somewhat lower than the corresponding treatment in the other soils.

In an attempt to clarify whether or not the genotypes were still suffering from copper deficiency in the +Cu+Zn (complete) treatment or possibly from manganese deficiency, bulked grain and straw (stem, leaf and chaff) samples were analysed for plants grown in the acid and calcareous soils. Results revealed that concentrations of copper in this experiment were very low, particularly for the grain of plants grown in the acid soil. The concentration of copper in the grain of wheat grown in the acid soil was less than 1 $\mu g\ g^{-1}$, the critical level, below which grain yield responses to copper usually occur.

TABLE 5.3.1. Effect of level of copper and zinc on the relative grain yield of four genotypes grown in three soils of different pH. Grain yield is expressed as a % of the maximum yield for each genotype.

Treatment		Cu	-	-	+	+
		Zn	-	+	-	+
Genotype	Soil pH					
Wheat cv. Halberd	5.0		0	0	1	33
	7.1		0	0	74	100
	8.8		1	0	58	99
Wheat cv. Gatcher	5.0		0	0	6	18
	7.1		0	0	66	100
	8.8		0	0	35	94
Triticale	5.0		0	0	11	59
	7.1		37	2	78	100
	8.8		6	0	56	83
Rye	5.0		0	0	51	64
	7.1		77	53	97	100
	8.8		47	30	79	80

The manganese concentrations of these samples appeared to be above the critical level, below which deficiency symptoms appear, for both soils.

It seems that manganese was not deficient in either soil for the treatments analysed and that copper was indeed the major factor limiting plant growth and high yields in the acid soil.

Acid soils are usually associated with relatively high rainfall and, as a result of leaching, with low nutrient status (Graham, 1975b). There is the possibility of aluminium toxicity due to the considerable amounts of exchangeable and soluble aluminium in acid soils (Vlamis, 1953). Similarly, low soil pH increases the solubility of manganese oxides by reduction to the manganous ion, which may reach amounts toxic to plants (Graham, 1975b) but this was not the case in the Mt. Burr soil used here.

Despite the problems associated with the acid soil, the results were consistent with the results obtained in Experiments 1 and 2, in that rye was most tolerant of copper and zinc deficiency in all soils and that wheat was most sensitive. Triticale remained intermediate between its parent types in tolerance of copper and zinc deficiency in all soils, irrespective of the degree of deficiency or acidity of the soil.

Deficiency of copper or zinc depressed vegetative growth and grain production and delayed maturity, but copper deficiency depressed grain production and delayed maturity the greater amount. In this investigation, in all soils without added copper, application of zinc accentuated copper deficiency and resulted in decreased dry matter production (Figure 4.3.5), grain yields (Figure 4.3.6) and pollen viability (Table 4.3.4). This interaction has been reported on grain yield in the field (Graham and Nambiar, 1981) but these results offer the explanation

that the effect is mediated through effects on pollen viability. In the absence of zinc, application of copper promoted growth thus increasing dry matter production, pollen viability (except on Halberd at pH 5.0) and grain yields.

The basic difference in physiological effects of copper and zinc was on pollen viability. Graham (1975, 1976b) showed that copper deficiency induced pollen sterility. The similarity in pattern of responses between the grain yield (or grain number) and pollen viability (Tables 4.3.7 and 4.3.4) provided evidence that the effect of copper deficiency on grain production was mediated through its effect on the pollen. Zinc exerted its influence on grain production mainly through its effect on plant growth as demonstrated in both Experiments 2 and 3.

The antagonistic action between copper and zinc in affecting the growth and yield of plants (both vegetative and grain yields), as previously shown by Lucas (1945), Dunne (1956), Schmid *et al.* (1965), Bowen (1969) and Chaudhry and Loneragan (1970), also occurred in this experiment. Zinc fertilizers (such as zinc sulphate) depressed copper concentrations in the tops of plants (Lucas, 1945; Hooper and Davies, 1968) and roots (Chaudhry and Loneragan, 1970), and induced or accentuated copper deficiency symptoms (Gilbert, 1951) resulting in drastic reductions in the grain yields of cereals (Mulder, 1950; Dunne, 1956; Hooper and Davies, 1968). Zinc application depressed the copper concentration by decreasing the amount of copper absorbed and the rate of copper absorption per gram root in early growth (Chaudhry and Loneragan, 1970). Copper fertilizers (such as copper sulphate) decreased zinc concentrations in plant tops (Lucas, 1945) and roots (Chaudhry and Loneragan, 1970) and induced or accentuated the response of plants to zinc (Anderson, 1946; Riceman, 1948) by promoting plant growth. Copper application decreased

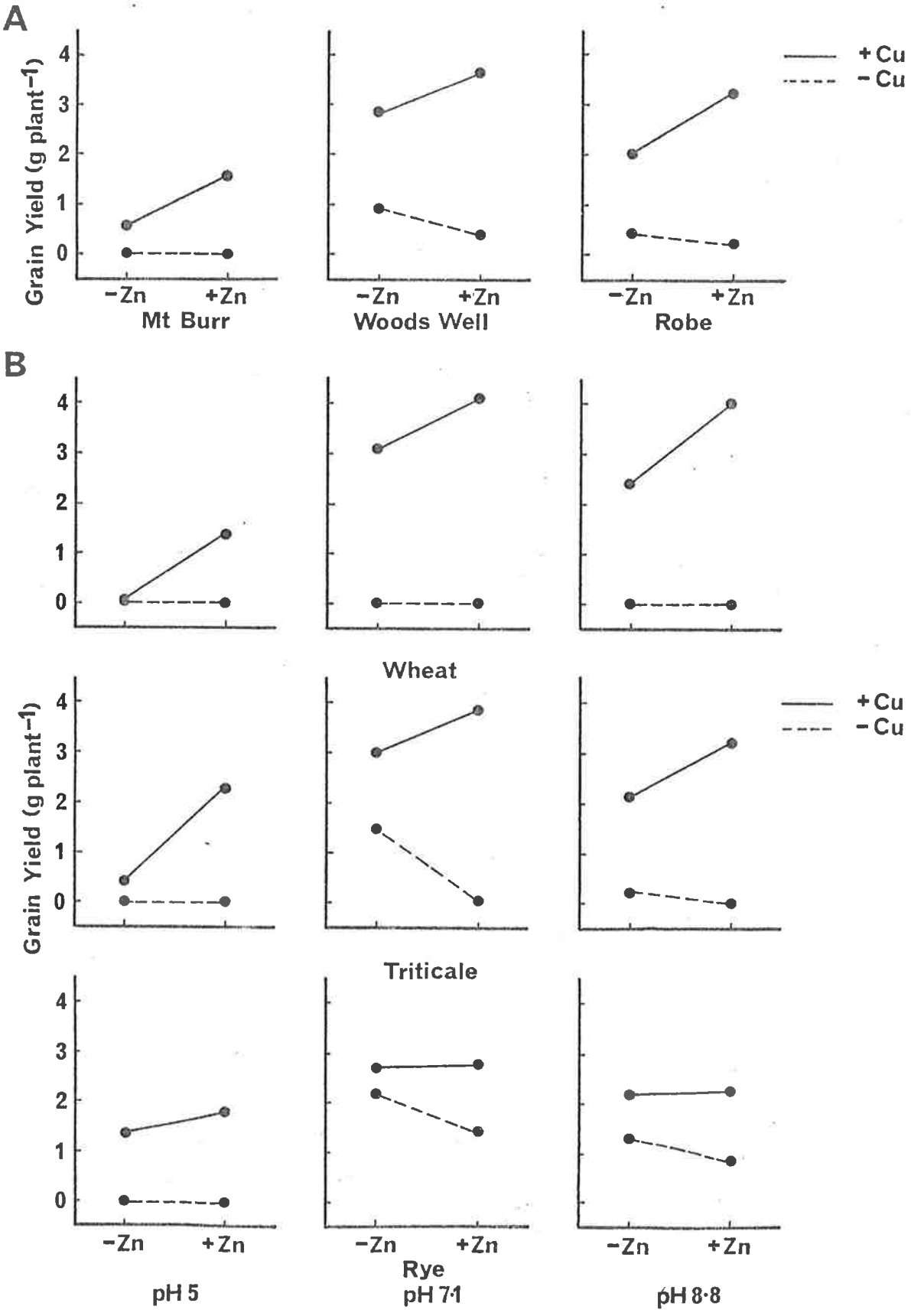
zinc concentration in plants partly by increasing growth but primarily by reducing the amount of zinc absorbed and the rate of zinc absorption per gram root in early growth (Chaudhry and Loneragan, 1970).

These results were somewhat different. Application of copper promoted growth both in the absence and presence of zinc. However, application of zinc aggravated the copper deficiency in the absence of applied copper; in the presence of applied copper the application of zinc alleviated the imbalance and promoted growth. It can be concluded from the results obtained in this experiment that copper deficiency in the three soils under examination was considerably more severe than zinc deficiency in the same soils.

The copper-zinc interaction in each soil depended upon the nature of the antagonistic action between them and on the extent of the copper and zinc deficiencies. Typically positive copper-zinc interactions were observed in all soils for vegetative yield, and grain yield (Figure 5.3.1A), but most strikingly in pollen viability on which the patterns of grain yield were based. Both wheat cultivars responded similarly to copper and zinc in the three soils and so only wheat cv. Halberd was graphed and compared with triticale and rye in the copper-zinc interaction graphs of grain yield (Figure 5.3.1B). Genotypic differences in the copper-zinc interaction showed up more strongly in the higher pH soils (pH 7.1 and pH 8.8).

Although there were marked differences among the genotypes in their sensitivity to a single deficiency of copper or of zinc, the copper-zinc interaction was physiologically similar for all genotypes in each soil.

FIGURE 5.3.1. Response to application of copper and/or zinc on grain yield (g plant^{-1}) as a function of soil pH. A. Grain yield (g plant^{-1}) independent of genotype (average for all genotypes). B. Grain yield (g plant^{-1}) for each genotype.


A
B
Grain Yield (g plant⁻¹)
0
1
2
3
4
+Cu
-Cu
-Zn
+Zn
Mt Burr
Woods Well
Robe
Wheat
Triticale
Rye
pH 5
pH 7·1
pH 8·8

5.4 GENERAL DISCUSSION

Little is known about the tolerance of triticale to low concentrations of available trace elements in soils at extremes of soil pH, because of the relatively short history of the crop. Mugwira *et al.* (1976) and Mugwira and Patel (1977) showed, however, that triticale was intermediate between wheat (sensitive) and rye (tolerant) in tolerance of aluminium toxicity in acid soils.

Literature was cited by Zillinsky (1974) which showed that triticale performed well on sandy soils in Spain and Hungary and often equalled the wheat yields on such soils, but did not perform as well as wheat under conditions of high soil fertility. Hulse and Spurgeon (1974) also stated that triticale was adaptable to unfavourable environmental conditions such as soils that were light and sandy or acid. In contrast Zillinsky and Borlaug (1971) reported that triticale had higher nutritional requirements than wheat or rye.

Many sandy soils in Australia have low or high soil pH and low concentrations of available copper and zinc. Such soils often contain adequate total copper and zinc for many crops, but it is relatively unavailable to genotypes of wheat, barley and oats currently grown (Graham, 1978b): these genotypes are unable to extract sufficient quantities of copper and zinc from the soil reserve to maintain optimum growth. In contrast, rye rarely shows responses to copper (Graham, 1978a; Graham and Pearce, 1979) and zinc (this study) on these soils. It is of agricultural interest, then, to know if triticale has inherited tolerance to extreme pH and low concentrations of available copper and zinc from its rye parent.

This study investigated the tolerance of triticale in a number of environments, combining both extreme soil pHs with low levels of copper and zinc, both separately and together. Three levels of copper and zinc deficiency were examined in the copper-zinc interaction study (experiment 3), compared to the effect of pH adjustment on one level of copper deficiency (experiment 1) and one level of zinc deficiency (experiment 2) in the earlier experiments. Three naturally copper- and zinc-deficient soils were selected on the basis of their pH (pH 5.0, pH 7.1, pH 8.8) for the copper-zinc interaction study whilst a neutral soil (pH 7.0, deficient in both copper and zinc) was selected for the earlier investigations and adjusted to acid (pH 5.0) and alkaline (pH 8.4) extremes to create three pH environments.

Soil reaction (pH) is the most important single characteristic of a soil governing the availability of nutrients to plants, and is of particular importance in connection with liming, fertilizing and soil management. The availability of all trace elements, with the exception of molybdenum increased with a decrease in pH (Lutz *et al.*, 1972). Soil reaction was a principal factor influencing fixation and leaching of many fertilizer constituents and played an important role in the availability and utilization of ions in light sandy soils (Peech, 1941). Likewise, the availability of the more insoluble nutrients from primary minerals in soils were governed by soil reaction.

Under acid soil conditions, many nutrients became depleted because of faster dissolution and leaching of the soil minerals and less soluble compounds (Peech, 1941). This was the situation for the natural soil with a pH of 5.0, however it did not apply to the neutral soil adjusted to acid pH. The effect of adding acid (H_2SO_4) to the soil was to increase the availability of copper and zinc, and in the case of zinc

to alleviate the deficiency completely, whilst for copper the deficiency still existed but it was less severe.

It was evident that the severity of copper deficiency was markedly greater than that of zinc deficiency on the neutral soil, after examination of the yield data in experiments 1 and 2 (Figures 4.1.4 and 4.2.4). Examination of the uptake data (Figure 4.2.5b) revealed that wheat and triticale plants were able to extract adequate zinc for their growth requirements from the soil at pH 5.0 and pH 7.0 but failed to do so at pH 8.4. In the copper study there was inadequate uptake of copper for grain production at all pHs for wheat and at pH 8.4 for triticale (Figure 4.1.5b). The decrease in availability of copper with increasing pH was insufficient to affect the response of wheat (highly sensitive) or of rye (highly tolerant), however, triticale responded strongly to the pH treatment.

Soil pH had a more marked influence on the availability of zinc than of copper, but pH did indeed affect the availability of copper, which conflicted with the findings of Piper and Beckwith (1949), who found that all species under examination in their investigation absorbed as much copper from neutral and alkaline soils as from acid soils.

Allowing for the fact that the soil was less deficient in zinc than in copper, the results had general similarities to those of copper, except that effects on grain yield were mediated more through vegetative yield than was the case for copper. Vegetative yield was reduced very little by severe copper deficiency whilst grain production was low or nil. In contrast, zinc deficiency reduced both the vegetative (straw) yield and the grain yield by similar proportions. Decreased grain production by zinc-deficient plants was associated with less vigorous growth of the plant, whereas grain yield reduction in copper-deficient plants was the

result of lower seed set caused by ~~inviable~~ non-viable pollen, as shown by Graham (1975, 1976b). The results of experiment 3 reiterated the findings of the first two experiments with respect to the influence of copper and zinc on plants and with respect to the ranking of the genotypes in order of sensitivity to the deficiencies. Thus artificial pH adjustment led to the same conclusions as natural extremes of pH.

Geneticists generally predict intermediacy for characters in a hybrid such as triticale, but clearly the interpretation is restricted when such studies are conducted only in one environment (for example, Graham and Pearce, 1979). In the copper study, grain yield of triticale varied from better than rye to nil, the equal of wheat. These results showed that, overall, triticale was indeed intermediate between wheat and rye in tolerance of copper deficiency in this soil. In the zinc study, grain yield of triticale ranged from superior to wheat and rye (zinc nonlimiting) to intermediate (zinc limiting). Thus, triticale was also intermediate between wheat and rye in tolerance to zinc deficiency in this soil. Results in experiment 3 further confirmed the tolerance of rye to extremes of soil pH and to both copper and zinc deficiency occurring separately and together, the sensitivity of wheat and the intermediacy of triticale.

Studies on genotypes and their hybrids when grown at various levels of an environmental factor have suggested that even within a species there may be different response curves, with optima at different levels of the environment, different yields at the optima, and differences in the range over which the genotypes will grow (Griffing and Langridge, 1963). Consequently, difficulties existed in the interpretation of average dominance or potence (Knight, 1973). When the F1 was precisely intermediate between its parents in its response, its yield values varied

between negative, positive and overdominance depending on the environment. In addition, when the F1 had a response more similar to one parent than another, (as in the case of triticale), thus exhibiting "dominance" in its response, its yield values again showed a range from negative to overdominance depending on the environment.

The concept of hybrid vigour can be applied to these experiments (although with caution as this is not "hybrid vigour" in the true meaning of the word since in these studies the triticale was compared to its parent types only, and was not the F1 resulting from the cross between the particular rye and wheat used).

The high yield of the hybrid, triticale, (in the absence of copper) relative to the parental species, wheat and rye, at pH 5.0 in the copper experiment, resembled "hybrid vigour" but this superiority disappeared at pH 7.0 and pH 8.4 where triticale was intermediate. In the zinc experiment, triticale (in the absence of zinc) again showed "hybrid vigour", this time at pH 5.0 and pH 7.0, whilst being intermediate between its parent species in grain production at pH 8.4.

For all experiments, in this investigation the same conclusion was reached regarding tolerance to copper and zinc deficiency of the three genotypes under examination. Triticale was intermediate between its parent species, wheat and rye, in tolerance of copper and zinc deficiency, irrespective of the soil pH and whether or not it was a natural or adjusted pH condition. In circumstances of marginal deficiency, triticale was tolerant like rye and under some conditions outperformed that genotype. When deficiency was severe, however, triticale was more sensitive than rye and sometimes performed like wheat. This applied to both copper and zinc deficiency whether or not they occurred separately or together in the soil. Evidence strongly supported the view that

copper and zinc efficiency in triticale and rye was due to greater absorption of copper and zinc and greater retranslocation to the shoot, especially to the ear, the pollen and grain.

The greater uptake of copper and zinc by these genotypes may be due to greater exploration of the soil by roots, greater apparent surface conductance of the roots, greater transpiration rate or a specific genotype - rhizosphere interaction (Barley, 1970). Graham *et al.* (1981) sought to determine the physiological basis of genotypic differences in efficiency of absorption of copper from soils deficient in that element. They found that the greater copper efficiency of rye compared to wheat appeared to depend on a number of properties of its root system, and perhaps of the shoot as well, triticale appeared to be intermediate in expression of these characters inherited from its rye parentage.

The physiological basis of genotypic differences in efficiency of absorption of zinc from soils deficient in that element have not been undertaken. It seems highly likely, however, that it could be attributed to properties of the root system, probably the same properties influencing the absorption of copper, although copper and zinc are known to have antagonistic effects on the absorption of one another (Lucas, 1945; Chaudhry and Loneragan, 1970).

Triticale appeared, like rye, to be generally tolerant of soil acidity. Slootmaker (1974) showed that the high degree of tolerance of triticale to soil acidity occurred as a result of the addition of the rye genome, creating a new species which could be cultivated in areas less well suited for cultivation of bread wheat.

Although the soil pH in Experiments 1 and 2 was varied artificially, this approach was validated by the results of Experiment 3 with natural soils covering a wide pH range.

The degree of copper deficiency in all soils (Experiment 3) and at all pHs in the adjusted neutral soil (Experiment 1) was severe and as a consequence it seemed likely that the tolerance of triticale would be adequate for most field situations when copper deficiency is a possibility. Preliminary field work supports this view (Graham and Davies, pers. comm.). The Mt. Burr sand (acid sand) used in Experiment 3 had such an acute deficiency of copper that even rye responded to copper application. It was unlikely, therefore, that any cereal would grow adequately on this soil, and from the maximum yields obtained, it appeared that there were other problems associated with it.

Although the degree of zinc deficiency in all soils was less severe than that of copper, it was severe enough in both Experiments 2 (pH 8.4) and 3 to define clearly the genetic differences under study. In all situations encountered in this investigation where zinc deficiency occurred, the tolerance of triticale was greater than that of wheat and likely to be adequate for most field situations where cereals are grown.

6.0 CONCLUSION

The conclusions attained in this study are:-

(1) Triticale is intermediate between wheat and rye in tolerance of copper deficiency, and zinc deficiency, in the neutral soil used in Pot Experiments 1 and 2.

(2) Triticale is intermediate between wheat and rye in tolerance of copper and zinc deficiency in all soils used in Pot Experiment 3, irrespective of the degree of deficiency or acidity of the soil.

(3) The outstanding performance of rye in the adverse conditions of serious copper deficiency and extremes of pH is well known: this study established that rye is also tolerant of zinc deficiency.

(4) Triticale has the tolerance of rye to both deficiencies of copper and zinc, and to extremes of pH.

(5) The same conclusions were reached for all experiments with respect to the influence of copper and zinc on plants and with respect to the ranking of the genotypes in order of sensitivity to the deficiencies: artificial pH adjustment led to the same conclusion as natural extremes of pH.

(6) Availability of copper and zinc is affected by soil pH.

(7) The response to copper deficiency was greater than that to zinc deficiency in the neutral soil.

(8) Since the level of copper and zinc deficiency in these pots was severe, the tolerance of triticale is likely to be adequate for most field situations when these deficiencies occur. Preliminary field work supports this view.

7.0 APPENDICES

APPENDIX 1

Details of soils used in Pot Experiments 1, 2 and 3.

Woods Well Soil (Prescott, 1944; Anderson and Neal-Smith, 1950).

No soil survey has been undertaken on this soil. Four inches of grey sand with slight to moderate organic matter accumulation, overlying two feet of light grey sand, and a further three feet of yellow sand. The yellow sand overlies about two feet of brown to yellow-brown sandy clay loam to sandy clay, which rests on limestone.

Copper and Zinc Analysis+

Pot Experiment	1	2	3
Copper (ppm)	.034	.016	.020
Zinc (ppm)	.080	.090	.038

Mt. Burr Soil Young Sand: Mt. Burr sand complex (Stephens, Crocker, Butler and Smith, 1941).

A1. Up to 1 ft. of grey non-coherent sand darkened by fairly large amounts of organic matter in a very coarse state of subdivision.
A2. Up to 5 ft. of light grey to white non-coherent sand.
B1. Black and brown accumulation of illuviated organic matter in sand frequently indurated into a hardpan and often two feet thick.
B2. Yellow sand to clayey sand of variable depth.

Mechanical analyses and chemical data on the soils.

Analytical data of Mt. Burr sand complex.

Soil Type (locality)	Young Sand			Hundred of Riddoch		
Horizon	A1	A2	A3	A4	B1	B2
Depth (inches)	0-10	10-21	21-45	45-96	91-114	114-132
%						
Coarse sand	63.2	49.7	48.4	36.7	41.5	21.4
Fine sand	29.0	46.8	49.3	60.6	53.9	44.3
Silt	1.2	1.0	1.3	1.3	1.4	4.3
Clay	1.9	1.5	0.9	0.8	2.7	24.1
L. on acid treatment	0.3	0.2	0.1	0.1	0.2	0.7
Moisture	2.5	0.2	0.1	0.0	0.3	5.1
Loss on Ignition	2.7	0.9	0.2	0.1	0.5	4.2
Hydrochloric acid extract) % K_2O	0.021	0.016	-	-	0.022	0.125
% P_2O_5	0.004	0.002	-	-	0.003	0.012
N%	0.058	0.017	-	-	-	-
Reaction (pH)	5.4	4.9	5.7	6.2	5.9	7.3

Copper and Zinc Analysis+

Copper not detectable Zinc .007 ppm

Robe Soil (Thomas, 1937)

Chemical analysis on major constituents in two unconsolidated dune sand soils from Robe (%).

From the site of the C.S.I.R. paddocks on the property of Mr. R. Dawson

Soil Sample	Calcium expressed as Carbonate	Siliceous Residue Insoluble in HCl	Magnesium expressed as Carbonate	Total Organic Matter	Iron and Aluminium as Oxides	Phosphorus expressed as Pentoxide	Sulphate Radicle SO_2	H_2O at 100°C	Total
1A 0"- 9"	65.83	27.77	2.28	4.07	0.62	0.071	0.19	0.64	101.47
1B 9"-18"	68.57	26.07	2.13	3.13	0.38	0.064	0.16	0.37	100.87
1C 18"-27"	71.07	23.84	2.36	3.11	0.39	0.057	0.18	0.25	101.26
2A 0"- 9"	62.41	29.66	1.94	4.16	0.63	0.073	0.16	1.29	100.32
2B 9"-18"	66.07	27.53	2.05	2.07	0.49	0.062	0.20	0.60	99.07
2C 18"-27"	70.36	24.62	1.94	1.08	0.46	0.055	0.22	0.24	98.98

Copper and Zinc Analysis+

Copper .018 ppm Zinc .106 ppm

+ These soil analyses were undertaken in this study.
40 g of soil was shaken for 16 hours with 80 mls of extractant. The extracting solution was:-
1 M NH_4Ac + .05M EDTA disodium
Copper and zinc were read following the methods outlined in Sections 3.3.1 and 3.3.2.

APPENDIX 2, Figure 1

Experiment 1

Effect of level of copper supply on the weekly water use (ml plant^{-1}) throughout the season of triticale at pH 5.0. Data are the means of 9 plants (3 plants per pot for each of 3 replicates). Vertical bars indicate LSD values for $P < 0.05$.

APPENDIX 2, Figure 2

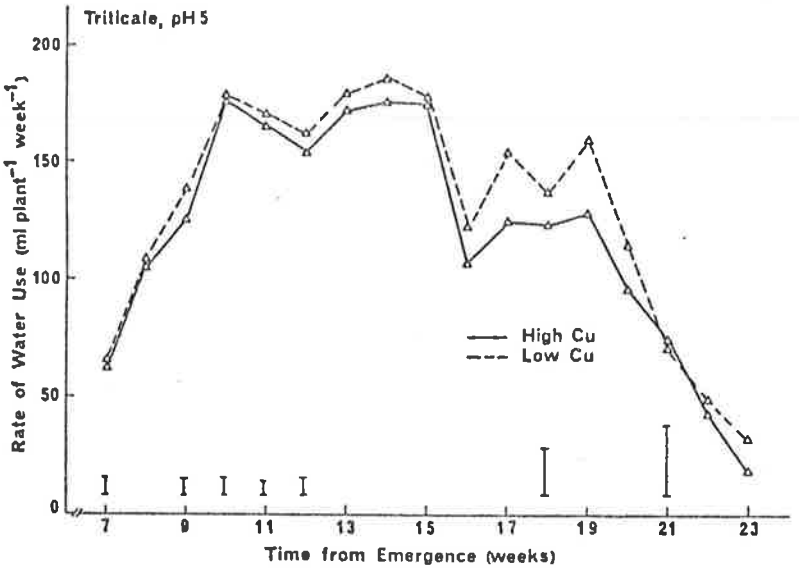
Experiment 1

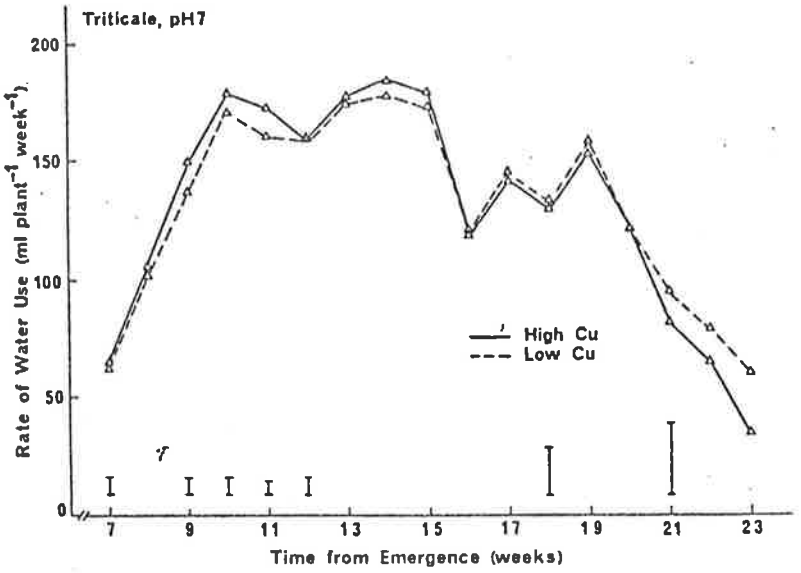
Effect of level of copper supply on the weekly water use (ml plant^{-1}) throughout the season of triticale at pH 7.0. Data are the means of 9 plants (3 plants per pot for each of 3 replicates). Vertical bars indicate LSD values for $P < 0.05$.

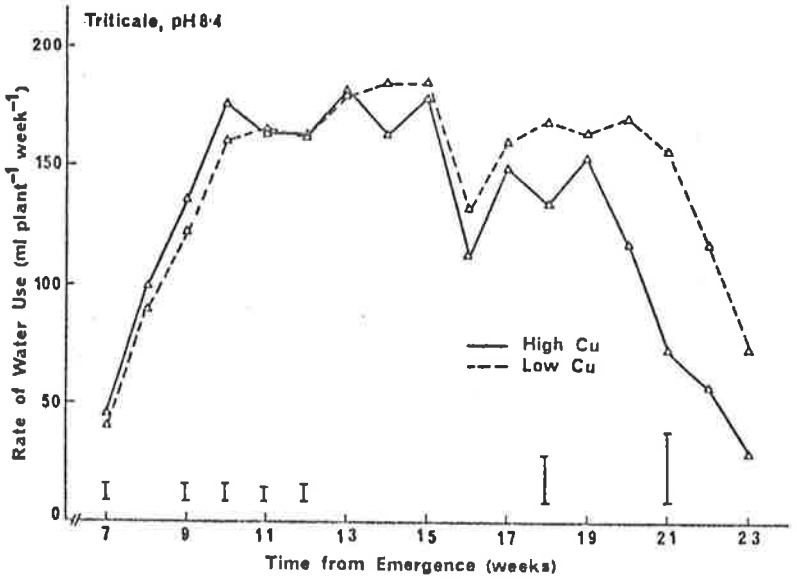
APPENDIX 2, Figure 3

Experiment 1

Effect of level of copper supply on the weekly water use (ml plant^{-1}) throughout the season of triticale at pH 8.4. Data are the means of 9 plants (3 plants per pot for each of 3 replicates). Vertical bars indicate LSD values for $P < 0.05$.


Triticale, pH 5
Rate of Water Use (ml plant^{-1} week^{-1})
200
150
100
50
0
High Cu
Low Cu
7
9
11
13
15
17
19
21
23
Time from Emergence (weeks)


Triticale, pH 7
Rate of Water Use (ml plant^{-1} week^{-1})
200
150
100
50
0
High Cu
Low Cu
7
9
11
13
15
17
19
21
23
Time from Emergence (weeks)


Triticale, pH 8·4
Rate of Water Use (ml plant^{-1} week^{-1})
200
150
100
50
0
High Cu
Low Cu
7
9
11
13
15
17
19
21
23
Time from Emergence (weeks)

APPENDIX 2, Figure 4

Experiment 1

Effect of level of copper supply on the weekly water use (ml $plant^{-1}$) throughout the season of rye at pH 5.0. Data are the means of 9 plants (3 plants per pot for each of 3 replicates). Vertical bars indicate LSD values for $P < 0.05$.

APPENDIX 2, Figure 5

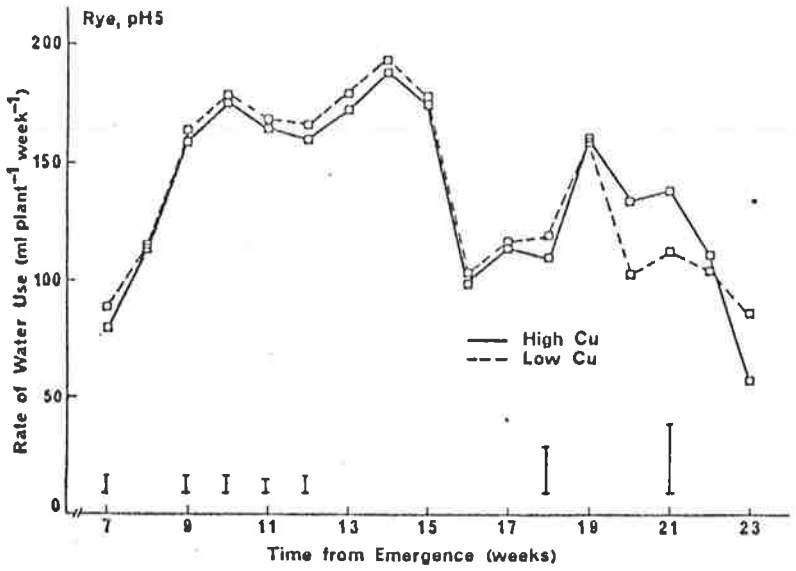
Experiment 1

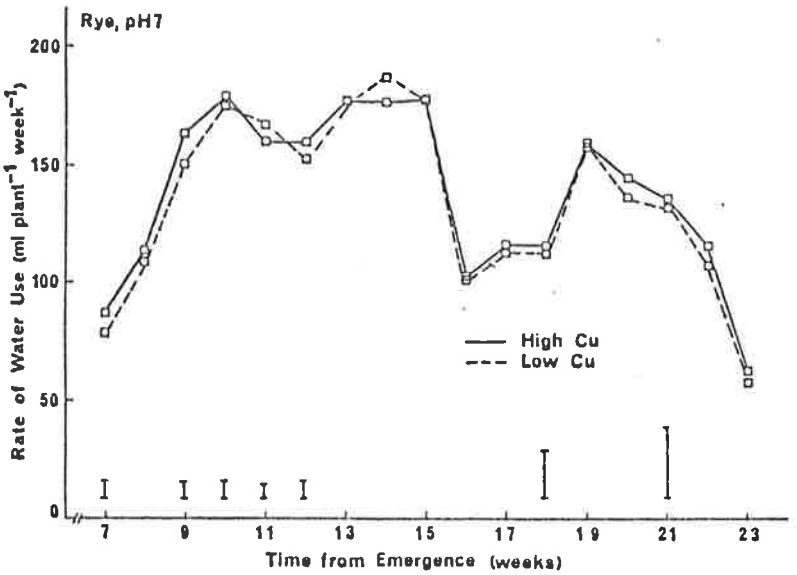
Effect of level of copper supply on the weekly water use (ml $plant^{-1}$) throughout the season of rye at pH 7.0. Data are the means of 9 plants (3 plants per pot for each of 3 replicates). Vertical bars indicate LSD values for $P < 0.05$.

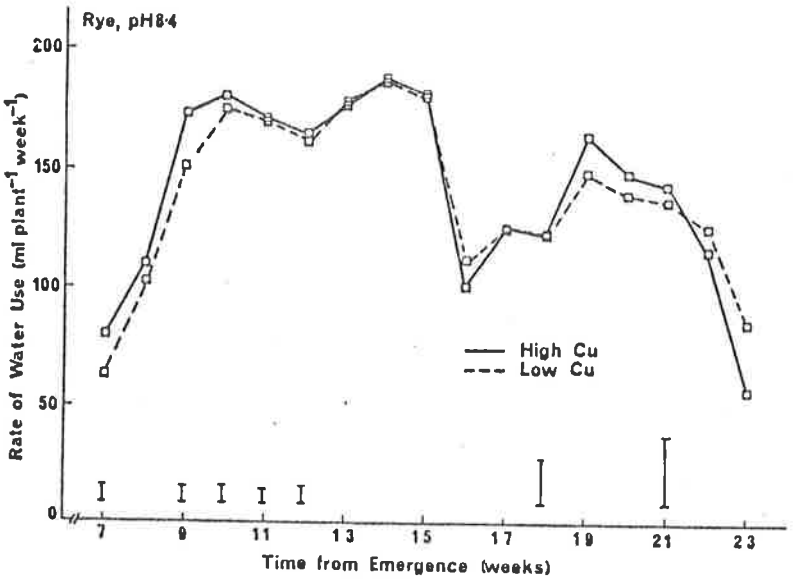
APPENDIX 2, Figure 6

Experiment 1

Effect of level of copper supply on the weekly water use (ml $plant^{-1}$) throughout the season of rye at pH 8.4. Data are the means of 9 plants (3 plants per pot for each of 3 replicates). Vertical bars indicate LSD values for $P < 0.05$.


Rye, pH5
Rate of Water Use (ml plant^{-1} week^{-1})
200
150
100
50
0
High Cu
Low Cu
7
9
11
13
15
17
19
21
23
Time from Emergence (weeks)


Rye, pH7
Rate of Water Use (ml plant^{-1} week^{-1})
200
150
100
50
0
High Cu
Low Cu
7
9
11
13
15
17
19
21
23
Time from Emergence (weeks)


Rye, pH8·4
Rate of Water Use (ml plant^{-1} week^{-1})
200
150
100
50
0
High Cu
Low Cu
7
9
11
13
15
17
19
21
23
Time from Emergence (weeks)

APPENDIX 3

Experiment 1

(a) Total water use over the whole season (ml plant^{-1})[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Cu added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	2493	2490	2473	2313	2170	2232
	Rep 2	2503	2493	2412	2358	2175	2343
	Rep 3	2497	2375	2265	2270	2217	2320
Triticale	Rep 1	2130	2003	2267	2108	2430	2138
	Rep 2	2202	1883	2247	2200	2400	2198
	Rep 3	2255	2165	2150	2315	2467	2060
Rye	Rep 1	2308	2290	2397	2345	2447	2303
	Rep 2	2170	2228	2283	2387	2422	2450
	Rep 3	2435	2420	2188	2307	2252	2478

1 = mean of 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	9118069			
Replication	2	2670	1335	0.02	NS
Genotype (G)	2	2338362	1169181	17.51	***
pH	2	12626	6313	0.09	NS
Cu	1	231412	231412	3.46	NS
G-pH	4	2525694	631423	9.45	***
G-Cu	2	903473	451737	6.76	**
pH-Cu	2	83181	41591	0.62	NS
G-pH-Cu	4	750771	187693	2.81	*
Residual	34	2269880	66761		

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; NS = not significant

APPENDIX 4

Experiment 1

(a) Height of main culms to top of ears (cm)[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Cu added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	31.8	89.4	41.2	91.1	35.1	101.1
	Rep 2	42.5	80.4	39.3	91.2	31.9	93.8
	Rep 3	34.2	87.1	48.6	92.8	29.0	92.6
Triticale	Rep 1	98.0	99.5	82.5	95.7	72.6	93.8
	Rep 2	89.9	105.5	92.8	96.8	81.3	100.6
	Rep 3	90.6	91.7	83.0	93.1	65.3	93.5
Rye	Rep 1	104.2	107.9	114.5	113.7	92.4	111.3
	Rep 2	119.4	116.0	125.7	114.0	124.6	117.7
	Rep 3	117.0	121.3	125.9	116.2	104.3	117.3

[1] = mean of 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	39657.6			
Replication	2	223.9	111.9	3.07	NS
Genotype (G)	2	23039.9	11519.9	316.90	***
pH	2	290.5	145.3	3.99	*
Cu	1	6829.9	6829.9	187.90	***
G-pH	4	374.7	93.7	2.57	NS
G-Cu	2	7014.1	3507.0	96.40	***
pH-Cu	2	582.3	291.1	8.00	**
G-pH-Cu	4	66.2	16.5	0.45	NS
Residual	34	1236.2	36.4		

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; NS = not significant

APPENDIX 5

Experiment 1

(a) Number of culms produced per plant[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Cu added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	5.3	3.0	5.7	2.7	4.7	3.0
	Rep 2	8.3	4.0	6.7	2.7	5.7	2.3
	Rep 3	8.0	3.7	4.3	2.7	3.7	2.3
Triticale	Rep 1	1.0	1.0	4.0	2.0	5.7	2.3
	Rep 2	1.7	1.0	2.7	2.0	4.3	2.0
	Rep 3	2.0	1.7	3.7	2.0	5.7	1.3
Rye	Rep 1	3.1	2.7	3.3	2.7	3.7	3.0
	Rep 2	2.7	2.0	2.3	3.7	5.7	3.0
	Rep 3	3.0	3.0	2.0	3.3	3.0	3.0

[1] = mean of 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	1266.000			
Replication	2	5.444	2.722	0.516	NS
Genotype (G)	2	283.111	141.556	26.854	***
pH	2	14.333	7.167	1.360	NS
Cu	1	322.667	322.667	61.213	***
G-pH	4	224.556	56.139	10.650	***
G-Cu	2	136.444	68.222	12.942	***
pH-Cu	2	20.111	10.056	1.908	NS
G-pH-Cu	4	80.111	20.028	3.799	*
Residual	34	179.222	5.271		

* = $P < 0.05$; *** = $P < 0.001$; NS = not significant

APPENDIX 6

Experiment 1

(a) Number of ears produced per plant[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Cu added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	0.7	3.0	1.0	2.3	0.0	2.0
	Rep 2	0.7	3.0	0.7	2.7	0.3	2.3
	Rep 3	0.7	3.0	1.7	2.7	1.3	2.3
Triticale	Rep 1	1.0	1.0	3.7	1.7	4.7	2.0
	Rep 2	1.3	1.0	2.7	1.7	3.7	1.7
	Rep 3	2.0	1.7	3.3	2.0	5.7	1.3
Rye	Rep 1	3.0	2.7	3.3	2.7	3.7	3.0
	Rep 2	2.3	2.0	2.3	3.3	4.3	2.7
	Rep 3	2.7	3.0	2.0	2.7	3.0	2.7

[1] = mean of 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	598.093			
Replication	2	6.259	3.130	1.571	NS
Genotype (G)	2	110.704	55.352	27.782	***
pH	2	36.926	18.463	9.267	***
Cu	1	0.019	0.019	0.009	NS
G-pH	4	74.630	18.657	9.364	***
G-Cu	2	233.370	116.685	58.566	***
pH-Cu	2	40.704	20.352	10.215	***
G-pH-Cu	4	27.741	6.935	3.481	*
Residual	34	67.741	1.992		

* = $P < 0.05$; *** = $P < 0.001$; NS = not significant

APPENDIX 7

Experiment 1

(a) Number of days to ear emergence of main culms[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Cu added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	163	91	161	86	-[+]	90
	Rep 2	165	89	167	83	167	92
	Rep 3	165	92	163	88	161	93
Triticale	Rep 1	83	85	87	83	95	84
	Rep 2	85	84	90	81	92	85
	Rep 3	85	85	88	82	91	85
Rye	Rep 1	99	92	94	93	96	96
	Rep 2	93	94	96	93	94	96
	Rep 3	94	93	91	94	97	99

[1] = mean of 3 plants/pot

[+] = not reached by harvest date

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	41861.43			
Replication	2	0.93	0.46	0.124	NS
Genotype (G)	2	16403.37	8201.68	2194.447	***
pH	2	91.59	45.80	12.253	***
Cu	1	9520.17	9520.17	2547.220	***
G-pH	4	28.96	7.24	1.937	NS
G-Cu	2	15592.11	7796.06	2085.916	***
pH-Cu	2	21.00	10.50	2.809	NS
G-pH-Cu	4	76.22	19.06	5.099	**
Residual	34	127.07	3.74		

** = $P < 0.01$; *** = $P < 0.001$; NS = not significant

APPENDIX 8

Experiment 1

(a) Number of days to anthesis of main culms[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Cu added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	-[+]	101	-[+]	95	-[+]	98
	Rep 2	-[+]	100	-[+]	92	-[+]	99
	Rep 3	-[+]	101	-[+]	97	-[+]	101
Triticale	Rep 1	93	94	96	92	105	94
	Rep 2	94	93	97	91	100	95
	Rep 3	96	94	96	92	99	94
Rye	Rep 1	108	102	104	103	108	105
	Rep 2	103	102	105	102	107	105
	Rep 3	104	103	103	103	109	108

[1] = mean of 3 plants/pot

[+] = not reached by harvest date

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	43794.15			
Replication	2	7.37	3.68	1.959	NS
Genotype (G)	2	16902.26	8451.13	4492.262	***
pH	2	100.04	50.02	26.588	***
Cu	1	10305.85	10305.85	5478.154	***
G-pH	4	37.85	9.46	5.030	**
G-Cu	2	16314.93	8157.46	4336.162	***
pH-Cu	2	21.15	10.57	5.621	**
G-pH-Cu	4	40.74	10.18	5.414	**
Residual	34	63.96	1.88		

** = $P < 0.01$; *** = $P < 0.001$; NS = not significant

APPENDIX 9

Experiment 1

(a) Number of days to maturity of main culms[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Cu added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	-[+]	151	-[+]	148	-[+]	150
	Rep 2	-[+]	149	-[+]	148	-[+]	151
	Rep 3	-[+]	161	-[+]	157	-[+]	151
Triticale	Rep 1	139	141	152	140	165	139
	Rep 2	142	138	152	140	162	140
	Rep 3	145	144	150	140	161	139
Rye	Rep 1	160	157	159	156	163	156
	Rep 2	159	159	160	152	160	156
	Rep 3	158	158	158	158	165	161

[1] = mean of 3 plants/pot

[+] = not reached by harvest date

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	6936.98			
Replication	2	44.59	22.30	3.893	*
Genotype (G)	2	2885.48	1442.74	251.890	***
pH	2	108.26	54.13	9.451	***
Cu	1	2204.17	2204.17	384.828	***
G-pH	4	199.07	49.77	8.689	***
G-Cu	2	905.33	452.67	79.032	***
pH-Cu	2	215.44	107.72	18.807	***
G-pH-Cu	4	179.89	44.97	7.852	***
Residual	34	194.74			

* = $P < 0.05$; *** = $P < 0.001$

APPENDIX 10

Experiment 1

(a) Total dry matter production per plant (g)[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Cu added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	2.48	10.02	3.16	9.72	2.30	8.98
	Rep 2	3.68	9.83	2.89	10.21	2.51	9.31
	Rep 3	3.12	9.04	3.33	8.81	2.75	9.50
Triticale	Rep 1	7.15	8.41	7.48	8.88	5.11	9.66
	Rep 2	7.63	7.37	7.51	8.69	5.90	9.17
	Rep 3	7.47	8.46	6.16	8.96	5.16	8.37
Rye	Rep 1	6.18	6.46	7.45	7.73	7.21	6.52
	Rep 2	6.95	7.25	7.30	7.93	7.50	7.68
	Rep 3	7.38	8.48	6.55	6.69	5.95	8.00

[1] = mean of 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	2306.672			
Replication	2	7.686	3.843	1.227	NS
Genotype (G)	2	174.976	87.488	27.943	***
pH	2	16.609	8.305	2.652	NS
Cu	1	1116.934	1116.934	356.736	***
G-pH	4	6.875	1.719	0.549	NS
G-Cu	2	813.482	406.741	129.908	***
pH-Cu	2	24.348	12.174	3.888	*
G-pH-Cu	4	39.308	9.827	3.139	*
Residual	34	2298.986	45.078		

* = $P < 0.05$; *** = $P < 0.001$; NS = not significant

APPENDIX 11

Experiment 1

(a) Dry weight of straw+ per plant (g)[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Cu added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	2.48	5.87	3.16	5.70	2.30	5.45
	Rep 2	3.68	6.12	2.89	5.92	2.51	5.50
	Rep 3	3.12	5.61	3.33	5.20	2.75	5.79
Triticale	Rep 1	3.90	4.63	5.91	4.90	5.11	5.37
	Rep 2	4.33	4.53	4.95	4.80	5.89	5.22
	Rep 3	5.10	5.03	6.13	5.17	5.16	4.63
Rye	Rep 1	5.35	4.57	6.09	6.08	6.13	5.42
	Rep 2	5.29	5.07	5.17	6.53	7.00	5.68
	Rep 3	5.74	6.44	4.70	5.70	4.84	6.24

1 = mean of 3 plants/pot

+ = weight of (stem, leaf and chaff)

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	601.066			
Replication	2	2.077	1.039	0.407	NS
Genotype (G)	2	152.436	76.218	29.878	***
pH	2	8.109	4.055	1.589	NS
Cu	1	97.231	97.231	38.116	***
G-pH	4	20.518	5.130	2.011	NS
G-Cu	2	216.991	108.496	42.532	***
pH-Cu	2	0.507	0.254	0.099	NS
G-pH-Cu	4	16.464	4.116	1.614	NS
Residual	34	86.732	2.551		

*** = $P < 0.001$; NS = not significant

APPENDIX 12

Experiment 1

(a) Grain yield per plant (g)[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Cu added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	0.00	4.15	0.00	4.02	0.00	3.52
	Rep 2	0.00	3.71	0.00	4.29	0.00	3.81
	Rep 3	0.00	3.43	0.00	3.62	0.00	3.71
Triticale	Rep 1	3.25	3.79	1.57	8.98	0.00	4.28
	Rep 2	3.30	2.84	2.55	3.90	0.01	3.95
	Rep 3	2.37	3.43	0.03	3.80	0.00	3.75
Rye	Rep 1	0.83	1.89	1.37	1.65	1.09	1.10
	Rep 2	1.66	2.18	2.13	1.40	0.50	2.00
	Rep 3	1.65	2.04	1.85	0.99	1.11	1.76

[1] = mean of 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	1105.486			
Replication	2	5.672	2.836	1.790	NS
Genotype (G)	2	98.459	49.229	31.072	***
pH	2	25.445	12.723	8.030	**
Cu	1	555.074	555.074	350.345	***
G-pH	4	17.530	4.383	2.766	*
G-Cu	2	248.442	124.221	78.404	***
pH-Cu	2	29.947	14.974	9.451	***
G-pH-Cu	4	71.049	17.762	11.211	***
Residual	34	53.868	1.584		

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; NS = not significant

APPENDIX 13

Experiment 1

(a) Harvest index of the plant[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Cu added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	0.00	0.41	0.00	0.41	0.00	0.39
	Rep 2	0.00	0.38	0.00	0.42	0.00	0.41
	Rep 3	0.00	0.38	0.00	0.41	0.00	0.39
Triticale	Rep 1	0.45	0.45	0.21	0.45	0.00	0.44
	Rep 2	0.43	0.39	0.34	0.45	0.00	0.43
	Rep 3	0.32	0.41	0.01	0.42	0.00	0.45
Rye	Rep 1	0.13	0.29	0.18	0.21	0.15	0.17
	Rep 2	0.24	0.30	0.29	0.18	0.07	0.26
	Rep 3	0.22	0.24	0.28	0.15	0.19	0.22

[1] = mean of 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	1.499395			
Replication	2	0.007036	0.003518	1.269	NS
Genotype (G)	2	0.141610	0.070805	25.547	***
pH	2	0.061050	0.030525	11.014	***
Cu	1	0.664975	0.664975	239.931	***
G-pH	4	0.056436	0.014109	5.091	**
G-Cu	2	0.312008	0.156004	56.288	***
pH-Cu	2	0.051426	0.025713	9.278	***
G-pH-Cu	4	0.110622	0.027656	9.978	***
Residual	34	0.094232	0.002772		

** = $P < 0.01$; *** = $P < 0.001$; NS = not significant

APPENDIX 14

Experiment 1

(a) Number of grains per plant[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Cu added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	0.0	113.0	0.0	102.3	0.0	90.7
	Rep 2	0.0	95.7	0.0	114.3	0.0	96.7
	Rep 3	0.0	99.7	0.0	104.3	0.0	102.3
Triticale	Rep 1	66.7	74.0	42.0	87.0	0.0	100.3
	Rep 2	75.0	69.7	64.3	55.7	3.0	94.3
	Rep 3	59.3	68.0	9.3	86.3	0.0	75.3
Rye	Rep 1	35.3	68.0	53.3	58.3	59.7	50.3
	Rep 2	84.7	94.3	92.7	59.7	38.7	89.3
	Rep 3	65.0	99.0	93.3	38.3	50.7	72.7

[1] = mean of 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	679693			
Replication	2	4588	2294	1.317	NS
Genotype (G)	2	20528	10264	5.892	**
pH	2	14885	7442	4.272	*
Cu	1	311296	311296	178.709	***
G-pH	4	5980	1495	0.858	NS
G-Cu	2	189030	94515	54.259	***
pH-Cu	2	20765	10383	5.961	**
G-pH-Cu	4	53395	13349	7.663	***
Residual	34	59225	1742		

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; NS = not significant

APPENDIX 15

Experiment 1

(a) Number of spikelets per ear[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Cu added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	12.00	20.11	11.67	18.43	-[+]	19.67
	Rep 2	11.50	18.22	11.50	18.63	13.00	*
	Rep 3	12.50	18.00	11.20	18.00	11.50	20.86
Triticale	Rep 1	22.67	25.00	17.91	21.40	-[#]	22.00
	Rep 2	23.75	22.67	21.50	25.00	17.73	23.20
	Rep 3	20.83	24.00	18.00	23.67	12.94	23.25
Rye	Rep 1	33.22	35.88	34.00	34.75	30.73	33.44
	Rep 2	33.14	40.50	33.86	31.50	30.69	38.63
	Rep 3	32.38	31.56	37.17	33.38	34.56	32.75

1 = mean of 3 plants/pot

\+ = no ears emerged by harvest date

* = missing value

\# = spikelets could not be distinguished as ears were so small

(b) Analysis of Variance

Source of variance	D.F. (MV)	S.S.	M.S.	v-ratio	
Total	51	4302.78			
Replication	2	30.58	15.29	1.943	NS
Genotype (G)	2	3311.93	1655.97	210.415	***
pH	2	45.55	22.78	2.894	NS
Cu	1	338.94	338.94	43.068	***
G-pH	4	103.31	25.83	3.282	*
G-Cu	2	92.46	46.23	5.874	**
pH-Cu	2	67.77	33.88	4.306	*
G-pH-Cu	4	60.39	15.10	1.918	NS
Residual	32 (2)	251.84	7.87		

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; NS = not significant

APPENDIX 16

Experiment 1

(a) Number of grains per ear[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Cu added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	0.00	37.67	0.00	43.86	-[+]	45.33
	Rep 2	0.00	31.89	0.00	42.88	0.00	41.43
	Rep 3	0.00	33.22	0.00	39.13	0.00	43.86
Triticale	Rep 1	66.67	74.00	11.45	52.20	0.00	50.17
	Rep 2	56.25	69.67	24.13	33.40	0.82	56.60
	Rep 3	29.67	40.80	2.80	43.17	0.00	56.50
Rye	Rep 1	11.78	25.50	16.00	21.88	16.27	16.78
	Rep 2	36.29	47.17	39.71	17.90	8.92	33.50
	Rep 3	24.38	33.00	46.67	14.38	16.89	27.25

[1] = mean of 3 plants/pot

[+] = no ears emerged by harvest date

(b) Analysis of Variance

Source of variance	D.F. (MV)	S.S.	M.S.	v-ratio	
Total	50	23514.01			
Replication	2	221.07	110.54	1.257	NS
Genotype (G)	2	2789.71	1394.85	15.865	***
pH	2	1319.31	659.66	7.503	**
Cu	1	8184.42	8184.42	93.089	***
G-pH	4	2311.19	577.80	6.572	***
G-Cu	2	3528.02	1764.01	20.064	***
pH-Cu	2	959.39	479.70	5.456	**
G-pH-Cu	4	1299.53	324.88	3.695	*
Residual	33 (1)	2901.37	87.92		

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; NS = not significant

APPENDIX 17

Experiment 1

(a) Weight per grain (mg)[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Cu added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	0.0	36.8	0.0	39.3	0.0	38.9
	Rep 2	0.0	38.8	0.0	37.5	0.0	39.4
	Rep 3	0.0	34.4	0.0	34.7	0.0	36.3
Triticale	Rep 1	48.8	51.2	37.4	45.7	0.0	42.7
	Rep 2	44.0	40.8	39.7	70.0	0.0	41.9
	Rep 3	39.9	50.4	0.0	44.0	0.0	49.7
Rye	Rep 1	23.5	27.8	25.6	28.3	18.2	21.9
	Rep 2	19.6	23.1	22.9	23.4	13.0	22.4
	Rep 3	25.3	20.6	19.8	25.9	21.9	24.2

[1] = mean of 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F. (MV)	S.S.	M.S.	v-ratio	
Total	42	10.119			
Replication	2	0.160	0.080	1.488	NS
Genotype (G)	2	1.748	0.874	16.213	***
pH	2	1.232	0.616	11.423	***
Cu	1	2.443	2.443	45.308	***
G-pH	4	0.656	0.164	3.044	*
G-Cu	1 (1)	0.976	0.976	18.098	***
pH-Cu	2	1.041	0.521	9.657	***
G-pH-Cu	2 (2)	0.462	0.231	4.281	*
Residual	26 (8)	1.402	0.054		

* = $P < 0.05$; *** = $P < 0.001$; NS = not significant

APPENDIX 18

Experiment 1

(a) Dry weight of roots per plant (g)[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Cu added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	0.31	0.78	0.60	0.93	0.34	1.60
	Rep 2	0.78	0.92	0.45	1.38	0.36	0.99
	Rep 3	0.67	0.93	0.49	0.98	0.57	1.11
Triticale	Rep 1	0.91	1.18	1.25	0.90	2.24	1.01
	Rep 2	0.91	1.38	1.54	1.12	1.49	1.54
	Rep 3	0.82	1.08	1.19	1.38	1.10	1.61
Rye	Rep 1	2.77	2.88	3.50	2.41	2.56	2.95
	Rep 2	2.86	2.86	3.73	7.05	2.52	3.16
	Rep 3	2.30	2.37	2.29	3.71	2.37	3.07

[1] = mean of 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	693.204			
Replication	2	14.283	7.142	2.057	NS
Genotype (G)	2	472.995	236.498	68.111	***
pH	2	16.715	8.358	2.407	NS
Cu	1	17.670	17.670	5.089	*
G-pH	4	29.545	7.386	2.127	NS
G-Cu	2	10.363	5.182	1.492	NS
pH-Cu	2	1.934	0.967	0.279	NS
G-pH-Cu	4	11.642	2.910	0.838	NS
Residual	34	118.056	3.472		

* = $P < 0.05$; *** = $P < 0.001$; NS = not significant

APPENDIX 19

Experiment 1

(a) Concentration of copper in the straw ($\mu g\ g^{-1}$)[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Cu added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	2.33	2.40	2.10	2.27	1.69	2.88
	Rep 2	4.00	3.48	3.00	3.53	3.05	3.23
	Rep 3	3.10	3.85	3.08	3.15	3.23	2.65
Triticale	Rep 1	1.60	5.08	1.48	2.65	1.39	2.25
	Rep 2	2.78	4.80	2.45	4.50	2.83	3.38
	Rep 3	3.05	4.23	2.28	3.43	2.25	3.23
Rye	Rep 1	1.60	3.98	2.38	3.43	1.20	2.50
	Rep 2	1.88	4.50	1.58	3.40	1.33	3.38
	Rep 3	2.60	3.68	2.68	4.60	1.95	3.08

[1] = bulked sample of straw for 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	46.5210			
Replication	2	6.6770	3.3885	14.775	***
Genotype (G)	2	0.4887	0.2444	1.081	NS
pH	2	5.0196	2.5098	11.107	***
Cu	1	17.3967	17.3967	76.991	***
G-pH	4	1.5332	0.3833	1.696	NS
G-Cu	2	5.9208	2.9604	13.102	***
pH-Cu	2	0.8168	0.4084	1.808	NS
G-pH-Cu	4	0.9855	0.2464	1.090	NS
Residual	34	7.6826	0.2260		

*** = $P < 0.001$; NS = not significant

APPENDIX 20

Experiment 1

(a) Concentration of copper in main culm grain ($\mu g\ g^{-1}$)[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Cu added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	-*	3.32	-*	2.99	-*	1.70
	Rep 2	-*	3.33	-*	3.00	-*	2.17
	Rep 3	-*	3.51	-*	2.93	-*	1.82
Triticale	Rep 1	0.38	4.25	0.38	2.89	-*	2.47
	Rep 2	0.36	4.08	0.50*	3.57	-*	2.50
	Rep 3	0.44	4.84	-*	3.98	-*	2.76
Rye	Rep 1	1.55	6.91	1.53	6.33	0.46	4.66
	Rep 2	1.68	5.29	0.83	5.72	0.70	3.39
	Rep 3	0.98	6.08	1.67	7.94	1.34	3.37

[1] = bulked sample of main culm grain for 3 plants/pot

* = no grain

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	234.8847			
Replication	2	0.5794	0.2897	1.446	NS
Genotype (G)	2	38.4580	19.2290	95.967	***
pH	2	12.5983	6.2992	31.438	***
Cu	1	160.1667	160.1667	799.351	***
G-pH	4	2.7150	0.6788	3.388	*
G-Cu	2	5.8319	2.9159	14.553	***
pH-Cu	2	6.3376	3.1688	15.815	***
G-pH-Cu	4	1.3851	0.3463	1.728	NS
Residual	34	6.8126	0.2004		

* = $P < 0.05$; *** = $P < 0.001$; NS = not significant

APPENDIX 21

Experiment 1

(a) Concentration of copper in primary tiller grain ($\mu g\ g^{-1}$)[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Cu added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	-*	3.22	-*	2.85	-*	1.65
	Rep 2	-*	3.13	-*	2.80	-*	1.85
	Rep 3	-*	2.71	-*	3.24	-*	1.51
Triticale	Rep 1	-*	-*	0.50*	3.19	-*	2.16
	Rep 2	0.58	-*	-*	3.43	-*	1.90
	Rep 3	0.63	5.36	-*	2.69	-*	2.36
Rye	Rep 1	1.46	5.46	1.56	5.98	0.57*	4.12
	Rep 2	2.31	5.10	1.09	4.90	-*	3.19
	Rep 3	1.11	5.91	1.51	5.28	1.13	3.36

[1] = bulked sample of primary tiller grain for 3 plants/pot

* = no grain

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	183.7266			
Replication	2	1.2057	0.6029	0.931	NS
Genotype (G)	2	35.9617	17.9808	27.755	***
pH	2	7.5837	3.7919	5.853	**
Cu	1	103.8891	103.8891	160.360	***
G-pH	4	3.4386	0.8596	1.327	NS
G-Cu	2	5.1609	2.5805	3.983	*
pH-Cu	2	2.4048	1.2024	1.856	NS
G-pH-Cu	4	2.0552	0.5138	0.793	NS
Residual	34	22.0269	0.6479		

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; NS = not significant

APPENDIX 22

Experiment 1

(a) Concentration of copper in secondary tiller grain ($\mu g\ g^{-1}$)[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Cu added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	-*	2.66	-*	2.55	-*	-*
	Rep 2	-*	2.92	-*	2.22	-*	1.50
	Rep 3	-	3.89	-	3.02	-	1.55
Triticale	Rep 1	-*	-*	-*	-*	-*	1.60*
	Rep 2	-*	-	-*	-*	-*	-*
	Rep 3	-	4.54	-	-	-	-
Rye	Rep 1	0.90	6.48	1.21	5.64	-*	4.55
	Rep 2	1.21*	6.48	0.82*	4.04	-	2.61
	Rep 3	-	6.31	-	7.09	1.20	2.64

[1] = bulked sample of secondary tiller grain for 3 plants/pot

* = no grain

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	230.0402			
Replication	2	1.9856	0.9928	1.307	NS
Genotype (G)	2	58.9324	29.4662	38.778	***
pH	2	10.8665	5.4333	7.150	**
Cu	1	83.0056	83.0056	109.236	***
G-pH	4	4.3314	1.0829	1.425	NS
G-Cu	2	33.1303	16.5651	21.800	***
pH-Cu	2	8.9240	4.4620	5.872	*
G-pH-Cu	4	3.0289	0.7572	0.997	NS
Residual	34	25.8356	0.7599		

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; NS = not significant

APPENDIX 23

Experiment 1

(a) Copper content of straw per plant (µg)[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Cu added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	5.78	14.09	6.63	12.94	3.89	15.71
	Rep 2	14.72	21.30	8.67	20.89	7.65	17.75
	Rep 3	9.68	21.60	10.26	16.37	8.89	15.33
Triticale	Rep 1	6.24	23.50	8.75	12.99	7.19	12.09
	Rep 2	12.05	21.73	12.14	21.58	16.66	17.65
	Rep 3	15.56	21.28	13.97	17.72	11.62	14.94
Rye	Rep 1	8.55	18.18	14.49	20.85	7.35	13.55
	Rep 2	9.95	22.83	8.17	22.21	9.31	19.20
	Rep 3	14.92	23.70	12.60	26.20	9.44	19.23

[1] = mean of 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	14885.23			
Replication	2	1690.89	845.45	15.664	***
Genotype (G)	2	631.63	315.81	5.851	**
pH	2	888.72	444.36	8.233	**
Cu	1	8848.29	8848.29	163.938	***
G-pH	4	248.10	62.03	1.149	NS
G-Cu	2	258.94	129.47	2.399	NS
pH-Cu	2	185.32	92.66	1.717	NS
G-pH-Cu	4	298.25	74.56	1.381	NS
Residual	34	1835.09	53.97		

** = $P < 0.01$; *** = $P < 0.001$; NS = not significant

APPENDIX 24

Experiment 1

Copper content (μg plant^{-1}) in grain of wheat, triticale and rye grown at two levels of copper supply at three soil pHs.

Treatment	Cu added per pot (mg)	Soil pH 5.0	7.0	8.4
Genotype				
Wheat	0	0.00	0.00	0.00
	4	12.27	11.51	6.68
Triticale	0	1.21	0.61	0.00
	4	14.79	13.16	9.84
Rye	0	1.90	2.35	0.71
	4	11.47	8.17	5.94

LSD (P = 0.05) for the genotype-Cu interaction and soil pH-Cu interaction: 0.96

APPENDIX 25

Experiment 1

(a) Total copper uptake by grain ($\mu g\ plant^{-1}$)[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Cu added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	-*	13.20	-*	11.66	-*	5.93
	Rep 2	-*	11.89	-*	11.96	-*	7.62
	Rep 3	-*	11.74	-*	10.92	-*	6.49
Triticale	Rep 1	1.24	16.09	0.59	11.77	-*	10.01
	Rep 2	1.31	11.59	1.24	13.83	-*	9.39
	Rep 3	1.10	16.69	-*	13.89	-*	10.12
Rye	Rep 1	1.12	10.49	1.98	9.97	0.53	4.88
	Rep 2	2.87	11.55	2.12	7.13	0.22	6.39
	Rep 3	1.72	12.37	2.97	7.41	1.36	6.54

[1] = mean of 3 plants/pot

* = no grain

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	13786.963			
Replication	2	5.468	2.734	0.308	NS
Genotype (G)	2	249.232	124.616	14.044	***
pH	2	803.646	401.823	45.284	***
Cu	1	11367.714	11367.714	1281.104	***
G-pH	4	15.866	3.967	0.447	NS
G-Cu	2	544.774	272.387	30.697	***
pH-Cu	2	425.170	212.585	23.958	***
G-pH-Cu	4	73.398	18.349	2.068	NS
Residual	34	301.695	8.873		

*** = $P < 0.001$; NS = not significant

APPENDIX 26

Experiment 1

(a) Copper content of main culm grain per plant (µg)[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Cu added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	*	7.98	*	6.69	*	4.06
	Rep 2	*	6.26	*	6.82	*	4.53
	Rep 3	*	6.76	*	6.09	*	4.04
Triticale	Rep 1	1.24	16.09	0.59	8.86	*	7.65
	Rep 2	1.00	11.59	1.24	11.80	*	7.86
	Rep 3	0.91	13.34	*	11.36	*	8.83
Rye	Rep 1	0.64	4.95	0.89	4.30	0.30	2.13
	Rep 2	1.34	6.37	0.93	3.18	0.22	3.19
	Rep 3	0.82	6.22	1.98	3.76	0.58	3.26

[1] = mean of 3 plants/pot

* = no grain

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	7984.495			
Replication	2	0.866	0.433	0.072	NS
Genotype (G)	2	961.060	480.530	80.260	***
pH	2	379.844	189.922	31.722	***
Cu	1	5121.682	1521.682	855.444	***
G-pH	4	61.015	15.254	2.548	NS
G-Cu	2	1004.827	502.414	83.915	***
pH-Cu	2	214.022	107.011	17.873	***
G-pH-Cu	4	37.614	9.404	1.571	NS
Residual	34	203.564	5.987		

*** = $P < 0.001$; NS = not significant

APPENDIX 27

Experiment 1

(a) Copper content of primary tiller grain per plant (µg)[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Cu added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	-*	3.23	-*	4.11	-*	1.88
	Rep 2	-*	4.06	-*	3.18	-*	2.68
	Rep 3	-	1.97	-	2.72	-	1.71
Triticale	Rep 1	-*	-*	-*	2.90	-*	1.79
	Rep 2	0.31	-	-*	2.02	-*	1.53
	Rep 3	0.18	1.98	-	2.54	-	1.29
Rye	Rep 1	0.48	4.22	0.61	3.37	0.23*	1.76
	Rep 2	1.02	3.26	1.01	3.17	-	2.38
	Rep 3	0.90	3.88	0.99	1.48	0.48	1.90

[1] = mean of 3 plants/pot

* = no grain

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	894.216			
Replication	2	2.242	1.121	0.427	NS
Genotype (G)	2	71.204	35.602	13.547	***
pH	2	29.784	14.892	5.666	**
Cu	1	576.371	476.371	219.310	***
G-pH	4	37.887	9.472	3.604	*
G-Cu	2	35.828	17.914	6.816	**
pH-Cu	2	11.132	5.566	2.118	NS
G-pH-Cu	4	40.413	10.103	3.844	*
Residual	34	89.356	2.628		

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; NS = not significant

APPENDIX 28

Experiment 1

(a) Copper content of secondary tiller grain per plant (µg)[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Cu added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	-*	1.99	-*	0.86	-*	-*
	Rep 2	-*	1.57	-*	1.95	-*	0.42
	Rep 3	-	3.00	-	2.10	-	0.74
Triticale	Rep 1	-*	-*	-*	-*	-*	0.57*
	Rep 2	-*	-	-*	-*	-*	-*
	Rep 3	-	1.36	-	-	-	-
Rye	Rep 1	0.08	1.32	0.48	2.29	-*	1.00
	Rep 2	0.51*	1.92	0.18*	0.78	-	0.82
	Rep 3	-	2.27	-	2.17	0.30	1.38

[1] = mean of 3 plants/pot

* = no grain

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	323.515			
Replication	2	8.309	4.154	3.018	NS
Genotype (G)	2	51.154	25.577	18.583	***
pH	2	19.795	9.897	7.191	**
Cu	1	121.260	121.260	88.101	***
G-pH	4	10.884	2.721	1.977	NS
G-Cu	2	37.373	18.686	13.576	***
pH-Cu	2	17.103	8.551	6.213	**
G-pH-Cu	4	10.841	2.710	1.969	NS
Residual	34	46.797	1.376		

** = $P < 0.01$; *** = $P < 0.001$; NS = not significant

APPENDIX 29

Experiment 1

(a) Weight of main culm grain per plant (g)[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Cu added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	0.00	2.40	0.00	2.24	0.00	2.39
	Rep 2	0.00	1.88	0.00	2.27	0.00	2.09
	Rep 3	0.00	1.93	0.00	2.08	0.00	2.10
Triticale	Rep 1	3.25	3.79	1.56	3.07	0.00	3.10
	Rep 2	2.77	2.84	2.47	3.31	0.00	3.14
	Rep 3	2.07	2.76	0.00	2.85	0.00	3.20
Rye	Rep 1	0.41	0.92	0.58	0.68	0.66	0.46
	Rep 2	0.80	1.20	0.98	0.56	0.32	0.94
	Rep 3	0.84	1.02	1.18	0.41	0.43	0.67

[1] = mean of 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	669.500			
Replication	2	5.299	2.649	2.083	NS
Genotype (G)	2	201.511	100.755	79.224	***
pH	2	22.044	11.022	8.667	**
Cu	1	215.400	215.400	169.369	***
G-pH	4	28.767	7.192	5.655	**
G-Cu	2	99.264	49.632	39.026	***
pH-Cu	2	17.569	8.785	6.907	**
G-pH-Cu	4	36.406	9.101	7.156	**
Residual	34	43.241	1.272		

** = $P < 0.01$; *** = $P < 0.001$; NS = not significant

APPENDIX 30

Experiment 1

(a) Weight of primary tiller grain per plant (g)[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Cu added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	0.00	1.00	0.00	1.44	0.00	1.14
	Rep 2	0.00	1.30	0.00	1.14	0.00	1.45
	Rep 3	0.00	0.73	0.00	0.84	0.00	1.13
Triticale	Rep 1	0.00	0.00	0.00	0.91	0.00	0.83
	Rep 2	0.53	0.00	0.07	0.59	0.00	0.81
	Rep 3	0.29	0.37	0.03	0.94	0.00	0.55
Rye	Rep 1	0.33	0.77	0.39	0.56	0.40	0.43
	Rep 2	0.44	0.64	0.93	0.65	0.11	0.75
	Rep 3	0.81	0.66	0.66	0.28	0.43	0.57

[1] = mean of 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	88.5259			
Replication	2	0.4406	0.2203	0.703	NS
Genotype (G)	2	5.4921	2.7461	8.759	***
pH	2	0.6132	0.3066	0.978	NS
Cu	1	37.6501	37.6501	120.094	***
G-pH	4	2.0152	0.5038	1.607	NS
G-Cu	2	22.5433	11.2717	35.954	***
pH-Cu	2	3.3631	1.6815	5.364	*
G-pH-Cu	4	5.7490	1.4373	4.584	**
Residual	34	10.6592	0.3135		

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; NS = not significant

APPENDIX 31

Experiment 1

(a) Weight of secondary tiller grain per plant (g)[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Cu added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	0.00	0.75	0.00	0.34	0.00	0.00
	Rep 2	0.00	0.54	0.00	0.88	0.00	0.28
	Rep 3	0.00	0.77	0.00	0.70	0.00	0.48
Triticale	Rep 1	0.00	0.00	0.00	0.00	0.00	0.36
	Rep 2	0.00	0.00	0.02	0.00	0.00	0.00
	Rep 3	0.00	0.30	0.00	0.00	0.00	0.00
Rye	Rep 1	0.09	0.20	0.39	0.41	0.03	0.22
	Rep 2	0.42	0.31	0.22	0.19	0.07	0.31
	Rep 3	0.00	0.36	0.01	0.31	0.25	0.52

[1] = mean of 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	27.3338			
Replication	2	0.2120	0.1060	0.565	NS
Genotype (G)	2	5.0050	2.5025	13.335	***
pH	2	0.4130	0.2065	1.100	NS
Cu	1	7.5488	7.5488	40.224	***
G-pH	4	1.2283	0.3071	1.636	NS
G-Cu	2	4.7609	2.3804	12.684	***
pH-Cu	2	0.2242	0.1121	0.597	NS
G-pH-Cu	4	1.5609	0.3902	2.079	NS
Residual	34	6.3807	0.1877		

*** = $P < 0.001$; NS = not significant

APPENDIX 32, Figure 1

Experiment 2

Effect of level of zinc supply on the weekly water use (ml plant^{-1}) throughout the season of wheat at pH 5.0. Data are the means of 9 plants (3 plants per pot for each of 3 replicates). Vertical bars indicate LSD values for $P < 0.05$.

APPENDIX 32, Figure 2

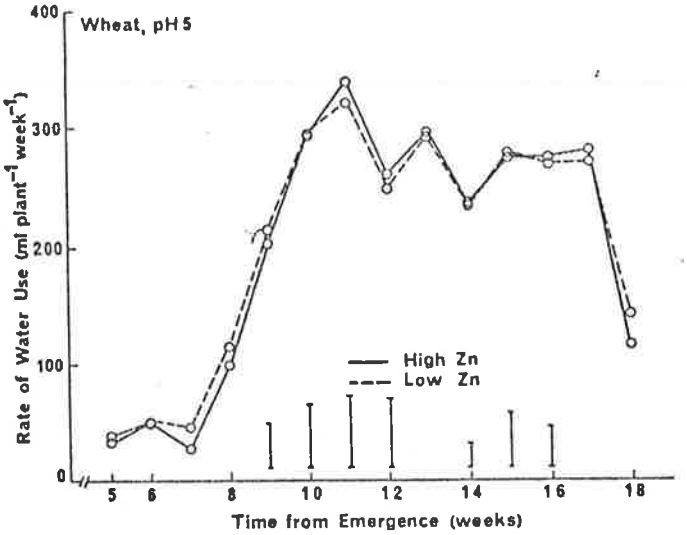
Experiment 2

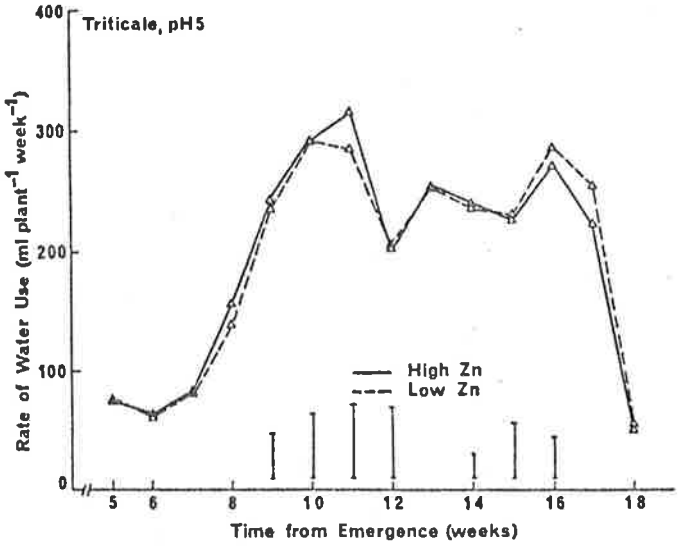
Effect of level of zinc supply on the weekly water use (ml plant^{-1}) throughout the season of triticale at pH 5.0. Data are the means of 9 plants (3 plants per pot for each of 3 replicates). Vertical bars indicate LSD values for $P < 0.05$.

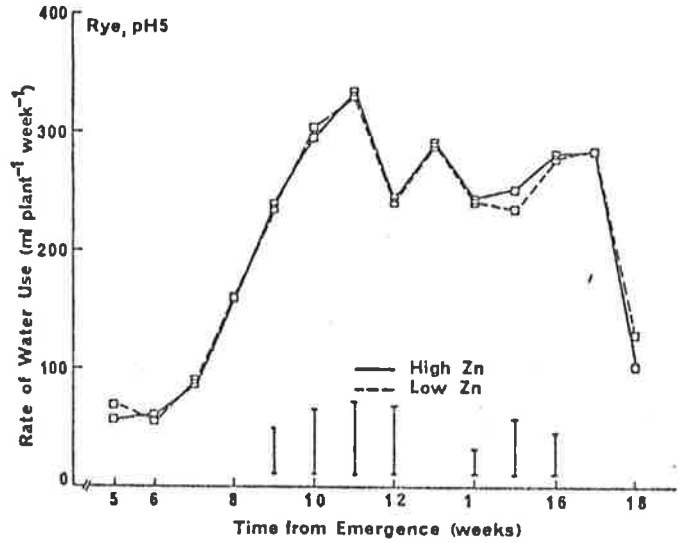
APPENDIX 32, Figure 3

Experiment 2

Effect of level of zinc supply on the weekly water use (ml plant^{-1}) throughout the season of rye at pH 5.0. Data are the means of 9 plants (3 plants per pot for each of 3 replicates). Vertical bars indicate LSD values for $P < 0.05$.


Wheat, pH 5
Rate of Water Use (ml plant^{-1} week^{-1})
400
300
200
100
0
High Zn
Low Zn
5 6 8 10 12 14 16 18
Time from Emergence (weeks)


Triticale, pH5
Rate of Water Use (ml plant^{-1} week^{-1})
400
300
200
100
0
High Zn
Low Zn
5 6 8 10 12 14 16 18
Time from Emergence (weeks)


Rye, pH5
Rate of Water Use (ml plant^{-1} week^{-1})
400
300
200
100
0
High Zn
Low Zn
5 6 8 10 12 1 16 18
Time from Emergence (weeks)

APPENDIX 32, Figure 4

Experiment 2

Effect of level of zinc supply on the weekly water use (ml plant^{-1}) throughout the season of wheat at pH 7.0. Data are the means of 9 plants (3 plants per pot for each of 3 replicates). Vertical bars indicate LSD values for $P < 0.05$.

APPENDIX 32, Figure 5

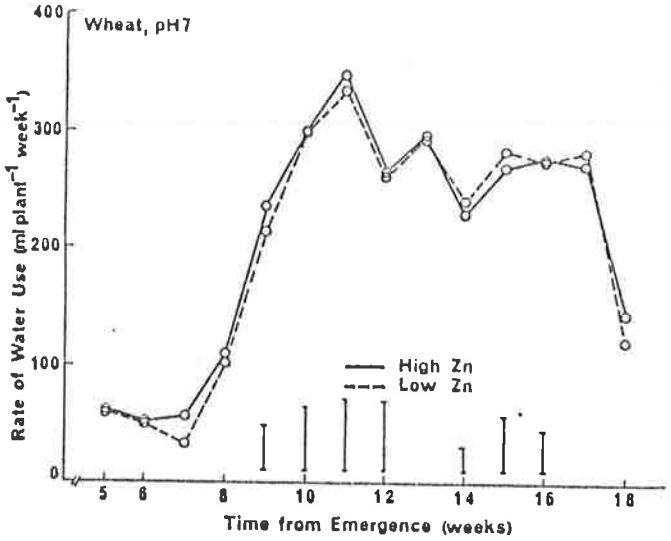
Experiment 2

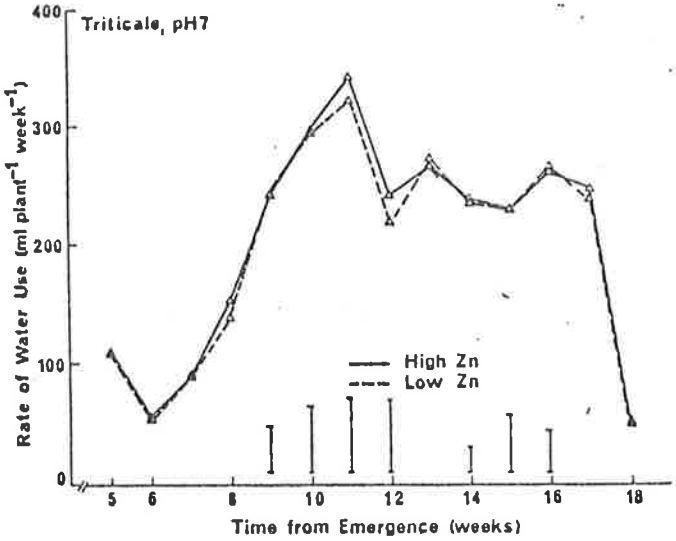
Effect of level of zinc supply on the weekly water use (ml plant^{-1}) throughout the season of triticale at pH 7.0. Data are the means of 9 plants (3 plants per pot for each of 3 replicates). Vertical bars indicate LSD values for $P < 0.05$.

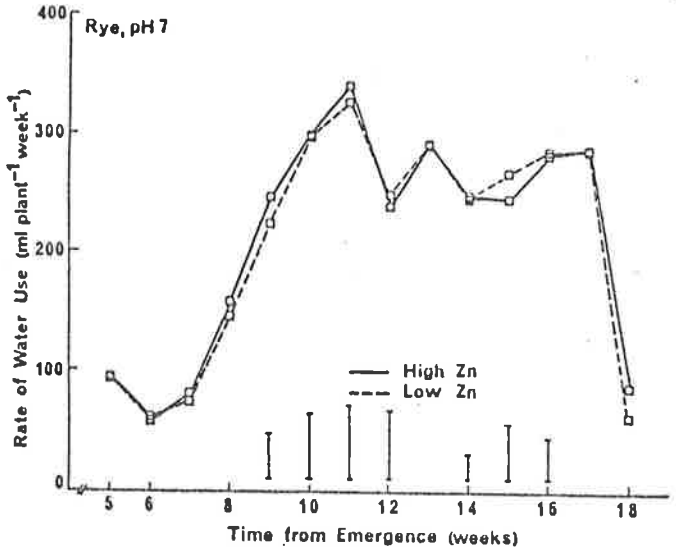
APPENDIX 32, Figure 6

Experiment 2

Effect of level of zinc supply on the weekly water use (ml plant^{-1}) throughout the season of rye at pH 7.0. Data are the means of 9 plants (3 plants per pot for each of 3 replicates). Vertical bars indicate LSD values for $P < 0.05$.


Wheat, pH7
Rate of Water Use (ml plant^{-1} week^{-1})
400
300
200
100
0
High Zn
Low Zn
5
6
8
10
12
14
16
18
Time from Emergence (weeks)


Triticale, pH7
Rate of Water Use (ml plant^{-1} week^{-1})
400
300
200
100
0
High Zn
Low Zn
5
6
8
10
12
14
16
18
Time from Emergence (weeks)


Rye, pH7
Rate of Water Use (ml plant^{-1} week^{-1})
400
300
200
100
0
High Zn
Low Zn
5
6
8
10
12
14
16
18
Time from Emergence (weeks)

APPENDIX 33

Experiment 2

(a) Total water use over the whole season (ml plant^{-1})[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Zn added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	2790	2828	2878	2912	938	2840
	Rep 2	2788	2705	2872	2983	2035	2572
	Rep 3	2837	2775	2805	2833	1130	2800
Triticale	Rep 1	2683	2638	2660	2865	1707	2697
	Rep 2	2673	2812	2829	2787	2602	1925
	Rep 3	2700	2627	2718	2725	2173	2585
Rye	Rep 1	2952	2852	2928	2903	2712	2942
	Rep 2	2923	2928	2880	2895	2722	2943
	Rep 3	2925	2985	2907	3058	2738	2885

[1] = mean of 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	81728720			
Replication	2	327501	163750	0.402	NS
Genotype (G)	2	21485418	10742709	26.372	***
pH	2	10904362	5452181	13.385	***
Zn	1	5613113	5613113	13.779	***
G-pH	4	8375966	2093991	5.140	**
G-Zn	2	9267479	4633739	11.375	***
pH-Zn	2	3776984	1888492	5.363	*
G-pH-Zn	4	8127849	2031962	4.988	**
Residual	34	13850049	407354		

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; NS = not significant

APPENDIX 34

Experiment 2

(a) Height of main culms to top of ears (cm)[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Zn added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	107.0	102.0	95.0	93.0	25.0	100.0
	Rep 2	99.0	105.0	104.0	102.0	52.0	93.0
	Rep 3	112.0	94.0	105.0	99.0	30.0	100.0
Triticale	Rep 1	105.0	105.0	97.0	94.0	70.0	104.0
	Rep 2	99.0	105.0	105.0	105.0	93.0	102.0
	Rep 3	102.0	103.0	107.0	101.0	94.0	106.0
Rye	Rep 1	139.0	137.0	130.0	147.0	123.0	125.0
	Rep 2	151.0	117.0	128.0	129.0	123.0	144.0
	Rep 3	142.0	138.0	149.0	131.0	143.0	144.0

[1] = mean of 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	35203.04			
Replication	2	290.81	145.41	2.195	NS
Genotype (G)	2	20799.59	10399.80	156.977	***
pH	2	2756.70	1378.35	20.805	***
Zn	1	711.41	711.41	10.738	**
G-pH	4	2384.07	596.02	8.996	***
G-Zn	2	863.37	431.69	6.516	**
pH-Zn	2	3348.93	1674.46	25.275	***
G-pH-Zn	4	1795.63	448.91	6.776	***
Residual	34	2252.52	66.25		

** = $P < 0.01$; *** = $P < 0.001$; NS = not significant

APPENDIX 35

Experiment 2

(a) Number of culms produced per plant[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Zn added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	3.0	2.3	3.3	3.3	8.7	2.0
	Rep 2	3.0	3.0	3.7	3.3	5.0	3.0
	Rep 3	4.0	3.0	3.7	3.3	8.0	4.0
Triticale	Rep 1	1.7	2.0	1.7	2.3	2.0	2.3
	Rep 2	2.0	2.3	1.7	2.0	1.3	2.0
	Rep 3	2.7	2.3	2.7	2.7	1.3	2.0
Rye	Rep 1	3.0	3.0	3.0	2.7	2.3	3.7
	Rep 2	3.0	3.0	3.0	3.3	3.3	3.3
	Rep 3	3.3	3.7	3.0	3.7	3.3	3.3

[1] = mean of 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	786.537			
Replication	2	22.481	11.241	3.645	*
Genotype (G)	2	271.259	135.630	43.980	***
pH	2	32.148	16.074	5.212	*
Zn	1	15.574	15.574	5.050	*
G-pH	4	100.963	25.241	8.185	***
G-Zn	2	104.148	52.074	16.886	***
pH-Zn	2	32.148	16.074	5.212	*
G-pH-Zn	4	102.963	25.741	8.347	***
Residual	34	104.852	3.084		

* = $P < 0.05$; *** = $P < 0.001$

APPENDIX 36

Experiment 2

(a) Number of ears produced per plant[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Zn added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	2.7	2.0	3.3	3.0	0.7	2.0
	Rep 2	2.7	1.7	2.0	2.3	2.7	2.7
	Rep 3	2.0	3.0	3.0	2.7	0.3	2.3
Triticale	Rep 1	1.7	1.7	1.7	2.0	1.3	1.7
	Rep 2	2.0	2.0	1.7	1.3	1.3	1.7
	Rep 3	2.0	1.3	2.0	1.7	1.3	1.7
Rye	Rep 1	2.7	2.3	2.7	2.0	2.0	3.0
	Rep 2	2.7	2.7	2.3	2.3	2.3	2.0
	Rep 3	3.0	2.7	3.0	3.0	2.7	2.7

[1] = mean of 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	189.500			
Replication	2	1.333	0.667	0.318	NS
Genotype (G)	2	67.000	33.500	15.967	***
pH	2	16.778	8.389	3.998	*
Zn	1	0.463	0.463	0.221	NS
G-pH	4	11.222	2.806	1.337	NS
G-Zn	2	2.481	1.241	0.591	NS
pH-Zn	2	14.926	7.463	3.557	*
G-pH-Zn	4	3.963	0.991	0.472	NS
Residual	34	71.333	2.098		

* = $P < 0.05$ *** = $P < 0.001$; NS = not significant

APPENDIX 37

Experiment 2

(a) Number of days to ear emergence of main culms[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Zn added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	83	83	90	85	100	86
	Rep 2	87	85	85	84	105	91
	Rep 3	83	88	90	86	95	88
Triticale	Rep 1	75	74	74	77	80	77
	Rep 2	74	74	75	75	78	79
	Rep 3	75	74	75	74	77	78
Rye	Rep 1	83	77	81	82	86	76
	Rep 2	75	79	84	80	82	84
	Rep 3	79	83	78	78	87	85

[1] = mean of 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	2366.148			
Replication	2	1.370	0.685	0.091	NS
Genotype (G)	2	1472.259	736.130	98.037	***
pH	2	326.926	163.463	21.770	***
Zn	1	54.000	54.000	7.192	*
G-pH	4	67.630	16.907	2.252	NS
G-Zn	2	50.778	25.389	3.381	*
pH-Zn	2	70.778	35.389	4.713	*
G-pH-Zn	4	67.111	16.778	2.234	NS
Residual	34	255.296	7.509		

* = $P < 0.05$; *** = $P < 0.001$; NS = not significant

APPENDIX 38

Experiment 2

(a) Number of days to anthesis of main culms[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Zn added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	93	93	98	94	106	99
	Rep 2	96	96	93	94	113	100
	Rep 3	98	99	98	96	100	99
Triticale	Rep 1	86	85	86	89	91	89
	Rep 2	85	85	87	88	92	91
	Rep 3	88	85	88	86	89	88
Rye	Rep 1	91	94	95	94	97	94
	Rep 2	91	94	98	91	90	99
	Rep 3	94	97	92	93	98	92

[1] = mean of 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	1620.833			
Replication	2	2.333	1.167	0.157	NS
Genotype (G)	2	990.111	495.056	66.705	***
pH	2	194.778	97.389	13.122	***
Zn	1	15.574	15.574	2.098	NS
G-pH	4	75.778	18.944	2.553	NS
G-Zn	2	21.370	10.685	1.440	NS
pH-Zn	2	26.704	13.352	1.799	NS
G-pH-Zn	4	41.852	10.463	1.410	NS
Residual	34	252.333	7.422		

*** = $P < 0.001$; NS = not significant

APPENDIX 39

Experiment 2

(a) Number of days to maturity of main culms[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Zn added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	130	130	131	129	-[+]	131
	Rep 2	131	129	130	130	-[+]	132
	Rep 3	130	131	131	130	-[+]	129
Triticale	Rep 1	122	120	120	122	129	122
	Rep 2	120	121	121	120	129	123
	Rep 3	123	121	122	121	122	120
Rye	Rep 1	133	130	130	134	137	124
	Rep 2	124	133	132	130	131	131
	Rep 3	127	130	127	124	133	130

[1] = mean of 3 plants/pot

[+] = not reached by harvest date

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	2170.593			
Replication	2	16.926	8.463	1.455	NS
Genotype (G)	2	1138.815	569.407	97.905	***
pH	2	228.259	114.130	19.624	***
Zn	1	112.667	112.667	19.372	***
G-pH	4	107.852	26.963	4.636	**
G-Zn	2	59.111	29.556	5.082	*
pH-Zn	2	236.333	118.167	20.318	***
G-pH-Zn	4	72.889	18.222	3.133	*
Residual	34	197.741	5.816		

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; NS = not significant

APPENDIX 40. Dry weight of straw (stem, leaf and chaff), grain and total dry weight at maturity.

Data are means of 3 replicates.

Treatment	Zn added per pot (mg)	Soil pH 5.0	Soil pH 7.0	Soil pH 8.4	Soil pH 5.0	Soil pH 7.0	Soil pH 8.4	Soil pH 5.0	Soil pH 7.0	Soil pH 8.4
		A. Straw (g plant^{-1})			B. Grain (g plant^{-1})			C. Total (g plant^{-1})		
Genotype										
Wheat	0	6.15	6.05	2.37	3.63	3.32	0.08	9.78	9.37	2.45
	4	6.02	6.08	6.02	3.67	3.59	3.38	9.69	9.67	9.40
Triticale	0	5.63	5.69	3.56	3.76	3.57	1.56	9.39	9.26	5.12
	4	5.68	5.88	5.39	3.81	3.61	3.48	9.49	9.49	8.87
Rye	0	6.70	6.49	5.31	1.67	1.99	1.77	8.37	8.48	7.08
	4	6.26	6.10	6.17	2.03	1.99	1.88	8.29	8.09	8.05
LSD (P = 0.05) for the genotype-soil pH-Zn interaction:			0.57			0.48			0.92	

APPENDIX 41

Experiment 2

(a) Total dry matter production per plant (g)[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Zn added per pot	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	9.42	9.66	8.84	9.15	2.04	9.38
	Rep 2	9.73	9.53	9.63	9.94	3.31	8.98
	Rep 3	10.19	9.88	9.62	9.91	2.00	9.86
Triticale	Rep 1	9.20	9.24	9.03	9.27	3.25	8.60
	Rep 2	9.46	9.83	9.40	9.38	5.49	8.80
	Rep 3	9.49	9.39	9.35	9.80	6.63	9.20
Rye	Rep 1	8.01	8.61	8.22	7.62	6.29	8.04
	Rep 2	8.91	8.00	7.55	7.79	7.71	7.68
	Rep 3	8.18	8.25	9.65	8.85	7.23	8.44

[1] = mean of 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	1734.853			
Replication	2	36.691	18.346	6.727	**
Genotype (G)	2	24.365	12.183	4.467	*
pH	2	563.117	281.559	103.236	***
Zn	1	207.094	207.094	75.933	***
G-pH	4	158.752	39.688	14.552	***
G-Zn	2	99.738	49.869	18.285	***
pH-Zn	2	406.563	203.281	74.535	***
G-pH-Zn	4	145.803	36.451	13.365	***
Residual	34	92.729	2.727		

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$

APPENDIX 42

Experiment 2

(a) Dry weight of straw+ per plant (g)[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Zn added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	6.13	5.89	5.94	5.71	2.04	5.90
	Rep 2	6.07	5.91	5.88	6.21	3.09	5.75
	Rep 3	6.24	6.26	6.33	6.32	2.00	6.42
Triticale	Rep 1	5.56	5.50	5.50	5.87	2.48	5.28
	Rep 2	5.56	5.94	5.69	5.80	3.69	5.28
	Rep 3	5.75	5.60	5.87	5.94	4.53	5.64
Rye	Rep 1	6.57	6.39	6.08	5.83	4.75	6.07
	Rep 2	6.72	6.26	6.10	5.83	5.47	5.91
	Rep 3	6.79	6.13	7.30	6.63	5.68	6.53

1 = mean of 3 plants/pot

+ = weight of (stem, leaf and chaff)

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	561.711			
Replication	2	18.117	9.058	8.537	***
Genotype (G)	2	69.375	34.687	32.691	***
pH	2	169.504	84.752	79.875	***
Zn	1	48.091	48.091	45.324	***
G-pH	4	28.327	7.082	6.674	***
G-Zn	2	28.056	14.028	13.221	***
pH-Zn	2	134.333	67.167	63.301	***
G-pH-Zn	4	29.832	7.458	7.029	***
Residual	34	36.076	1.061		

*** = $P < 0.001$

APPENDIX 43

Experiment 2

(a) Grain yield per plant (g)[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Zn added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	3.29	3.77	2.90	3.44	0.00	3.48
	Rep 2	3.66	3.62	3.75	3.73	0.23	3.23
	Rep 3	3.95	3.61	3.30	3.59	0.00	3.44
Triticale	Rep 1	3.64	3.74	3.53	3.40	0.78	3.33
	Rep 2	3.90	3.90	3.71	3.59	1.80	3.53
	Rep 3	3.74	3.79	3.48	3.86	2.09	3.57
Rye	Rep 1	1.44	2.22	2.15	1.79	1.54	1.97
	Rep 2	2.19	1.74	1.46	1.96	2.24	1.77
	Rep 3	1.39	2.13	2.35	2.22	1.55	1.91

[1] = mean of 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	575.3753			
Replication	2	4.2450	2.1225	2.853	NS
Genotype (G)	2	173.7874	86.8937	116.793	***
pH	2	114.8103	57.4052	77.158	***
Zn	1	55.6321	55.6321	74.775	***
G-pH	4	57.0812	14.2703	19.181	***
G-Zn	2	22.1254	11.0627	14.869	***
pH-Zn	2	73.7405	36.3702	49.557	***
G-pH-Zn	4	48.6574	12.1643	16.350	***
Residual	34	25.2959	0.7440		

*** = $P < 0.001$; NS = not significant

APPENDIX 44

Experiment 2

(a) Number of grains per plant[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Zn added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	102.7	110.7	102.3	105.3	0.0	114.0
	Rep 2	113.7	104.0	105.3	113.7	19.7	113.0
	Rep 3	115.3	102.7	104.0	107.0	0.0	117.3
Triticale	Rep 1	94.3	96.3	85.0	94.7	25.0	99.0
	Rep 2	100.0	96.0	88.0	83.3	48.0	96.7
	Rep 3	97.7	85.7	90.7	95.7	50.7	97.0
Rye	Rep 1	100.7	93.3	110.7	85.3	72.0	119.3
	Rep 2	147.0	89.0	105.0	88.0	112.0	72.3
	Rep 3	78.7	110.0	135.7	129.3	73.3	117.3

[1] = mean of 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	411361			
Replication	2	2785	1392	0.691	NS
Genotype (G)	2	25172	12586	6.249	**
pH	2	78967	39483	19.604	***
Zn	1	35063	35063	17.409	***
G-pH	4	24654	6163	3.060	*
G-Zn	2	31735	15867	7.878	**
pH-Zn	2	115870	57935	28.765	***
G-pH-Zn	4	28638	7159	3.555	*
Residual	34	68479	2014		

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; NS = not significant

APPENDIX 45

Experiment 2

(a) Number of spikelets per ear[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Zn added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	18.63	19.33	18.80	19.00	15.50	20.17
	Rep 2	18.88	20.80	19.67	19.43	16.00	20.13
	Rep 3	19.33	17.56	18.78	18.88	21.00	19.71
Triticale	Rep 1	21.40	21.20	19.80	21.17	15.25	21.60
	Rep 2	21.50	19.83	21.20	22.25	18.25	22.20
	Rep 3	21.33	20.75	21.00	21.00	20.00	22.60
Rye	Rep 1	37.63	36.00	35.00	42.83	35.17	32.44
	Rep 2	35.63	38.38	37.71	35.86	35.71	36.00
	Rep 3	32.78	38.00	37.22	37.33	34.25	38.25

[1] = mean of 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	3521.22			
Replication	2	2.80	1.40	0.467	NS
Genotype (G)	2	3342.60	1671.30	558.615	***
pH	2	14.72	7.36	2.461	NS
Zn	1	23.06	23.06	7.706	*
G-pH	4	6.86	1.71	0.573	NS
G-Zn	2	0.97	0.48	0.161	NS
pH-Zn	2	9.09	4.54	1.519	NS
G-pH-Zn	4	19.41	4.85	1.622	NS
Residual	34	101.72	2.99		

* = $P < 0.05$; *** = $P < 0.001$; NS = not significant

APPENDIX 46

Experiment 2

(a) Number of grains per ear[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Zn added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	38.50	55.33	30.70	35.11	0.00	57.00
	Rep 2	42.63	62.40	52.67	48.71	7.38	42.38
	Rep 3	57.67	34.22	34.67	40.13	0.00	50.29
Triticale	Rep 1	56.60	57.80	51.00	47.33	18.75	59.40
	Rep 2	50.00	48.00	52.80	62.50	36.00	58.00
	Rep 3	48.83	64.25	45.33	57.40	38.00	58.20
Rye	Rep 1	37.75	40.00	41.50	42.67	36.00	39.78
	Rep 2	55.13	33.38	45.00	37.71	48.00	36.17
	Rep 3	26.22	41.25	45.22	43.11	27.50	44.00

[1] = mean of 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	10569.79			
Replication	2	175.07	87.54	1.327	NS
Genotype (G)	2	1584.43	792.22	12.009	***
pH	2	1170.11	585.06	8.869	***
Zn	1	1376.89	1376.89	20.871	***
G-pH	4	727.54	181.89	2.757	*
G-Zn	2	812.72	406.36	6.160	***
pH-Zn	2	1698.24	849.12	12.871	***
G-pH-Zn	4	781.81	195.45	2.963	*
Residual	34	2242.97	65.97		

* = $P < 0.05$; *** = $P < 0.001$; NS = not significant

APPENDIX 47

Experiment 2

(a) Weight per grain (mg)[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Zn added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	32.0	34.1	28.4	32.7	0.0	30.5
	Rep 2	32.2	34.8	35.6	32.8	11.5	28.6
	Rep 3	34.2	35.2	31.7	33.6	0.0	29.3
Triticale	Rep 1	38.6	38.8	41.5	35.9	31.1	33.6
	Rep 2	39.0	40.6	42.2	43.0	37.5	36.6
	Rep 3	38.3	44.2	38.4	40.3	41.3	36.8
Rye	Rep 1	14.3	23.8	19.4	21.0	21.4	16.5
	Rep 2	14.9	19.6	13.9	22.3	20.0	24.5
	Rep 3	17.6	19.3	17.3	17.2	21.1	16.2

[1] = mean of 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F. (MV)	S.S.	M.S.	v-ratio	
Total	53	5.12			
Replication	2	0.02	0.01	1.484	NS
Genotype (G)	2	3.55	1.77	262.213	***
pH	2	0.31	0.16	22.957	***
Zn	1	0.14	0.14	20.658	***
G-pH	4	0.43	0.11	15.930	***
G-Zn	2	0.11	0.06	8.444	**
pH-Zn	2	0.04	0.02	2.809	NS
G-pH-Zn	4	0.30	0.08	11.190	***
Residual	32 (2)	0.22	0.01		

** = $P < 0.01$; *** = $P < 0.001$; NS = not significant

APPENDIX 48

Experiment 2

(a) Dry weight of roots per plant (g)[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Zn added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	1.39	1.41	1.42	0.91	1.47	1.75
	Rep 2	1.72	3.36	3.14	3.76	1.85	1.77
	Rep 3	1.46	1.09	1.96	1.34	1.10	2.13
Triticale	Rep 1	2.44	1.76	1.63	1.81	1.25	1.98
	Rep 2	2.48	5.31	1.59	2.36	2.71	2.58
	Rep 3	2.41	2.31	2.82	2.01	1.92	2.03
Rye	Rep 1	6.07	2.46	2.40	2.90	5.03	7.82
	Rep 2	4.56	11.71	5.09	6.20	5.01	7.11
	Rep 3	4.96	3.68	3.68	4.44	4.26	6.16

[1] = mean of 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	2031.31			
Replication	2	203.61	101.80	6.479	*
Genotype (G)	2	1074.73	537.37	34.197	***
pH	2	33.58	16.79	1.068	NS
Zn	1	44.55	44.55	2.835	NS
G-pH	4	87.58	21.89	1.393	NS
G-Zn	2	27.02	13.51	0.860	NS
pH-Zn	2	11.33	5.67	0.361	NS
G-pH-Zn	4	14.65	3.66	0.233	NS
Residual	34	534.26	15.71		

* = $P < 0.05$; *** = $P < 0.001$; NS = not significant

APPENDIX 49

Experiment 2

(a) Concentration of zinc in the straw ($\mu g\ g^{-1}$)[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Zn added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	12.54	35.19	8.45	23.68	10.31	7.71
	Rep 2	15.51	36.67	12.91	25.16	4.74	13.65
	Rep 3	9.19	31.85	6.60	22.93	8.82	6.97
Triticale	Rep 1	16.62	66.01	22.56	23.68	9.94	17.73
	Rep 2	24.42	62.29	16.62	40.39	14.02	17.36
	Rep 3	11.79	52.64	9.94	28.13	12.54	9.94
Rye	Rep 1	16.62	52.64	9.19	20.33	12.91	11.42
	Rep 2	19.22	62.29	17.73	37.42	18.85	24.42
	Rep 3	14.76	53.75	9.94	42.24	8.45	14.02

[1] = bulked sample of straw for 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	13175.99			
Replication	2	367.94	183.97	8.820	***
Genotype (G)	2	933.82	466.91	22.385	***
pH	2	3842.48	1921.24	92.110	***
Zn	1	4361.77	4361.77	209.117	***
G-pH	4	202.62	50.66	2.429	NS
G-Zn	2	187.79	93.90	4.502	*
pH-Zn	2	2347.95	1173.97	56.284	***
G-pH-Zn	4	222.44	55.61	2.666	*
Residual	34	709.17	20.86		

* = $P < 0.05$; *** = $P < 0.001$; NS = not significant

APPENDIX 50

Experiment 2

(a) Concentration of zinc in main culm grain ($\mu g\ g^{-1}$)[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Zn added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	18.78	42.30	9.21	29.08	-*	11.66
	Rep 2	23.30	40.56	12.69	25.42	13.27	7.60
	Rep 3	18.28	34.76	7.96	29.32	-*	10.01
Triticale	Rep 1	29.33	55.11	13.29	48.07	9.94	15.89
	Rep 2	23.53	49.51	16.15	48.17	11.57	11.19
	Rep 3	18.36	51.21	9.54	41.56	8.35	10.41
Rye	Rep 1	34.14	46.25	15.62	39.72	17.76	23.06
	Rep 2	23.47	54.36	25.82	37.48	8.78	23.15
	Rep 3	33.71	50.25	11.07	45.16	8.37	32.50

[1] = bulked sample of main culm grain for 3 plants/pot

* = no grain

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	12597.49			
Replication	2	50.43	25.21	1.299	NS
Genotype (G)	2	1127.83	563.92	29.058	***
pH	2	5019.98	2509.99	129.337	***
Zn	1	4473.01	4473.01	230.489	***
G-pH	4	110.87	27.72	1.428	NS
G-Zn	2	120.52	60.26	3.105	NS
pH-Zn	2	786.81	393.41	20.272	***
G-pH-Zn	4	248.20	62.05	3.197	*
Residual	34	659.83	19.41		

* = $P < 0.05$; *** = $P < 0.001$; NS = not significant

APPENDIX 51

Experiment 2

(a) Concentration of zinc in primary tiller grain ($\mu g\ g^{-1}$)[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Zn added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	18.78	34.63	10.33	32.35	-*	11.21
	Rep 2	21.33	44.43	12.48	27.93	9.69	8.01
	Rep 3	15.20	33.37	7.16	27.10	-*	8.78
Triticale	Rep 1	27.44	38.29	12.01	37.25	10.73	13.91
	Rep 2	24.29	50.63	12.38	36.19	11.62	11.54
	Rep 3	17.67	47.08	6.86	33.63	10.35	8.79
Rye	Rep 1	31.87	46.53	15.45	33.54	20.67	23.34
	Rep 2	21.54	47.54	18.67	39.34	8.81	22.10
	Rep 3	29.92	47.68	10.04	42.42	8.42	26.95

1 = bulked sample of primary tiller grain for 3 plants/pot

* = no grain

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	10022.17			
Replication	2	67.61	33.81	2.118	NS
Genotype (G)	2	822.41	411.21	25.762	***
pH	2	4079.47	2039.74	127.791	***
Zn	1	3595.79	3595.79	225.278	***
G-pH	4	52.77	13.19	0.827	NS
G-Zn	2	27.87	13.94	0.873	NS
pH-Zn	2	730.50	365.25	22.883	***
G-pH-Zn	4	103.05	25.76	1.614	NS
Residual	34	542.69	15.96		

*** = $P < 0.001$; NS = not significant

APPENDIX 52

Experiment 2

(a) Concentration of zinc in secondary tiller grain ($\mu g\ g^{-1}$)[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Zn added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	19.15	37.84	10.41	30.78	-*	10.37
	Rep 2	20.37	42.68	-*	34.12	-*	7.95
	Rep 3	-*	41.94	8.41	27.64	-*	8.87
Triticale	Rep 1	-*	-*	-*	29.32	-*	-*
	Rep 2	-*	-*	-*	-*	-*	-*
	Rep 3	-*	-*	8.46	-*	-*	-*
Rye	Rep 1	36.52	45.40	15.51	29.35	17.72	26.28
	Rep 2	23.27	51.41	24.95	40.54	8.77	-*
	Rep 3	23.44	48.96	11.55	43.90	8.61	23.14

[1] = bulked sample of secondary tiller grain for 3 plants/pot

* = no grain

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	14294.99			
Replication	2	108.66	54.33	1.098	NS
Genotype (G)	2	5480.76	2740.38	55.366	***
pH	2	2316.23	1158.11	23.398	***
Zn	1	2183.13	2183.13	44.107	***
G-pH	4	1136.28	284.07	5.739	**
G-Zn	2	786.70	393.35	7.947	**
pH-Zn	2	446.64	223.32	4.512	*
G-pH-Zn	4	153.72	38.43	0.776	NS
Residual	34	1682.86	49.50		

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; NS = not significant

APPENDIX 53

Experiment 2

(a) Concentration of manganese in the straw ($\mu g\ g^{-1}$)[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Zn added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	164.59	198.64	83.76	72.29	37.88	9.20
	Rep 2	153.84	168.17	73.00	68.70	31.43	9.92
	Rep 3	155.45	143.98	80.17	65.84	54.37	7.77
Triticale	Rep 1	209.39	214.77	86.63	92.36	29.99	9.92
	Rep 2	141.29	169.97	108.13	92.36	14.94	7.77
	Rep 3	155.45	207.60	122.47	103.83	18.52	11.35
Rye	Rep 1	193.26	169.97	80.89	85.19	24.26	20.67
	Rep 2	95.94	243.45	70.85	77.31	13.50	22.11
	Rep 3	207.60	247.03	73.72	111.72	26.41	18.52

[1] = bulked sample of straw for 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	263503.4			
Replication	2	2068.2	1034.1	2.138	NS
Genotype (G)	2	1647.9	824.0	1.704	NS
pH	2	231512.3	115756.2	239.359	***
Zn	1	377.0	377.0	0.780	NS
G-pH	4	3458.5	864.6	1.788	NS
G-Zn	2	2541.8	1270.9	2.628	NS
pH-Zn	2	5195.9	2598.0	5.372	*
G-pH-Zn	4	259.1	64.8	0.134	NS
Residual	34	16442.7	438.6		

* = $P < 0.05$; *** = $P < 0.001$; NS = not significant

APPENDIX 54

Experiment 2

(a) Concentration of manganese in main culm grain ($\mu g\ g^{-1}$)[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Zn added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	72.47	96.85	49.44	48.62	-*	13.12
	Rep 2	77.38	75.94	42.40	42.55	34.30	10.81
	Rep 3	83.18	71.00	49.09	44.52	-*	11.57
Triticale	Rep 1	75.64	71.30	45.29	52.51	43.20	18.13
	Rep 2	53.10	60.39	51.68	54.54	30.06	14.53
	Rep 3	61.27	65.71	52.79	53.49	24.74	9.00
Rye	Rep 1	88.65	85.05	51.03	58.69	26.10	27.06
	Rep 2	54.44	86.88	60.30	46.45	22.63	24.19
	Rep 3	76.45	87.31	51.04	53.27	31.44	27.73

[1] = bulked sample of main culm grain for 3 plants/pot

* = no grain

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	31774.53			
Replication	2	212.07	106.04	1.489	NS
Genotype (G)	2	616.21	308.10	4.328	*
pH	2	26473.48	13236.74	185.935	***
Zn	1	0.18	0.18	0.002	NS
G-pH	4	1205.15	301.29	4.232	**
G-Zn	2	149.59	74.79	1.051	NS
pH-Zn	2	362.17	181.08	2.544	NS
G-pH-Zn	4	335.21	83.80	1.177	NS
Residual	34	2420.46	71.19		

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; NS = not significant

APPENDIX 55

Experiment 2

(a) Concentration of manganese in primary tiller grain ($\mu g\ g^{-1}$)[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Zn added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	101.43	80.44	57.93	56.22	-*	14.55
	Rep 2	84.26	97.91	46.01	50.90	21.21	10.82
	Rep 3	69.55	75.83	44.63	44.92	-*	10.79
Triticale	Rep 1	64.07	64.75	40.56	45.17	23.43	12.98
	Rep 2	47.79	59.82	50.12	41.43	18.28	12.99
	Rep 3	63.14	58.37	54.18	56.40	35.11	14.50
Rye	Rep 1	78.05	84.11	49.73	53.19	34.43	28.39
	Rep 2	60.52	80.83	51.39	45.56	23.45	27.34
	Rep 3	89.52	81.81	57.77	53.57	34.59	25.50

[1] = bulked sample of primary tiller grain for 3 plants/pot

* = no grain

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	33591.94			
Replication	2	99.86	49.93	0.733	NS
Genotype (G)	2	1075.63	537.82	7.900	**
pH	2	27546.22	13773.11	202.301	***
Zn	1	2.69	2.69	0.040	NS
G-pH	4	2198.41	549.60	8.073	***
G-Zn	2	64.99	32.50	0.477	NS
pH-Zn	2	94.10	47.05	0.691	NS
G-pH-Zn	4	195.25	48.81	0.717	NS
Residual	34	2314.79	68.09		

** = $P < 0.01$; *** = $P < 0.001$; NS = not significant

APPENDIX 56

Experiment 2

(a) Concentration of manganese in secondary tiller grain (μg g^{-1})[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Zn added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	92.40	80.51	62.81	54.77	-*	10.79
	Rep 2	79.90	82.86	-*	52.03	-*	9.27
	Rep 3	-*	80.74	61.29	44.51	-*	10.16
Triticale	Rep 1	-*	-*	-*	47.83	-*	-*
	Rep 2	-*	-*	-*	-*	-*	-*
	Rep 3	-*	-*	60.15	-*	-*	-*
Rye	Rep 1	88.05	90.16	49.95	57.03	26.50	27.10
	Rep 2	56.41	81.32	53.57	49.75	21.12	-*
	Rep 3	73.82	84.18	52.89	59.34	38.42	21.96

[1] = bulked sample of secondary tiller grain for 3 plants/pot

* = no grain

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	58386.8			
Replication	2	1129.7	564.9	1.651	NS
Genotype (G)	2	20356.9	10178.5	29.746	***
pH	2	15776.5	7888.3	23.053	***
Zn	1	298.8	298.8	0.873	NS
G-pH	4	7852.9	1963.2	5.737	**
G-Zn	2	643.2	321.6	0.940	NS
pH-Zn	2	399.7	199.8	0.584	NS
G-pH-Zn	4	295.1	73.8	0.216	NS
Residual	34	11633.9	342.2		

** = $P < 0.01$; *** = $P < 0.001$; NS = not significant

APPENDIX 57

Experiment 2

(a) Weight of main culm grain per plant (g)[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Zn added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	1.70	2.32	1.59	1.89	0.00	2.11
	Rep 2	1.97	2.33	2.25	2.20	0.10	1.92
	Rep 3	2.45	1.86	1.84	1.90	0.00	1.90
Triticale	Rep 1	2.46	2.65	2.57	2.02	0.61	2.37
	Rep 2	2.27	2.68	2.68	3.03	1.56	2.43
	Rep 3	2.51	2.87	2.43	2.94	1.94	2.29
Rye	Rep 1	0.61	1.14	1.00	1.11	1.07	0.88
	Rep 2	1.05	0.69	0.71	1.05	1.09	1.23
	Rep 3	0.81	1.01	0.91	0.88	0.77	0.84

[1] = mean of 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	312.1336			
Replication	2	2.5779	1.2890	1.896	NS
Genotype (G)	2	162.0724	81.0362	119.218	***
pH	2	33.9472	16.9736	24.971	***
Zn	1	22.3880	22.3880	32.936	***
G-pH	4	23.6923	5.9231	8.714	***
G-Zn	2	8.2651	4.1325	6.080	**
pH-Zn	2	18.6730	9.3365	13.736	***
G-pH-Zn	4	17.4067	4.3517	6.402	***
Residual	34	23.1109	0.6797		

** = $P < 0.01$; *** = $P < 0.001$; NS = not significant

APPENDIX 58

Experiment 2

(a) Weight of primary tiller grain per plant (g)[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Zn added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	0.98	1.18	0.77	0.77	0.00	0.89
	Rep 2	1.04	0.56	1.50	1.25	0.13	0.93
	Rep 3	1.50	0.86	0.88	0.79	0.00	1.06
Triticale	Rep 1	1.18	1.09	0.96	0.89	0.17	0.95
	Rep 2	1.64	1.22	1.03	0.56	0.24	1.10
	Rep 3	1.22	0.91	0.69	0.92	0.16	1.28
Rye	Rep 1	0.59	0.54	0.72	0.49	0.26	0.70
	Rep 2	0.68	0.68	0.37	0.65	0.82	0.54
	Rep 3	0.44	0.65	0.75	0.69	0.55	0.67

[1] = mean of 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	65.5471			
Replication	2	0.8132	0.4066	1.070	NS
Genotype (G)	2	8.2049	4.1024	10.798	***
pH	2	10.8850	5.4425	14.325	***
Zn	1	2.0612	2.0612	5.425	*
G-pH	4	7.0403	1.7601	4.633	**
G-Zn	2	0.4386	0.2193	0.577	NS
pH-Zn	2	16.3156	8.1578	21.471	***
G-pH-Zn	4	6.8705	1.7176	4.521	**
Residual	34	12.9179	0.3799		

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; NS = not significant

APPENDIX 59

Experiment 2

(a) Weight of secondary tiller grain per plant (g)[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Zn added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	0.61	0.28	0.54	0.79	0.00	0.48
	Rep 2	0.64	0.72	0.00	0.28	0.00	0.38
	Rep 3	0.00	0.90	0.57	0.90	0.00	0.47
Triticale	Rep 1	0.00	0.00	0.00	0.49	0.00	0.00
	Rep 2	0.00	0.00	0.00	0.00	0.00	0.00
	Rep 3	0.00	0.00	0.36	0.00	0.00	0.00
Rye	Rep 1	0.25	0.53	0.42	0.20	0.20	0.39
	Rep 2	0.45	0.37	0.38	0.26	0.33	0.00
	Rep 3	0.13	0.47	0.69	0.66	0.23	0.40

[1] = mean of 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	36.1888			
Replication	2	1.0291	0.5145	1.399	NS
Genotype (G)	2	12.8193	6.4097	17.423	***
pH	2	3.4873	1.7436	4.740	*
Zn	1	1.6678	1.6678	4.533	*
G-pH	4	1.2741	0.3185	0.866	NS
G-Zn	2	2.3833	1.1917	3.239	NS
pH-Zn	2	0.1551	0.0775	0.211	NS
G-pH-Zn	4	0.8648	0.2162	0.588	NS
Residual	34	12.5081	0.3679		

* = $P < 0.05$; *** = $P < 0.001$; NS = not significant

APPENDIX 60

Experiment 2

(a) Zinc content of straw per plant (µg)[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Zn added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	76.87	207.27	50.16	135.21	21.00	45.49
	Rep 2	94.15	216.72	75.95	156.33	14.63	78.44
	Rep 3	57.31	199.49	41.76	144.84	17.67	44.75
Triticale	Rep 1	92.46	363.28	124.00	139.08	24.62	93.56
	Rep 2	135.78	369.79	94.51	234.13	51.73	91.60
	Rep 3	67.83	294.78	58.31	167.19	56.85	56.03
Rye	Rep 1	109.14	336.19	55.84	118.59	61.32	69.28
	Rep 2	129.16	389.94	108.09	218.03	103.11	144.32
	Rep 3	100.27	329.31	72.56	279.91	48.02	91.55

[1] = mean of 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	4525253			
Replication	2	112339	56170	8.116	**
Genotype (G)	2	324030	162015	23.408	***
pH	2	1509202	754601	109.027	***
Zn	1	1572834	1572834	227.247	***
G-pH	4	56697	14174	2.048	NS
G-Zn	2	46864	23432	3.386	*
pH-Zn	2	592883	296442	42.831	***
G-pH-Zn	4	75080	18770	2.712	*
Residual	34	235323	6921		

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; NS = not significant

APPENDIX 61

Experiment 2

Zinc content (μg plant^{-1}) in grain of wheat, triticale and rye grown at two levels of zinc supply at three soil pHs.

Treatment	Zn added per pot (mg)	Soil pH 5.0	7.0	8.4
Genotype				
Wheat	0	70.3	33.7	0.8
	4	143.5	97.6	32.4
Triticale	0	88.5	44.2	15.5
	4	190.7	154.6	42.0
Rye	0	47.4	31.3	20.4
	4	100.3	82.0	47.3

LSD (P = 0.05) for the genotype-soil pH-Zn interaction: 16.1

APPENDIX 62

Experiment 2

(a) Total zinc uptake by grain ($\mu g\ plant^{-1}$)[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Zn added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	62.00	149.34	28.25	103.88	-*	39.52
	Rep 2	81.27	150.39	47.27	86.86	2.54*	25.06
	Rep 3	67.59	130.85	25.48	102.00	-*	32.55
Triticale	Rep 1	104.52	187.65	45.68	144.62	7.85	50.97
	Rep 2	93.09	194.29	56.09	166.10	20.84	39.92
	Rep 3	67.76	190.14	30.97	153.01	17.82	35.06
Rye	Rep 1	48.54	107.18	33.77	72.76	28.58	46.96
	Rep 2	49.91	89.05	34.64	75.59	19.66	40.48
	Rep 3	43.69	104.59	25.61	97.69	13.03	54.55

[1] = mean of 3 plants/pot

* = no grain

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	1277316.9			
Replication	2	1913.6	956.8	1.145	NS
Genotype (G)	2	104824.5	52412.3	62.747	***
pH	2	528847.1	264423.5	316.565	***
Zn	1	434488.7	434488.7	520.165	***
G-pH	4	75243.8	18811.0	22.520	***
G-Zn	2	27297.6	13648.8	16.340	***
pH-Zn	2	60284.7	30142.4	36.086	***
G-pH-Zn	4	16016.9	4004.2	4.794	**
Residual	34	28399.8	835.3		

** = $P < 0.01$; *** = $P < 0.001$; NS = not significant

APPENDIX 63

Experiment 2

(a) Zinc content of main culm grain per plant (µg)[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Zn added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	31.93	97.99	14.67	54.86	-*	24.56
	Rep 2	45.98	94.64	28.59	56.01	1.28*	14.59
	Rep 3	44.79	64.65	14.65	55.81	-	19.02
Triticale	Rep 1	72.05	146.04	34.16	97.10	6.03	37.71
	Rep 2	53.33	132.52	43.34	145.96	18.05	27.19
	Rep 3	46.14	147.14	23.21	122.19	16.17	23.80
Rye	Rep 1	20.71	52.88	15.62	43.96	19.06	20.37
	Rep 2	24.64	37.69	18.33	39.48	9.60	28.47
	Rep 3	27.31	50.58	10.07	39.59	6.44	27.40

[1] = mean of 3 plants/pot

* = no grain

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	697612.0			
Replication	2	1664.9	832.4	0.984	NS
Genotype (G)	2	133052.4	66526.2	78.610	***
pH	2	202780.4	101390.3	119.806	***
Zn	1	185877.4	185877.4	219.639	***
G-pH	4	57229.8	14307.5	16.906	***
G-Zn	2	37831.0	18915.5	22.351	***
pH-Zn	2	31686.6	15843.3	18.721	***
G-pH-Zn	4	18715.7	4678.9	5.529	**
Residual	34	28773.7	846.3		

** = $P < 0.01$; *** = $P < 0.001$; NS = not significant

APPENDIX 64

Experiment 2

(a) Zinc content of primary tiller grain per plant (µg)[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Zn added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	18.40	40.75	7.99	24.80	-*	9.94
	Rep 2	22.25	24.88	18.68	21.41	1.26	7.48
	Rep 3	22.80	28.59	6.32	21.32	-*	9.34
Triticale	Rep 1	32.47	41.61	11.53	33.15	1.82	13.26
	Rep 2	39.75	61.77	12.75	20.15	2.79	12.73
	Rep 3	21.62	43.00	4.71	30.83	1.65	11.25
Rye	Rep 1	18.70	30.09	11.59	23.03	5.44	16.34
	Rep 2	14.72	32.17	6.91	25.44	7.19	12.01
	Rep 3	13.26	30.83	7.53	29.13	4.60	17.97

[1] = mean of 3 plants/pot

* = no grain

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	81070.7			
Replication	2	481.2	240.6	1.099	
Genotype (G)	2	3458.6	1729.3	7.899	**
pH	2	40641.3	20320.6	92.817	***
Zn	1	21181.4	21181.4	96.748	***
G-pH	4	6234.9	1558.7	7.120	***
G-Zn	2	623.3	311.7	1.424	NS
pH-Zn	2	864.5	432.2	1.974	NS
G-pH-Zn	4	141.8	35.4	0.162	NS
Residual	34	7443.7	218.9		

** = $P < 0.01$; *** = $P < 0.001$; NS = not significant

APPENDIX 65

Experiment 2

(a) Zinc content of secondary tiller grain per plant (µg)[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Zn added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	11.68	10.60	5.59	24.21	*	5.01
	Rep 2	13.04	30.87	*	9.44	*	2.99
	Rep 3	*	37.61	4.51	24.88	*	4.20
Triticale	Rep 1	*	*	*	14.37	*	*
	Rep 2	*	*	*	*	*	*
	Rep 3	*	*	3.05	*	*	*
Rye	Rep 1	9.13	24.21	6.57	5.77	4.08	10.25
	Rep 2	10.55	19.19	9.40	0.68	2.86	*
	Rep 3	3.13	23.17	8.01	28.97	1.98	9.18

1 = mean of 3 plants/pot

* = no grain

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	42219.3			
Replication	2	395.4	197.7	0.631	NS
Genotype (G)	2	9461.7	4730.8	15.097	***
pH	2	6319.3	3159.7	10.083	***
Zn	1	6803.7	6803.7	21.712	***
G-pH	4	3292.8	823.2	2.627	NS
G-Zn	2	2739.5	1389.8	4.371	*
pH-Zn	2	1565.9	783.0	2.499	NS
G-pH-Zn	4	986.7	246.7	0.787	NS
Residual	34	10654.2	313.4		

* = $P < 0.05$; *** = $P < 0.001$; NS = not significant

APPENDIX 66

Experiment 2

(a) Manganese content of straw per plant (µg)[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Zn added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	1008.94	1169.99	497.26	412.78	77.15	54.28
	Rep 2	933.81	993.88	429.48	426.86	97.01	57.01
	Rep 3	969.49	901.79	507.21	415.89	108.92	49.88
Triticale	Rep 1	1164.91	1181.95	476.18	542.46	74.28	52.34
	Rep 2	785.57	1009.06	614.90	535.38	55.13	41.00
	Rep 3	894.36	1162.56	718.49	617.10	83.96	63.98
Rye	Rep 1	1269.07	1085.54	491.55	496.94	115.23	125.40
	Rep 2	644.72	1524.00	431.95	450.46	73.84	130.67
	Rep 3	1410.30	1513.47	538.16	740.33	150.10	120.94

[1] = mean of 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	92561176			
Replication	2	762844	381422	2.393	NS
Genotype (G)	2	1217530	608765	3.819	*
pH	2	82340198	41170099	258.244	***
Zn	1	262082	262082	1.644	NS
G-pH	4	1265981	316495	1.985	NS
G-Zn	2	370661	185330	2.163	NS
pH-Zn	2	817367	408683	2.564	NS
G-pH-Zn	4	104118	26029	0.163	NS
Residual	34	5420395	159423		

* = $P < 0.05$; *** = $P < 0.001$; NS = not significant

APPENDIX 67

Experiment 2

Manganese content (μg plant^{-1}) in grain of wheat, triticale and rye grown at two levels of zinc supply at three soil pHs.

Treatment		Soil pH		
	Zn added per pot (mg)	5.0	7.0	8.4
Genotype				
Wheat	0	292.9	161.4	2.0
	4	301.0	161.7	39.5
Triticale	0	230.5	177.6	45.0
	4	245.3	189.0	48.1
Rye	0	119.0	106.0	48.6
	4	175.2	108.9	49.3
LSD (P = 0.05) for the genotype-soil pH-Zn interaction:				28.8

APPENDIX 68

Experiment 2

(a) Manganese content of main culm grain per plant (µg)[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Zn added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	123.20	224.37	78.77	91.73	-*	27.64
	Rep 2	152.70	177.19	95.54	93.75	3.32	20.76
	Rep 3	203.79	132.06	90.33	84.74	-*	21.98
Triticale	Rep 1	185.82	188.94	116.40	106.07	26.21	43.03
	Rep 2	120.36	161.64	138.67	165.26	46.89	35.31
	Rep 3	153.99	188.81	128.46	157.26	47.91	20.58
Rye	Rep 1	53.78	97.24	51.03	64.95	28.01	23.90
	Rep 2	57.16	60.24	42.81	48.93	24.74	29.75
	Rep 3	61.92	87.89	46.45	46.70	24.21	23.39

1 = mean of 3 plants/pot

* = no grain

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	1718853			
Replication	2	887	444	0.117	NS
Genotype (G)	2	345109	172554	45.704	***
pH	2	998038	499019	132.175	***
Zn	1	17241	17241	4.567	*
G-pH	4	213603	53401	14.144	***
G-Zn	2	303	151	0.040	NS
pH-Zn	2	7437	3718	0.985	NS
G-pH-Zn	4	7870	1968	0.521	NS
Residual	34	128365	3775		

* = $P < 0.05$; *** = $P < 0.001$; NS = not significant

APPENDIX 69

Experiment 2

(a) Manganese content of primary tiller grain per plant (µg)[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Zn added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	99.40	94.65	44.80	43.10	-*	12.90
	Rep 2	87.91	54.83	68.86	39.02	2.76	10.10
	Rep 3	104.33	64.96	39.42	35.34	-*	11.47
Triticale	Rep 1	75.82	70.36	38.94	40.20	3.98	12.37
	Rep 2	78.22	72.98	51.62	23.06	4.39	14.33
	Rep 3	77.24	53.31	37.20	51.70	5.50	18.56
Rye	Rep 1	45.79	54.39	37.30	36.52	9.07	19.87
	Rep 2	41.36	54.69	19.01	29.46	19.15	14.85
	Rep 3	39.69	52.90	43.33	36.78	18.91	17.00

[1] = mean of 3 plants/pot

* = no grain

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	349548.8			
Replication	2	708.1	354.0	0.496	NS
Genotype (G)	2	12776.3	6388.1	8.945	***
pH	2	264008.4	132004.2	184.844	***
Zn	1	490.3	490.3	0.687	NS
G-pH	4	30001.6	7500.4	10.503	***
G-Zn	2	3846.7	1923.3	2.693	NS
pH-Zn	2	5766.1	2883.1	4.037	*
G-pH-Zn	4	7670.7	1917.7	2.685	*
Residual	34	24280.6	714.1		

* = $P < 0.05$: *** = $P < 0.001$; NS = not significant

APPENDIX 70

Experiment 2

(a) Manganese content of secondary tiller grain per plant (µg)[1]

Treatment		Soil pH					
		5.0		7.0		8.4	
	Zn added per pot (mg)	0	4	0	4	0	4
Genotype							
Wheat	Rep 1	56.36	22.54	33.71	43.09	-*	5.22
	Rep 2	51.14	59.94	-*	14.39	-*	3.49
	Rep 3	-*	72.40	32.89	40.06	-*	4.81
Triticale	Rep 1	-*	-*	-*	23.44	-*	-*
	Rep 2	-*	-*	-*	-*	-*	-*
	Rep 3	-*	-*	21.65	-*	-*	-*
Rye	Rep 1	22.01	48.09	21.15	11.22	6.09	10.57
	Rep 2	25.57	30.36	20.18	13.10	6.90	-*
	Rep 3	9.84	39.85	36.67	39.16	8.84	8.71

[1] = mean of 3 plants/pot

* = no grain

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	53	174284			
Replication	2	2391	1195	0.758	NS
Genotype (G)	2	43460	21730	13.779	***
pH	2	40391	20195	12.806	***
Zn	1	3147	3147	1.995	NS
G-pH	4	23459	5865	3.719	*
G-Zn	2	2030	1015	0.644	NS
pH-Zn	2	2937	1468	0.931	NS
G-pH-Zn	4	2850	712	0.452	NS
Residual	34	53620	1577		

* = $P < 0.05$; *** = $P < 0.001$; NS = not significant

APPENDIX 71, Figure 1

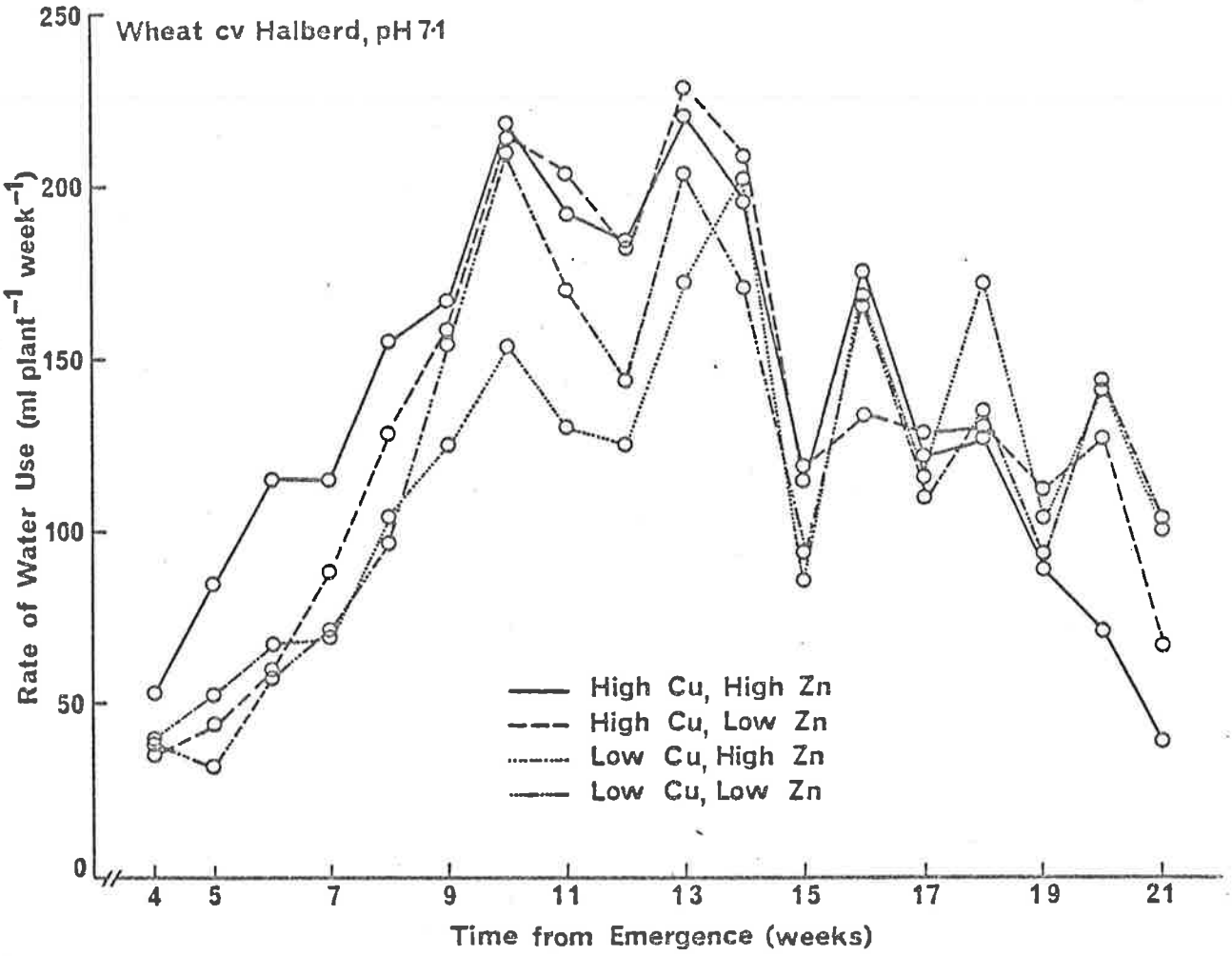
Experiment 3

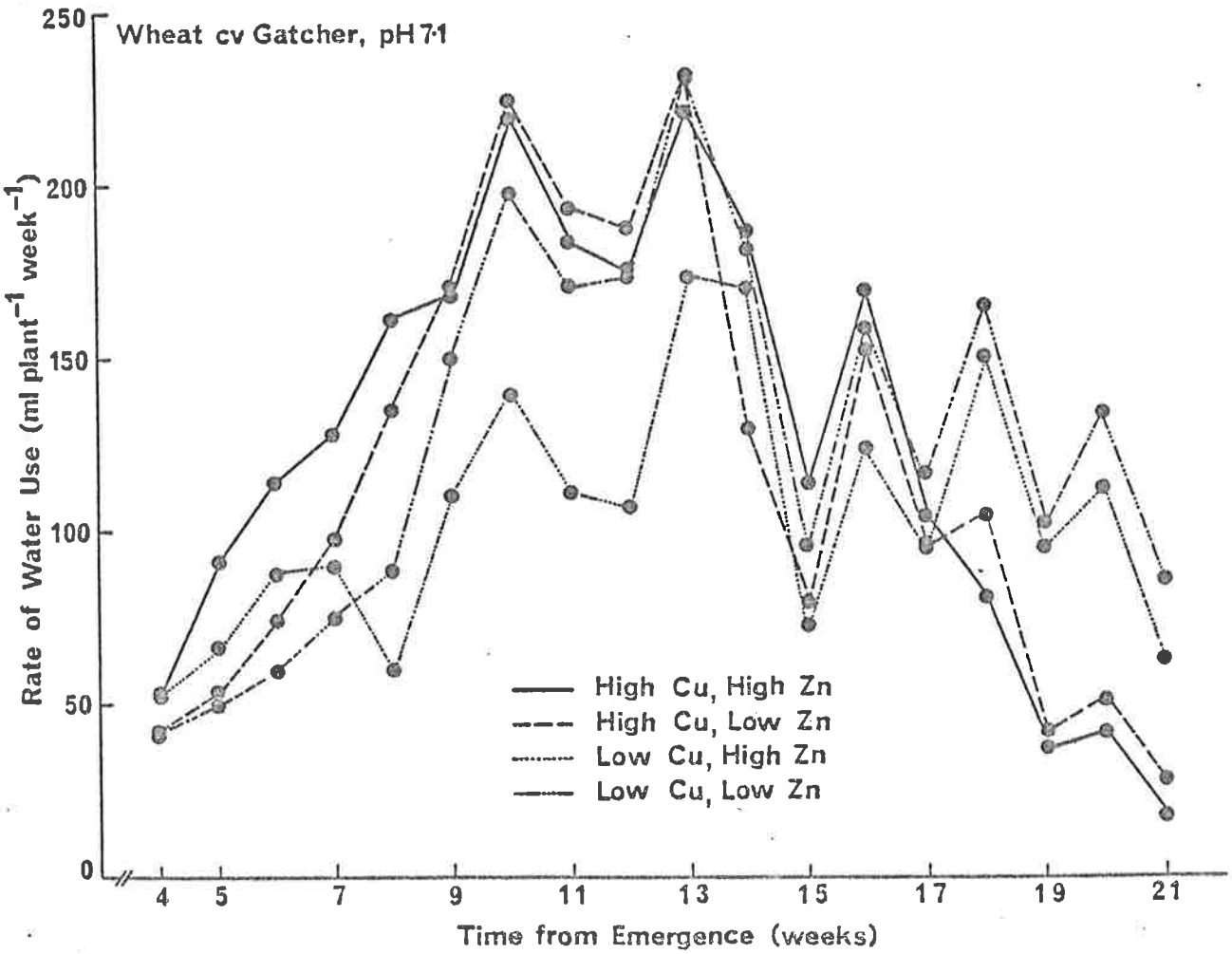
Effect of level of copper and zinc supply on the weekly water use (ml plant^{-1}) throughout the season of wheat cv. Halberd at pH 7.1. Data are means of 6 plants (3 plants per pot for each of 2 replicates).

APPENDIX 71, Figure 2

Experiment 3

Effect of level of copper and zinc supply on the weekly water use (ml plant^{-1}) throughout the season of wheat cv. Gatcher at pH 7.1. Data are means of 6 plants (3 plants per pot for each of 2 replicates).


Wheat cv Halberd, pH 7·1
Rate of Water Use (ml plant^{-1} week^{-1})
250
200
150
100
50
0
4
5
7
9
11
13
15
17
19
21
Time from Emergence (weeks)
High Cu, High Zn
High Cu, Low Zn
Low Cu, High Zn
Low Cu, Low Zn


Wheat cv Gatcher, pH 7·1
Rate of Water Use (ml plant^{-1} week^{-1})
250
200
150
100
50
0
4
5
7
9
11
13
15
17
19
21
Time from Emergence (weeks)
High Cu, High Zn
High Cu, Low Zn
Low Cu, High Zn
Low Cu, Low Zn

APPENDIX 71, Figure 3

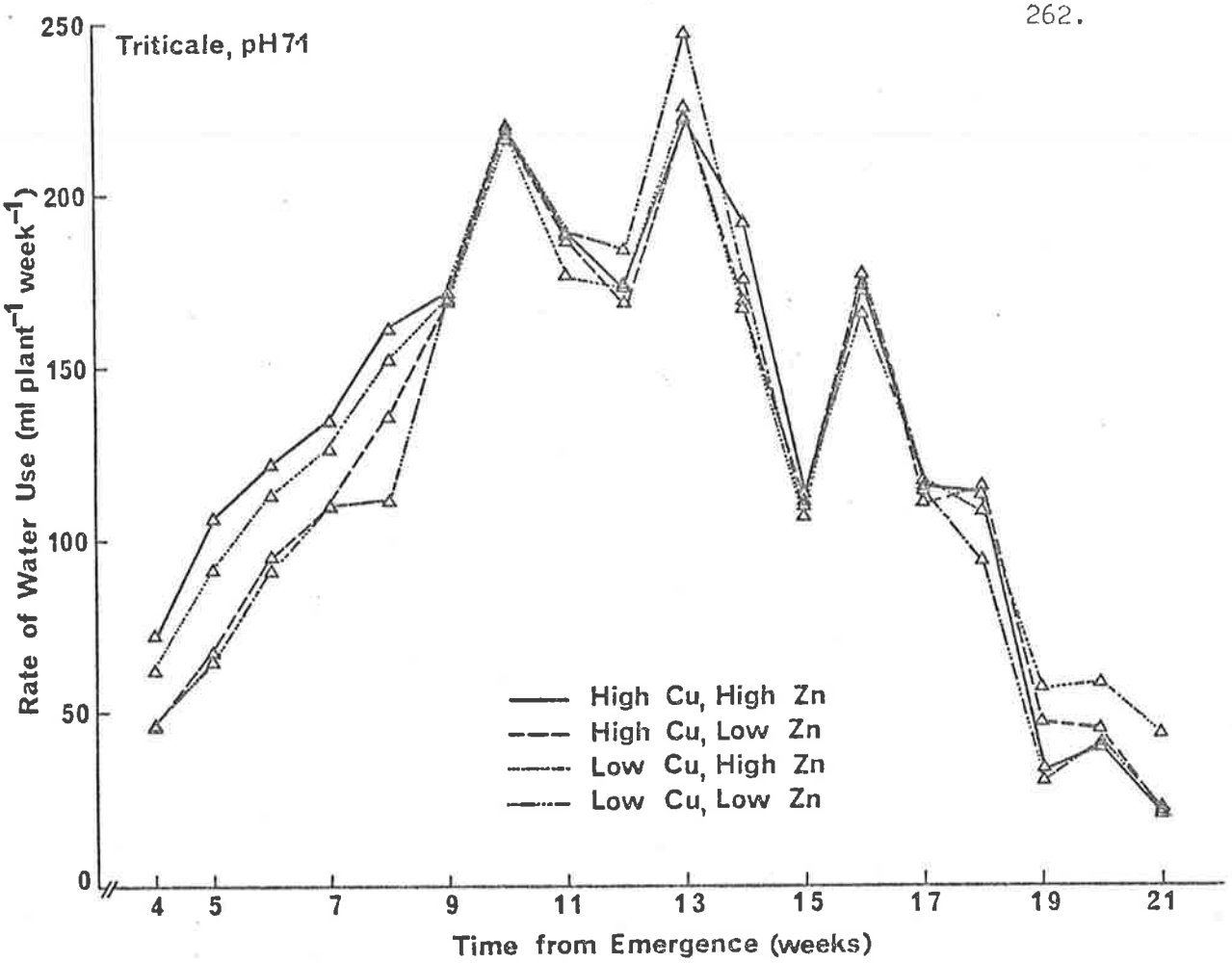
Experiment 3

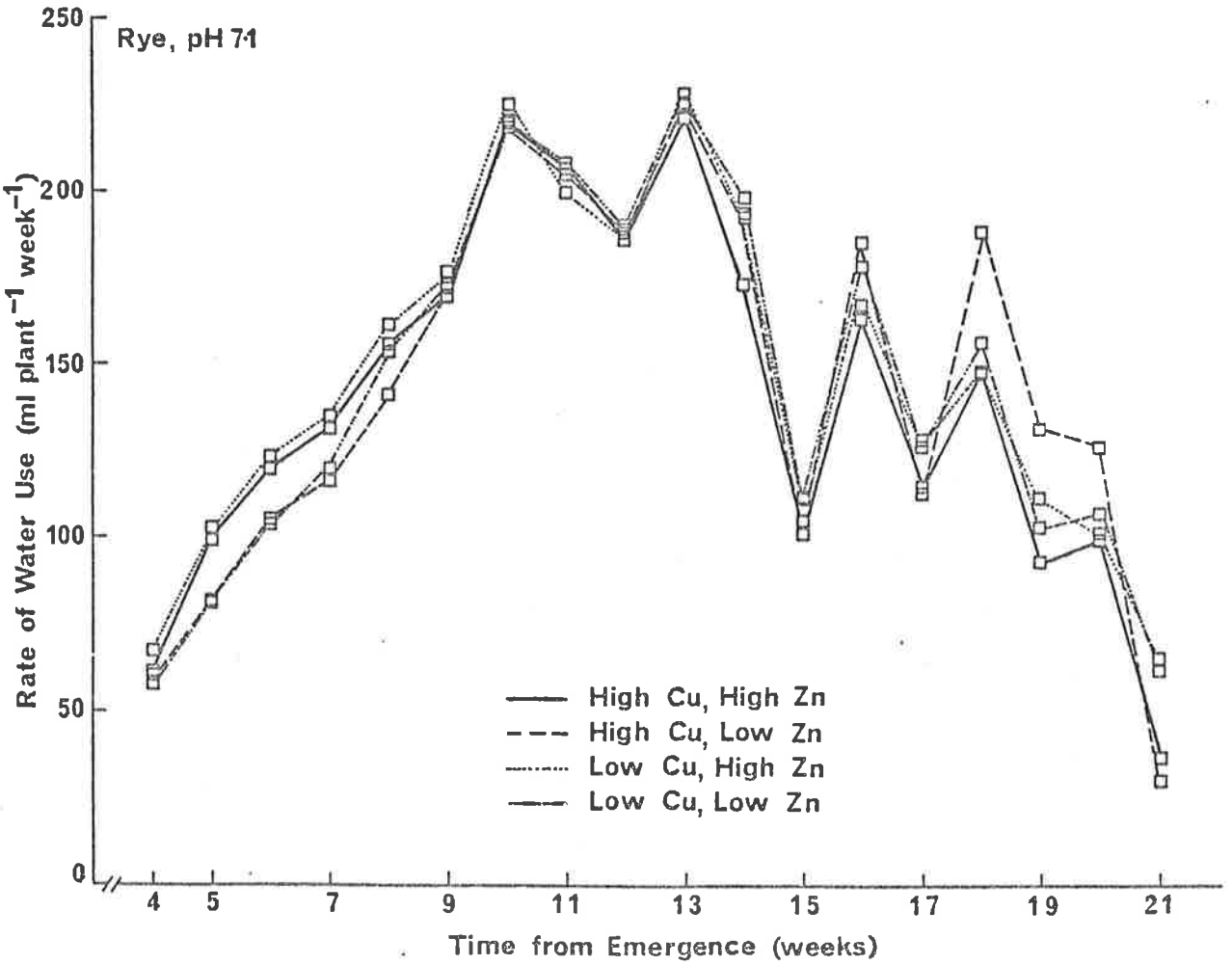
Effect of level of copper and zinc supply on the weekly water use (ml plant^{-1}) throughout the season of triticale at pH 7.1. Data are means of 6 plants (3 plants per pot for each of 2 replicates).

APPENDIX 71, Figure 4

Experiment 3

Effect of level of copper and zinc supply on the weekly water use (ml plant^{-1}) throughout the season of rye at pH 7.1. Data are means of 6 plants (3 plants per pot for each of 2 replicates).


Triticale, pH 7·1
Rate of Water Use (ml plant^{-1} week^{-1})
250
200
150
100
50
0
4
5
7
9
11
13
15
17
19
21
Time from Emergence (weeks)
High Cu, High Zn
High Cu, Low Zn
Low Cu, High Zn
Low Cu, Low Zn


Rye, pH 7·1
Rate of Water Use (ml plant^{-1} week^{-1})
250
200
150
100
50
0
4
5
7
9
11
13
15
17
19
21
Time from Emergence (weeks)
High Cu, High Zn
High Cu, Low Zn
Low Cu, High Zn
Low Cu, Low Zn

APPENDIX 71, Figure 5

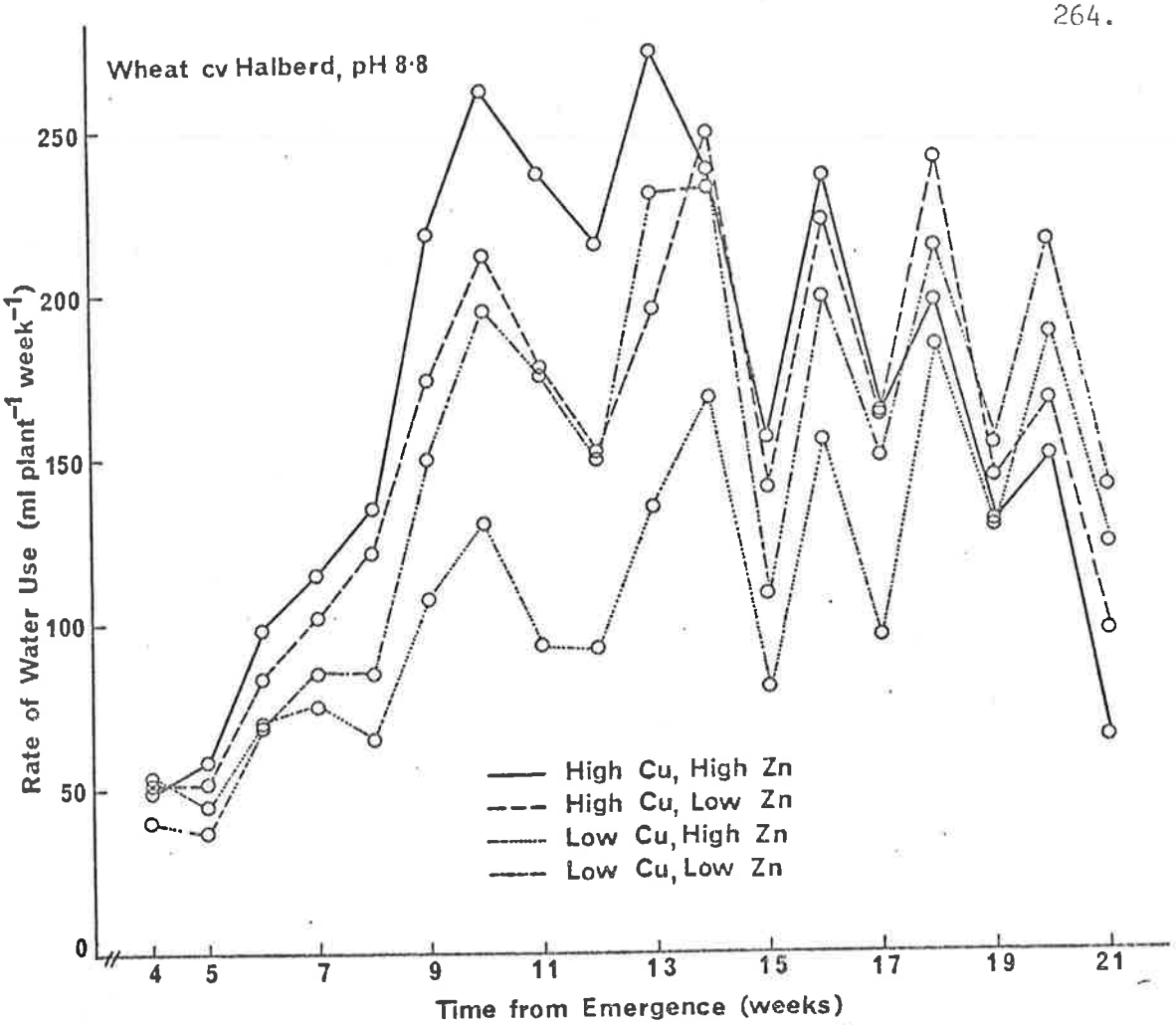
Experiment 3

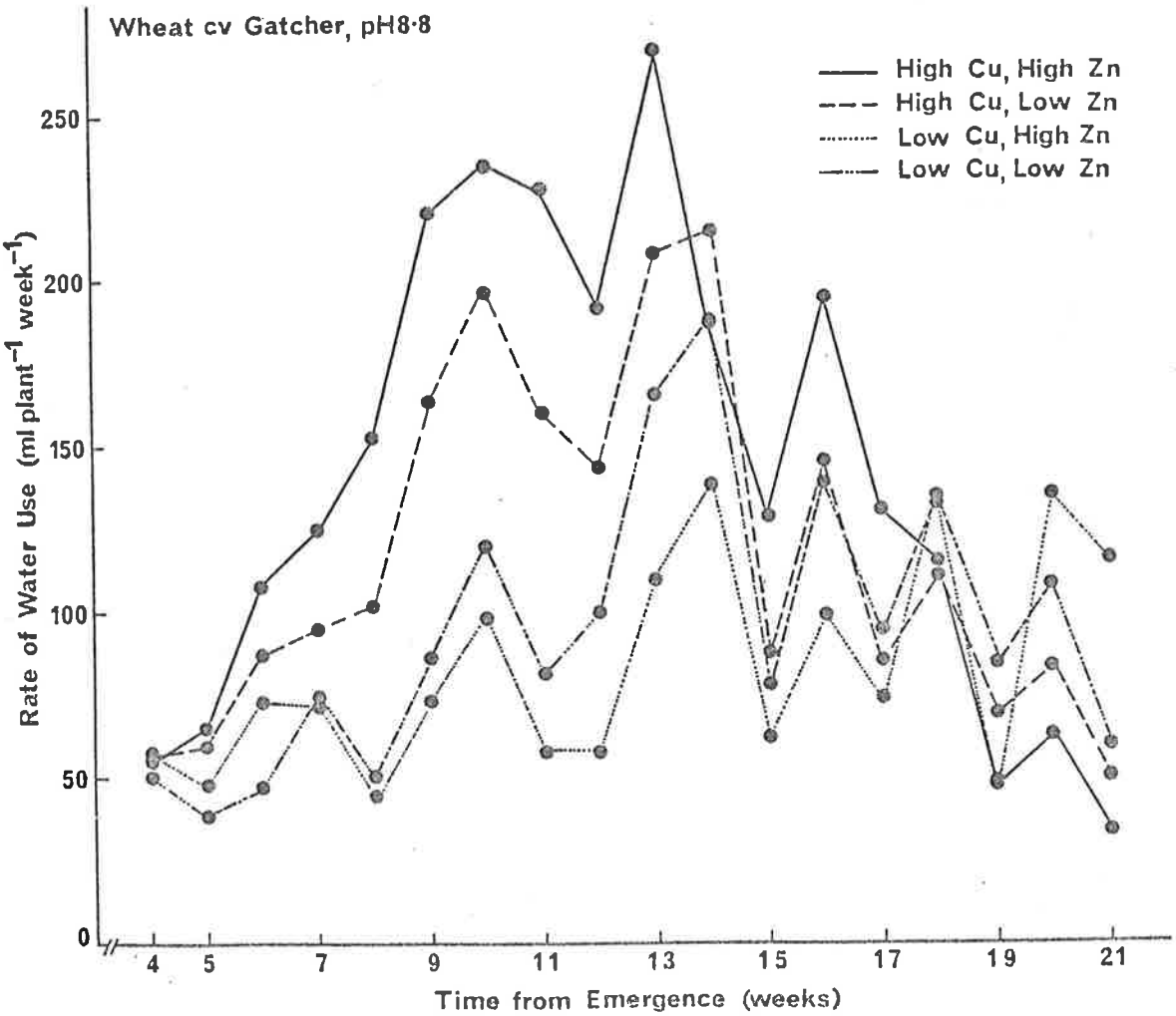
Effect of level of copper and zinc supply on the weekly water use (ml plant^{-1}) throughout the season of wheat cv. Halberd at pH 8.8. Data are means of 6 plants (3 plants per pot for each of 2 replicates).

APPENDIX 71, Figure 6

Experiment 3

Effect of level of copper and zinc supply on the weekly water use (ml plant^{-1}) throughout the season of wheat cv. Gatcher at pH 8.8. Data are means of 6 plants (3 plants per pot for each of 2 replicates).


Wheat cv Halberd, pH 8·8
Rate of Water Use (ml plant^{-1} week^{-1})
0
50
100
150
200
250
4
5
7
9
11
13
15
17
19
21
Time from Emergence (weeks)
High Cu, High Zn
High Cu, Low Zn
Low Cu, High Zn
Low Cu, Low Zn


Wheat cv Gatcher, pH8·8
Rate of Water Use (ml plant^{-1} week^{-1})
0
50
100
150
200
250
4
5
7
9
11
13
15
17
19
21
Time from Emergence (weeks)
High Cu, High Zn
High Cu, Low Zn
Low Cu, High Zn
Low Cu, Low Zn

APPENDIX 71, Figure 7

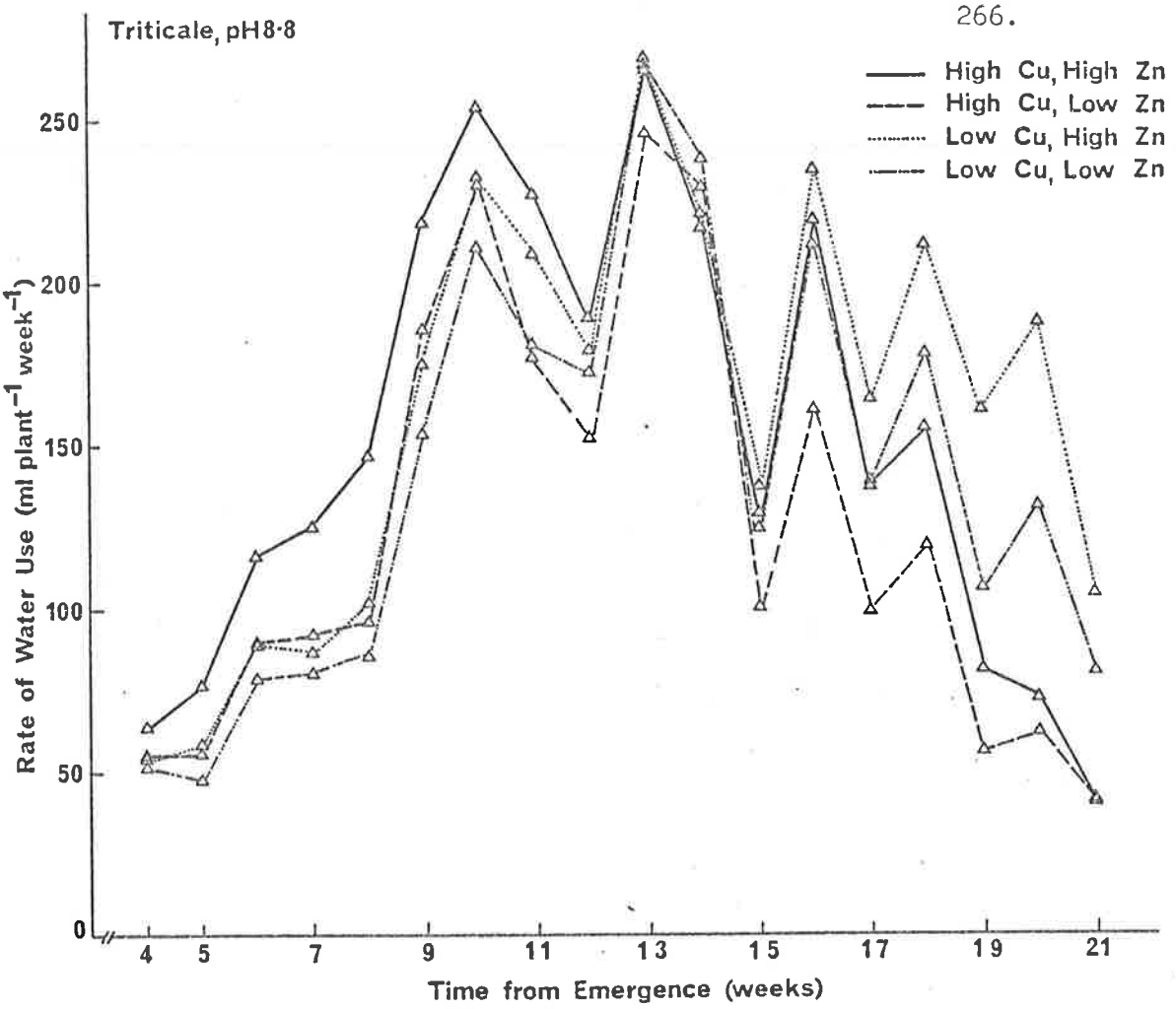
Experiment 3

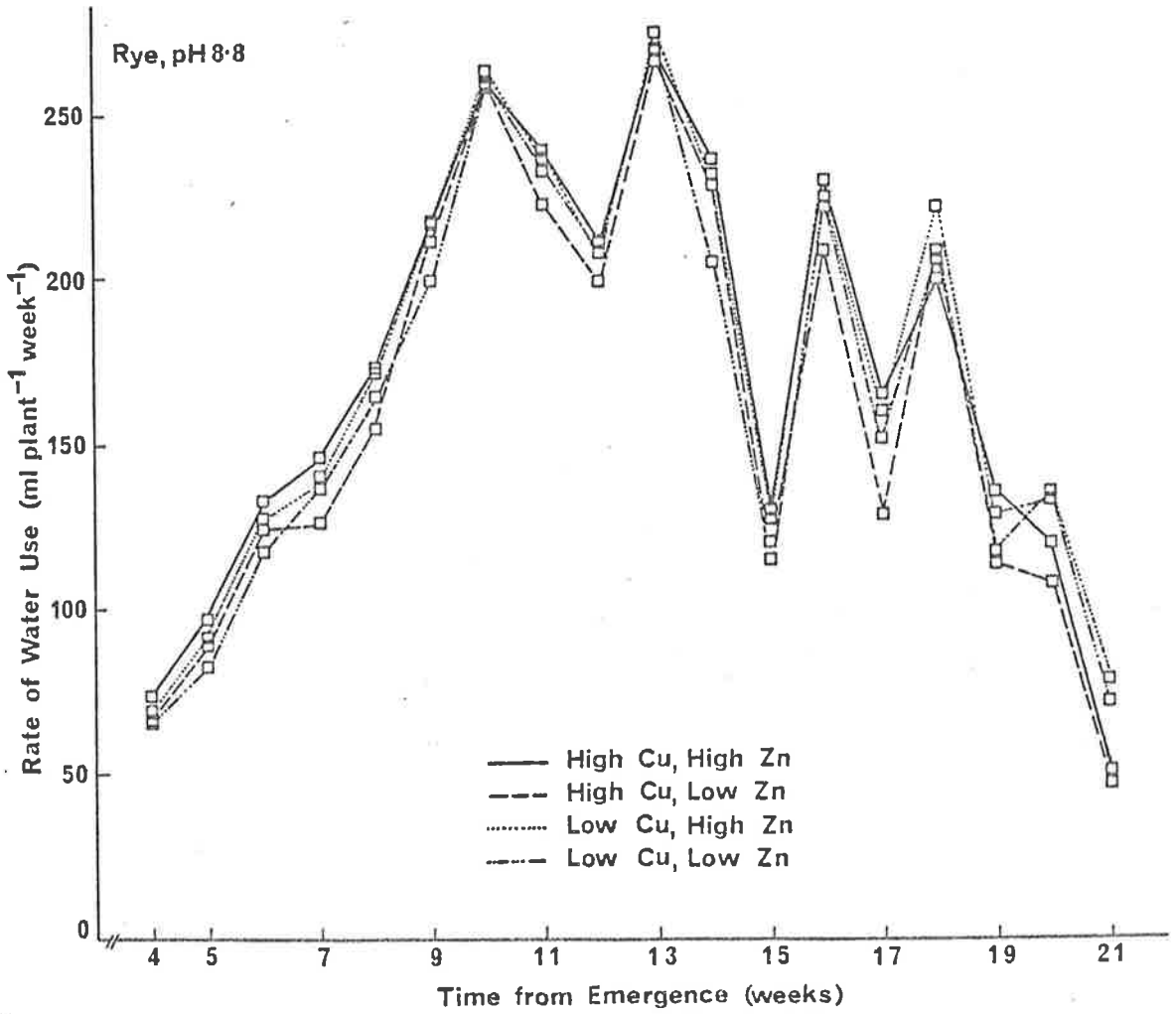
Effect of level of copper and zinc supply on the weekly water use (ml $plant^{-1}$) throughout the season of triticale at pH 8.8. Data are means of 6 plants (3 plants per pot for each of 2 replicates).

APPENDIX 71, Figure 8

Experiment 3

Effect of level of copper and zinc supply on the weekly water use (ml $plant^{-1}$) throughout the season of rye at pH 8.8. Data are means of 6 plants (3 plants per pot for each of 2 replicates).


Triticale, pH8·8
High Cu, High Zn
High Cu, Low Zn
Low Cu, High Zn
Low Cu, Low Zn
Rate of Water Use (ml plant⁻¹ week⁻¹)
0
50
100
150
200
250
4 5 7 9 11 13 15 17 19 21
Time from Emergence (weeks)


Rye, pH 8·8
High Cu, High Zn
High Cu, Low Zn
Low Cu, High Zn
Low Cu, Low Zn
Rate of Water Use (ml plant⁻¹ week⁻¹)
0
50
100
150
200
250
4 5 7 9 11 13 15 17 19 21
Time from Emergence (weeks)

APPENDIX 72

Experiment 3

(a) Total water use over the whole season (ml plant^{-1})[1]

Treatment			Soil pH					
			5.0		7.1		8.8	
		Replicate	1	2	1	2	1	2
	Cu added per pot (mg)	Zn added per pot (mg)						
Genotype								
Wheat cv. Halberd	0	0	413	238	1972	2407	2500	2747
	0	4	300	300	2077	2173	2127	1840
	4	0	1085	1333	2370	2355	2937	2538
	4	4	1873	1813	2405	2462	3030	2953
Wheat cv. Gatcher	0	0	285	215	2303	2242	1537	1868
	0	4	303	345	1833	1907	1202	1783
	4	0	1273	1475	2107	2073	1962	2278
	4	4	1482	1328	2265	2257	2545	2547
Triticale	0	0	798	860	2142	2233	2430	2618
	0	4	1180	1002	2415	2255	2677	3053
	4	0	1915	1797	2273	2153	2270	2205
	4	4	1915	2023	2380	2367	2688	2763
Rye	0	0	1005	1007	2595	2563	2860	3065
	0	4	2073	750	2625	2625	3013	3200
	4	0	2418	2410	2685	2485	2795	2978
	4	4	2372	2322	2483	2523	3090	3092

[1] = mean of 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	95	506341218			
Replication	1	30638	30638	0.093	NS
Genotype (G)	3	75934847	25311616	77.004	***
pH	2	273749944	136874972	416.404	***
Cu	1	50293388	50293388	143.004	***
Zn	1	2332825	2332825	7.097	*
G-pH	6	15855306	2642551	8.039	***
G-Cu	3	7038490	2346163	7.138	***
pH-Cu	2	43704985	21852492	66.480	***
G-Zn	3	1847257	615752	1.873	NS
pH-Zn	2	1102963	551482	1.678	NS
Cu-Zn	1	2005371	2005371	6.101	*
G-pH-Cu	6	5974365	995728	3.029	*
G-pH-Zn	6	2768670	461445	1.404	NS
G-Cu-Zn	3	4774161	1591387	4.841	**
pH-Cu-Zn	2	1769377	884688	2.691	NS
G-pH-Cu-Zn	6	1709407	284901	0.867	NS
Residual	47	15449225	328707		

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$: NS = not significant

APPENDIX 73

Experiment 3

(a) Height of main culms to top of ears (cm)[1]

Treatment	Cu added per pot (mg)	Zn added per pot (mg)	Soil pH 5.0 Rep 1	5.0 Rep 2	7.1 Rep 1	7.1 Rep 2	8.8 Rep 1	8.8 Rep 2
Genotype								
Wheat cv. Halberd	0	0	22.0	16.0	54.0	72.0	50.0	66.0
	0	4	18.0	20.0	54.0	34.0	33.0	36.0
	4	0	57.0	30.0	81.0	90.0	87.0	73.0
	4	4	65.0	65.0	101.0	109.0	93.0	99.0
Wheat cv. Gatcher	0	0	22.0	21.0	53.0	61.0	42.0	38.0
	0	4	23.0	27.0	34.0	40.0	25.0	49.0
	4	0	36.0	46.0	83.0	78.0	56.0	76.0
	4	4	57.0	75.0	98.0	110.0	114.0	111.0
Triticale	0	0	21.0	44.0	98.0	103.0	92.0	85.0
	0	4	27.0	22.0	92.0	95.0	72.0	85.0
	4	0	71.0	75.0	98.0	102.0	102.0	103.0
	4	4	87.0	87.0	102.0	112.0	102.0	112.0
Rye	0	0	60.0	20.0	147.0	141.0	133.0	119.0
	0	4	87.0	41.0	151.0	131.0	142.0	138.0
	4	0	115.0	133.0	125.0	142.0	134.0	151.0
	4	4	112.0	120.0	137.0	134.0	148.0	144.0

[1] = mean of 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	95	147460.0			
Replication	1	48.2	48.2	0.446	NS
Genotype (G)	3	63207.8	21069.3	195.246	***
pH	2	33636.3	16823.2	144.989	***
Cu	1	26070.0	26070.0	241.588	***
Zn	1	630.4	630.4	5.842	*
G-pH	6	1918.8	319.8	2.964	*
G-Cu	3	1528.5	509.5	4.721	**
pH-Cu	2	2510.1	1255.0	11.630	***
G-Zn	3	530.8	176.9	1.640	NS
pH-Zn	2	306.7	153.4	1.421	NS
Cu-Zn	1	2147.0	2147.0	19.896	***
G-pH-Cu	6	6346.4	1057.7	9.802	***
G-pH-Zn	6	464.6	77.4	0.718	NS
G-Cu-Zn	3	2347.5	782.5	7.251	***
pH-Cu-Zn	2	345.3	172.7	1.600	NS
G-pH-Cu-Zn	6	339.7	56.6	0.525	NS
Residual	47	5071.8	107.9		

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; NS = not significant

APPENDIX 74

Experiment 3

(a) Number of culms produced per plant[1]

Treatment	Cu added per pot (mg)	Zn added per pot (mg)	Soil pH 5.0 Rep 1	5.0 Rep 2	7.1 Rep 1	7.1 Rep 2	8.8 Rep 1	8.8 Rep 2
Genotype								
Wheat cv. Halberd	0	0	2.3	2.0	5.3	4.3	3.7	3.3
	0	4	2.0	2.0	6.0	6.3	4.3	4.7
	4	0	2.3	9.3	4.3	4.7	3.7	4.0
	4	4	2.3	2.3	3.3	3.7	3.7	3.7
Wheat cv. Gatcher	0	0	1.3	1.7	5.7	3.0	3.0	3.3
	0	4	1.7	2.0	5.3	6.0	4.3	5.7
	4	0	6.7	3.7	4.3	4.3	3.0	3.0
	4	4	2.3	1.7	3.0	3.0	3.3	3.0
Triticale	0	0	7.0	3.7	2.7	3.0	3.7	3.0
	0	4	6.7	3.0	4.7	5.0	7.0	5.0
	4	0	3.7	4.0	2.7	3.0	2.3	2.0
	4	4	2.7	2.7	3.0	3.0	2.3	2.7
Rye	0	0	5.3	3.7	4.3	3.7	3.7	4.0
	0	4	5.7	1.7	4.3	3.7	4.7	5.0
	4	0	5.3	2.7	6.3	3.0	4.0	3.7
	4	4	3.3	3.0	4.0	3.3	3.7	5.0

[1] = mean of 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	95	1760.24			
Replication	1	29.26	29.26	2.287	NS
Genotype (G)	3	37.03	12.34	0.965	NS
pH	2	72.33	36.17	2.827	NS
Cu	1	52.51	52.51	4.105	*
Zn	1	0.51	0.51	0.040	NS
G-pH	6	165.75	27.62	2.159	NS
G-Cu	3	106.61	35.54	2.778	*
pH-Cu	2	85.58	42.79	3.345	*
G-Zn	3	30.95	10.32	0.806	NS
pH-Zn	2	168.58	84.29	6.589	**
Cu-Zn	1	162.76	162.76	12.723	***
G-pH-Cu	6	165.67	27.61	2.158	NS
G-pH-Zn	6	17.33	2.89	0.226	NS
G-Cu-Zn	3	37.03	12.34	0.965	NS
pH-Cu-Zn	2	3.58	1.79	0.140	NS
G-pH-Cu-Zn	6	23.50	3.92	0.306	NS
Residual	47	601.24	12.79		

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; NS = not significant

APPENDIX 75

Experiment 3

(a) Number of ear produced per plant[1]

Treatment	Cu added per pot (mg)	Zn added per pot (mg)	Soil pH 5.0 Replicate 1	5.0 2	7.1 1	7.1 2	8.8 1	8.8 2
Genotype								
Wheat cv. Halberd	0	0	0.0	0.0	0.3	2.0	1.0	2.0
	0	4	0.0	0.0	0.7	0.3	0.0	0.0
	4	0	0.7	0.0	3.3	2.7	3.0	2.7
	4	4	2.0	2.0	3.0	2.7	3.0	2.3
Wheat cv. Gatcher	0	0	0.0	0.0	1.0	0.7	1.0	1.3
	0	4	0.0	0.0	0.3	1.3	0.3	2.3
	4	0	3.3	1.7	3.0	3.0	3.0	3.0
	4	4	2.0	1.0	3.0	3.0	2.7	2.7
Triticale	0	0	0.0	0.0	1.7	2.0	2.7	3.0
	0	4	0.0	0.0	3.0	4.0	4.0	5.0
	4	0	1.7	2.3	2.0	1.7	1.3	1.3
	4	4	1.7	2.0	2.0	2.0	2.3	1.7
Rye	0	0	0.3	0.0	2.3	2.3	2.7	2.7
	0	4	2.3	0.3	3.7	2.7	3.7	2.7
	4	0	2.3	2.0	2.3	2.7	2.3	2.3
	4	4	2.3	2.0	2.0	2.3	2.3	3.0

[1] = mean of 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	95	1203.740			
Replication	1	0.094	0.094	0.040	NS
Genotype (G)	3	86.031	28.677	12.098	***
pH	2	290.271	145.135	61.230	***
Cu	1	173.344	173.344	73.130	***
Zn	1	7.594	7.594	3.204	NS
G-pH	6	11.813	1.969	0.831	NS
G-Cu	3	196.615	65.538	27.649	***
pH-Cu	2	65.687	32.844	13.856	***
G-Zn	3	28.865	9.622	4.059	*
pH-Zn	2	0.062	0.031	0.013	NS
Cu-Zn	1	3.760	3.760	1.586	NS
G-pH-Cu	6	131.229	21.872	9.227	***
G-pH-Zn	6	46.354	7.726	3.259	*
G-Cu-Zn	3	38.031	12.677	5.348	**
pH-Cu-Zn	2	2.146	1.073	0.453	NS
G-pH-Cu-Zn	6	10.437	1.740	0.734	NS
Residual	47	111.406	2.370		

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; NS = not significant

APPENDIX 76

Experiment 3

(a) Pollen viability expressed as percentage of grains staining with iodine[1]

Treatment	Cu added per pot (mg)	Zn added per pot (mg)	Soil pH 5.0 Replicate 1	5.0 2	7.1 1	7.1 2	8.8 1	8.8 2
Genotype								
Wheat cv. Halberd	0	0	0.0	0.0	0.0	0.0	0.0	0.0
	0	4	0.0	0.0	0.0	0.0	0.0	0.0
	4	0	0.0	0.0	91.0	82.0	74.0	96.0
	4	4	93.0	96.0	90.0	93.0	75.0	95.0
Wheat cv. Gatcher	0	0	0.0	0.0	0.0	0.0	0.0	0.0
	0	4	0.0	0.0	0.0	0.0	0.0	0.0
	4	0	-+	96.0	81.0	95.0	91.0	94.0
	4	4	91.0	87.0	94.0	98.0	98.0	98.0
Triticale	0	0	0.0	0.0	87.0	81.0	69.0	83.0
	0	4	0.0	0.0	36.0	61.0	-+	83.0
	4	0	69.0	65.0	80.0	84.0	71.0	84.0
	4	4	92.0	87.0	93.0	90.0	66.0	94.0
Rye	0	0	0.0	0.0	91.0	96.0	84.0	78.0
	0	4	75.0	-+	59.0	90.0	48.0	90.0
	4	0	98.0	73.0	93.0	95.0	94.0	96.0
	4	4	84.0	95.0	88.0	87.0	91.0	82.0

1 = pollen collected from 1 plant/pot.

+ = anther undeveloped

(b) Analysis of Variance

Source of variance	D.F.(MV)	S.S.	M.S.	v-ratio	
Total	92	162831.73			
Replication	1	359.01	359.01	5.226	*
Genotype (G)	3	24128.70	8042.90	117.081	***
pH	2	8865.59	4432.80	64.528	***
Cu	1	74935.09	74935.09	1090.830	***
Zn	1	899.64	899.64	13.096	***
G-pH	6	3869.89	644.98	9.389	***
G-Cu	3	19452.19	6484.06	94.389	***
pH-Cu	2	1393.99	696.99	10.146	***
G-Zn	3	968.48	322.83	4.699	**
pH-Zn	2	3943.00	1971.50	28.699	***
Cu-Zn	1	560.14	560.14	8.154	**
G-pH-Cu	6	9285.88	1547.65	22.529	***
G-pH-Zn	6	3156.92	526.15	7.659	***
G-Cu-Zn	3	2345.04	781.68	11.379	***
pH-Cu-Zn	2	256.49	128.24	1.867	NS
G-pH-Cu-Zn	6	5389.08	898.18	13.075	***
Residual	44 (3)	3022.60	68.70		

* = P < 0.05; ** = P < 0.01; *** = P < 0.001; NS = not significant

APPENDIX 77

Experiment 3

(a) Number of days to ear emergence of main culms[1]

Treatment	Cu added per pot (mg)	Zn added per pot (mg)	Soil pH 5.0 Rep 1	Soil pH 5.0 Rep 2	Soil pH 7.1 Rep 1	Soil pH 7.1 Rep 2	Soil pH 8.8 Rep 1	Soil pH 8.8 Rep 2
Genotype								
Wheat cv. Halberd	0	0	-+	-+	106	110	113+	107+
	0	4	-+	-+	152	127	-+	-+
	4	0	145	-+	99	100	101	110
	4	4	99	97	84	82	93	90
Wheat cv. Gatcher	0	0	-+	-+	106	109	101	99
	0	4	-+	-+	113	131	123	124
	4	0	134	100	86	86	94	93
	4	4	85	83	69	69	73	75
Triticale	0	0	-+	-+	75	77	82	81
	0	4	-+	-+	77	79	93	82
	4	0	82	80	78	75	76	74
	4	4	79	76	73	77	82	79
Rye	0	0	137	-+	87	81	82	84
	0	4	110	96	77	80	82	87
	4	0	86	85	83	85	86	82
	4	4	81	83	80	82	83	82

[1] = mean of 3 plants/pot

\+ = not reached by harvest date

(b) Analysis of Variance

Source of variance	D.F. (MV)	S.S.	M.S.	v-ratio	
Total	79	71028.92			
Replication	1	70.06	70.06	2.010	NS
Genotype (G)	3	22385.02	7461.67	214.125	***
pH	2	13045.73	6522.87	187.184	***
Cu	1	14571.97	14571.97	418.167	***
Zn	1	958.81	958.81	27.515	***
G-pH	6	1822.59	303.76	8.717	***
G-Cu	3	4295.90	1431.97	41.093	***
pH-Cu	2	3197.92	1598.96	45.885	***
G-Zn	3	112.62	37.54	1.077	NS
pH-Zn	2	3623.41	1811.71	51.990	***
Cu-Zn	1	1009.26	1009.26	28.962	***
G-pH-Cu	3 (3)	382.36	127.45	3.657	*
G-pH-Zn	6	648.81	108.13	3.103	*
G-Cu-Zn	3	2654.31	884.77	25.390	***
pH-Cu-Zn	2	879.28	439.64	12.616	***
G-pH-Cu-Zn	2 (4)	46.67	23.34	0.670	NS
Residual	38 (9)	1324.20	34.85		

* = $P < 0.05$; *** = $P < 0.001$; NS = not significant

APPENDIX 78

Experiment 3

(a) Number of days to anthesis of main culms[1]

Treatment	Cu added per pot (mg)	Zn added per pot (mg)	Soil pH 5.0 Rep 1	5.0 Rep 2	7.1 Rep 1	7.1 Rep 2	8.8 Rep 1	8.8 Rep 2
Genotype								
Wheat cv. Halberd	0	0	-+	-+	115	115	119	115
	0	4	-+	-+	157	133	-+	-+
	4	0	154	-+	105	106	109	116
	4	4	105	106	92	91	99	99
Wheat cv. Gatcher	0	0	-+	-+	114	116	109	111
	0	4	-+	-+	120	136	-+	129
	4	0	-+	111	96	93	101	96
	4	4	93	92	78	78	84	84
Triticale	0	0	-+	-+	90	88	90	90
	0	4	-+	-+	88	89	104	91
	4	0	92	92	89	89	90	89
	4	4	91	88	87	86	89	90
Rye	0	0	140	-+	98	94	96	96
	0	4	116	103	90	96	96	100
	4	0	101	99	96	98	96	96
	4	4	96	97	95	97	97	97

[1] = mean of 3 plants/pot

\+ = not reached by harvest date

(b) Analysis of Variance

Source of variance	D.F. (MV)	S.S.	M.S.	v-ratio	
Total	77	49796.64			
Replication	1	16.29	16.29	0.867	NS
Genotype (G)	3	15753.99	5251.33	279.430	***
pH	2	7725.54	3862.77	205.543	***
Cu	1	10201.73	10201.73	542.847	***
Zn	1	614.70	614.70	32.709	***
G-pH	6	1764.71	294.12	15.650	***
G-Cu	3	4220.12	1406.71	74.853	***
pH-Cu	2	1308.24	654.12	34.806	***
G-Zn	3	90.03	30.01	1.597	NS
pH-Zn	2	2505.53	1252.77	66.661	***
Cu-Zn	1	894.74	894.74	47.610	***
G-pH-Cu	3 (3)	330.66	110.22	5.865	**
G-pH-Zn	6	1033.84	172.31	9.169	***
G-Cu-Zn	3	1997.86	665.95	35.436	***
pH-Cu-Zn	2	639.47	319.73	17.013	***
G-pH-Cu-Zn	2 (4)	22.64	11.32	0.602	NS
Residual	36 (11)	676.55	18.79		

** = P < 0.01; *** = P < 0.001; NS = not significant

APPENDIX 79

Experiment 3

(a) Number of days to maturity of main culms[1]

Treatment	Cu added per pot (mg)	Zn added per pot (mg)	Soil pH 5.0 Rep 1	5.0 Rep 2	7.1 Rep 1	7.1 Rep 2	8.8 Rep 1	8.8 Rep 2
Genotype								
Wheat cv. Halberd	0	0	-+	-+	-+	-+	-+	-+
	0	4	-+	-+	-+	-+	-+	-+
	4	0	-+	-+	148	137	143	150
	4	4	148	141	135	135	142	135
Wheat cv. Gatcher	0	0	-+	-+	151	151	142	145
	0	4	-+	-+	142	154	-+	-+
	4	0	-+	146	130	129	139	134
	4	4	138	137	126	123	125	124
Triticale	0	0	-+	-+	131	131	137	141
	0	4	-+	-+	137	137	141	139
	4	0	136	138	131	129	131	133
	4	4	129	128	126	128	131	130
Rye	0	0	154	-+	140	138	148	150
	0	4	-+	143	137	139	138	147
	4	0	154	137	138	151	142	136
	4	4	139	141	137	138	139	135

[1] = mean of 3 plants/pot

\+ = not reached by harvest date

(b) Analysis of Variance

Source of variance	D.F. (MV)	S.S.	M.S.	v-ratio	
Total	68	6977.29			
Replication	1	2.36	2.36	0.137	NS
Genotype (G)	3	2150.49	716.83	41.669	***
pH	2	717.53	358.76	20.855	***
Cu	1	1376.94	1376.94	80.041	***
Zn	1	647.97	647.97	37.666	***
G-pH	6	412.12	68.69	3.993	*
G-Cu	2 (1)	363.95	181.97	10.578	***
pH-Cu	2	25.76	12.88	0.749	NS
G-Zn	3	108.40	36.13	2.100	NS
pH-Zn	2	79.45	39.73	2.309	NS
Cu-Zn	1	32.31	32.31	1.878	NS
G-pH-Cu	2 (4)	359.08	179.54	10.437	***
G-pH-Zn	5 (1)	60.52	12.10	0.704	NS
G-Cu-Zn	2 (1)	32.43	16.22	0.943	NS
pH-Cu-Zn	2	33.88	16.94	0.985	NS
G-pH-Cu-Zn	1 (5)	23.62	23.62	1.373	NS
Residual	32 (15)	550.49	17.20		

* = $P < 0.05$; *** = $P < 0.001$; NS = not significant

APPENDIX 80

Experiment 3

(a) Total dry matter production per plant (g)[1]

Treatment	Cu added per pot (mg)	Zn added per pot (mg)	Soil pH 5.0 Rep 1	5.0 Rep 2	7.1 Rep 1	7.1 Rep 2	8.8 Rep 1	8.8 Rep 2
Genotype								
Wheat cv. Halberd	0	0	0.34	0.16	2.21	3.36	2.50	3.29
	0	4	0.18	0.18	2.16	1.83	1.52	1.32
	4	0	1.47	1.66	8.65	7.86	8.53	6.10
	4	4	3.96	3.77	10.14	10.15	10.16	9.92
Wheat cv. Gatcher	0	0	0.18	0.16	2.37	1.82	0.88	1.37
	0	4	0.21	0.27	1.39	1.63	0.67	1.59
	4	0	1.66	1.74	6.84	6.61	3.50	4.93
	4	4	1.87	2.39	8.43	8.48	8.09	8.03
Triticale	0	0	0.74	0.88	5.38	6.55	4.42	4.69
	0	4	0.99	0.79	6.42	6.64	3.92	6.12
	4	0	3.37	3.11	7.82	8.04	6.25	5.31
	4	4	5.62	5.83	9.39	9.47	8.99	9.42
Rye	0	0	0.89	0.71	7.87	8.54	7.01	8.16
	0	4	2.78	0.61	8.87	8.23	7.83	7.25
	4	0	5.55	5.34	8.54	8.77	8.57	8.57
	4	4	5.74	5.67	8.95	8.88	9.06	9.53

[1] = mean of 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	95	9324.494			
Replication	1	0.776	0.776	0.292	NS
Genotype (G)	3	1070.947	523.649	197.364	***
pH	2	3309.023	1654.512	623.587	***
Cu	1	2799.468	2799.468	1055.122	***
Zn	1	166.137	166.137	62.617	***
G-pH	6	113.531	18.922	7.132	***
G-Cu	3	326.171	108.724	40.978	***
pH-Cu	2	33.815	16.908	6.372	**
G-Zn	3	28.545	9.515	3.586	*
pH-Zn	2	13.176	6.588	2.483	NS
Cu-Zn	1	183.292	183.292	69.083	***
G-pH-Cu	6	508.608	84.768	31.949	***
G-pH-Zn	6	27.418	4.570	1.722	NS
G-Cu-Zn	3	68.298	22.766	8.580	***
pH-Cu-Zn	2	33.713	16.857	6.353	**
G-pH-Cu-Zn	6	16.875	2.813	1.060	NS
Residual	47	124.701	2.653		

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; NS = not significant

APPENDIX 81

Experiment 3

(a) Dry weight of straw+ per plant (g)[1]

Treatment	Cu added per pot (mg)	Zn added per pot (mg)	Soil pH 5.0 Rep 1	5.0 Rep 2	7.1 Rep 1	7.1 Rep 2	8.8 Rep 1	8.8 Rep 2
Genotype								
Wheat cv. Halberd	0	0	1.01	0.48	6.62	10.08	7.51	9.72
	0	4	0.53	0.54	6.48	5.50	4.55	3.96
	4	0	4.19	4.97	16.53	14.72	17.63	11.99
	4	4	7.44	7.50	18.10	18.16	18.62	17.36
Wheat cv. Gatcher	0	0	0.53	0.49	7.10	5.45	2.65	4.07
	0	4	0.64	0.82	4.16	4.89	2.02	4.77
	4	0	4.89	4.13	13.63	12.79	7.94	9.95
	4	4	4.78	4.15	14.73	14.77	14.35	14.04
Triticale	0	0	2.23	2.63	13.00	14.20	12.31	13.74
	0	4	2.97	2.37	19.10	19.66	11.75	18.36
	4	0	8.34	8.47	14.64	14.85	11.22	10.58
	4	4	10.20	10.51	16.39	16.93	18.68	17.20
Rye	0	0	2.68	2.12	18.34	18.15	18.46	19.15
	0	4	8.34	1.82	22.47	20.02	20.96	19.30
	4	0	13.31	10.92	17.28	18.44	18.45	19.87
	4	4	11.77	11.82	18.54	18.33	20.61	21.88

[1] = mean of 3 plants/pot

\+ = weight of (stem, leaf and chaff)

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	95	4149.45			
Replication	1	0.04	0.04	0.022	NS
Genotype (G)	3	1093.67	364.56	181.957	***
pH	2	1662.72	831.36	414.948	***
Cu	1	589.35	589.35	294.154	***
Zn	1	51.66	51.66	25.782	***
G-pH	6	106.74	17.79	8.879	***
G-Cu	3	176.71	58.90	29.400	***
pH-Cu	2	17.84	8.92	4.452	*
G-Zn	3	27.87	9.29	4.637	**
pH-Zn	2	5.33	2.66	1.329	NS
Cu-Zn	1	20.04	20.04	10.002	***
G-pH-Cu	6	208.44	34.74	17.340	***
G-pH-Zn	6	21.62	3.60	1.798	NS
G-Cu-Zn	3	36.34	12.11	6.046	**
pH-Cu-Zn	2	23.55	11.77	5.876	**
G-pH-Cu-Zn	6	13.37	2.23	1.113	NS
Residual	47	94.17	2.00		

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; NS = not significant

APPENDIX 82

Experiment 3

(a) Grain yield per plant (g)[1]

Treatment	Cu added per pot (mg)	Zn added per pot (mg)	Soil pH 5.0 Rep 1	5.0 Rep 2	7.1 Rep 1	7.1 Rep 2	8.8 Rep 1	8.8 Rep 2
Genotype								
Wheat cv. Halberd	0	0	0.00	0.00	0.00	0.00	0.00	0.05
	0	4	0.00	0.00	0.00	0.00	0.00	0.00
	4	0	0.07	0.00	3.14	2.95	2.65	2.10
	4	4	1.48	1.27	4.10	4.10	3.95	4.14
Wheat cv. Gatcher	0	0	0.00	0.00	0.00	0.00	0.00	0.01
	0	4	0.00	0.00	0.00	0.00	0.00	0.00
	4	0	0.03	0.37	2.29	2.35	0.85	1.62
	4	4	0.27	1.00	3.52	3.55	3.30	3.35
Triticale	0	0	0.00	0.00	1.04	1.82	0.32	0.11
	0	4	0.00	0.00	0.05	0.09	0.00	0.00
	4	0	0.59	0.29	2.94	3.09	2.51	1.78
	4	4	2.22	2.33	3.93	3.82	2.77	3.69
Rye	0	0	0.00	0.00	1.76	2.49	0.85	1.77
	0	4	0.00	0.00	1.38	1.56	0.84	0.82
	4	0	1.11	1.70	2.78	2.62	2.42	1.95
	4	4	1.82	1.73	2.77	2.77	2.19	2.23

[1] = mean of 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	95	1591.0953			
Replication	1	1.1948	1.1948	2.234	NS
Genotype (G)	3	45.6010	15.2003	28.419	***
pH	2	291.6135	145.8067	272.602	***
Cu	1	819.8782	819.8782	1532.853	***
Zn	1	32.5152	32.5152	60.791	***
G-pH	6	9.0062	1.5010	2.806	*
G-Cu	3	48.7035	16.2345	30.352	***
pH-Cu	2	95.8172	47.9086	89.570	***
G-Zn	3	20.8948	6.9649	13.022	***
pH-Zn	2	6.1733	3.0866	5.771	**
Cu-Zn	1	82.1215	82.1215	153.535	***
G-pH-Cu	6	76.6873	12.7812	23.896	***
G-pH-Zn	6	15.4863	2.5811	4.826	***
G-Cu-Zn	3	10.9287	3.6429	6.811	***
pH-Cu-Zn	2	1.6092	0.8046	1.504	NS
G-pH-Cu-Zn	6	7.7258	1.2876	2.407	*
Residual	47	25.1389	0.5349		

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; NS = not significant

APPENDIX 83

Experiment 3

(a) Number of grains per plant[1]

Treatment			Soil pH 5.0		7.1		8.8	
	Cu added per pot (mg)	Zn added per pot (mg)	Replicate 1	2	1	2	1	2
Genotype								
Wheat cv. Halberd	0	0	0.0	0.0	0.0	0.0	0.0	4.7
	0	4	0.0	0.0	0.0	0.0	0.0	0.0
	4	0	4.7	0.0	96.3	82.3	86.7	61.0
	4	4	45.3	41.0	115.3	118.0	107.7	75.3
Wheat cv. Gatcher	0	0	0.0	0.0	0.0	0.3	0.0	0.0
	0	4	0.0	0.0	0.0	0.0	0.0	0.0
	4	0	1.7	9.3	62.3	59.0	28.0	41.3
	4	4	7.3	23.3	98.0	95.0	98.3	92.0
Triticale	0	0	0.0	0.0	43.3	68.0	19.0	8.3
	0	4	0.0	0.0	10.0	12.3	0.0	0.0
	4	0	17.0	7.7	67.0	67.3	53.3	39.0
	4	4	64.7	66.3	89.7	89.3	72.7	98.7
Rye	0	0	0.0	0.0	82.7	93.0	62.0	89.3
	0	4	0.0	0.0	69.7	75.0	93.3	57.0
	4	0	42.3	66.0	118.7	103.3	91.0	68.7
	4	4	74.7	76.7	98.3	112.0	84.3	92.0

[1] = mean of 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	95	1438231.6			
Replication	1	15.0	15.0	0.020	NS
Genotype (G)	3	227774.2	75924.7	99.567	***
pH	2	282550.2	141275.1	185.266	***
Cu	1	549945.4	549945.4	721.190	***
Zn	1	24257.0	24257.0	31.810	***
G-pH	6	25092.2	4182.0	5.484	***
G-Cu	3	34122.7	11374.2	14.916	***
pH-Cu	2	32032.9	16016.5	21.004	***
G-Zn	3	7996.4	2665.5	3.495	*
pH-Zn	2	7331.8	3665.9	4.807	*
Cu-Zn	1	62322.0	62322.0	81.728	***
G-pH-Cu	6	110171.0	18361.8	24.079	***
G-pH-Zn	6	17307.3	2884.6	3.783	**
G-Cu-Zn	3	13678.2	4559.4	5.979	**
pH-Cu-Zn	2	192.0	96.0	0.126	NS
G-pH-Cu-Zn	6	7603.2	1267.2	1.662	NS
Residual	47	35840.0	762.6		

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; NS = not significant

APPENDIX 84

Experiment 3

(a) Dry weight of roots per plant (g)[1]

Treatment			Soil pH					
			5.0		7.1		8.8	
		Replicate	1	2	1	2	1	2
	Cu added per pot (mg)	Zn added per pot (mg)						
Genotype								
Wheat cv. Halberd	0	0	0.05	0.05	0.42	0.68	0.54	0.78
	0	4	0.03	0.04	0.16	0.23	0.11	0.15
	4	0	0.71	1.18	1.56	2.69	3.59	1.61
	4	4	0.99	0.86	1.51	2.22	1.75	2.44
Wheat cv. Gatcher	0	0	0.03	0.03	0.68	0.92	0.10	0.23
	0	4	0.04	0.07	0.08	0.15	0.06	0.31
	4	0	0.53	0.44	3.59	2.47	1.21	1.25
	4	4	0.46	0.35	1.80	1.65	1.43	1.46
Triticale	0	0	0.11	0.23	2.45	0.90	1.46	1.61
	0	4	0.13	0.19	1.94	2.18	0.69	1.90
	4	0	1.06	0.91	2.42	2.13	1.80	2.50
	4	4	0.87	1.03	4.32	6.04	2.53	3.10
Rye	0	0	0.12	0.11	6.00	7.05	3.94	6.40
	0	4	0.60	0.07	3.20	10.81	3.84	8.14
	4	0	1.62	1.36	4.56	5.79	4.13	6.64
	4	4	0.85	1.43	4.43	6.41	5.32	6.27

[1] = mean of 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	95	3999.685			
Replication	1	61.632	61.632	6.492	*
Genotype (G)	3	1503.888	501.296	52.808	***
pH	2	890.813	445.407	46.920	***
Cu	1	192.157	192.157	20.242	***
Zn	1	1.525	1.525	0.161	NS
G-pH	6	598.558	99.760	10.509	***
G-Cu	3	84.803	28.268	2.978	*
pH-Cu	2	2.457	1.228	0.129	NS
G-Zn	3	32.825	10.942	1.153	NS
pH-Zn	2	1.618	0.809	0.085	NS
Cu-Zn	1	1.157	1.157	0.122	NS
G-pH-Cu	6	98.959	16.493	1.737	NS
G-pH-Zn	6	47.334	7.889	0.831	NS
G-Cu-Zn	3	18.926	6.309	0.665	NS
pH-Cu-Zn	2	3.463	1.732	0.182	NS
G-pH-Cu-Zn	6	13.404	2.234	0.235	NS
Residual	47	446.165	9.493		

* = $P < 0.05$; *** = $P < 0.001$; NS = not significant

APPENDIX 85

Experiment 3

(a) Concentration of copper in the straw ($\mu g\ g^{-1}$)[1]

Treatment			Soil pH			
			5.0		8.8	
		Replicate	1	2	1	2
	Cu added per pot (mg)	Zn added per pot (mg)				
Genotype						
Wheat cv.	0	0	1.03	1.27	2.06	4.72
Halberd	4	4	2.07	2.90	1.82	2.18
Triticale	0	0	4.13	4.26	2.37	1.18
	4	4	2.82	1.89	2.43	2.95
Rye	0	0	1.57	1.45	1.16	1.91
	4	4	3.85	2.38	0.78	2.77

[1] = mean of 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	23	26.20			
Replication	1	0.59	0.59	0.813	NS
Genotype (G)	2	2.44	1.22	1.673	NS
pH	1	0.45	0.45	0.619	NS
CuZn	1	0.12	0.12	0.171	NS
G-pH	2	4.13	2.06	2.832	NS
G-CuZn	2	2.01	1.00	1.377	NS
pH-CuZn	1	0.30	0.30	0.408	NS
G-pH-CuZn	2	8.14	4.07	5.586	*
Residual	11	8.02	0.73		

* = $P < 0.05$; NS = not significant

APPENDIX 86

Experiment 3

(a) Concentration of copper in the grain ($\mu g\ g^{-1}$)[1]

Treatment			Soil pH			
			5.0		8.8	
	Cu added per pot (mg)	Zn added per pot (mg)	Replicate 1	2	1	2
Genotype						
Wheat cv. Halberd	0	0	-	-	-	0.38
	4	4	0.61	0.82	1.41	0.94
Triticale	0	0	-	-	0.67	0.38
	4	4	1.02	1.25	2.25	1.56
Rye	0	0	-	-	0.42	0.75
	4	4	2.09	1.66	3.11	4.23

[1] = bulked sample of grain for 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F. (MV)	S.S.	M.S.	v-ratio	
Total	16	34.49			
Replication	1	0.00	0.00	0.000	NS
Genotype (G)	2	1.90	0.95	5.477	*
pH	1	5.84	5.84	33.677	***
CuZn	1	17.98	17.98	103.770	***
G-pH	2	1.93	0.97	5.573	*
G-CuZn	2	5.63	2.81	16.234	***
pH-CuZn	0 (1)	0.00			
G-pH-CuZn	0 (2)	0.00			
Residual	7 (4)	1.21	0.17		

* = $P < 0.05$; *** = $P < 0.001$; NS = not significant

APPENDIX 87

Experiment 3

(a) Concentration of manganese in the straw ($\mu g\ g^{-1}$)[1]

Treatment			Soil pH			
			5.0		8.8	
	Cu added per pot (mg)	Replicate Zn added per pot (mg)	1	2	1	2
Genotype						
Wheat cv.	0	0	181.41	151.28	65.40	72.60
Halberd	4	4	28.00	28.60	26.40	20.60
Triticale	0	0	46.90	59.60	63.60	82.60
	4	4	17.00	16.30	14.70	16.60
Rye	0	0	87.40	62.90	84.70	168.60
	4	4	16.40	16.70	21.10	48.40

[1] = mean of 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	23	54854.1			
Replication	1	350.9	350.9	0.839	NS
Genotype (G)	2	4431.8	2215.9	5.297	*
pH	1	30.8	30.8	0.074	NS
CuZn	1	30544.2	30544.2	73.016	***
G-pH	2	7792.7	3896.4	9.314	**
G-CuZn	2	2048.0	1024.0	2.448	NS
pH-CuZn	1	245.7	245.7	0.587	NS
G-pH-CuZn	2	4808.4	2404.2	5.747	*
Residual	11	4601.5	418.3		

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; NS = not significant

APPENDIX 88

Experiment 3

(a) Concentration of manganese in the grain ($\mu g\ g^{-1}$)[1]

Treatment			Soil pH			
			5.0		8.8	
	Replicate		1	2	1	2
	Cu added per pot (mg)	Zn added per pot (mg)				
Genotype						
Wheat cv. Halberd	0	0	-	-	-	67.18
	4	4	28.31	15.04	13.09	11.07
Triticale	0	0	-	-	58.03	69.34
	4	4	13.84	11.85	17.53	15.86
Rye	0	0	-	-	-	48.49
	4	4	22.30	26.17	40.76	33.53

[1] = bulked sample of grain for 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F. (MV)	S.S.	M.S.	v-ratio	
Total	15	11914.54			
Replication	1	15.01	15.01	0.494	NS
Genotype (G)	2	288.41	144.20	4.743	NS
pH	1	38.01	38.01	1.250	NS
CuZn	1	8755.48	8755.48	288.000	***
G-pH	2	505.96	252.98	8.321	*
G-CuZn	2	2129.14	1064.57	35.018	***
pH-CuZn	0 (1)	0.10			
G-pH-CuZn	0 (2)	0.03			
Residual	6 (5)	182.41	30.40		

* = $P < 0.05$: *** = $P < 0.001$; NS = not significant

APPENDIX 89

Experiment 3

(a) Copper content of the straw per plant (µg)[1]

Treatment			Soil pH			
			5.0		8.8	
	Cu added per pot (mg)	Zn added per pot (mg)	Replicate 1	2	1	2
Genotype						
Wheat cv.	0	0	0.04	0.60	14.98	40.03
Halberd	4	4	13.14	18.53	28.10	31.48
Triticale	0	0	9.20	1.20	24.55	12.93
	4	4	23.10	15.67	37.23	41.48
Rye	0	0	4.07	3.07	18.54	31.36
	4	4	36.65	22.73	13.72	52.21

[1] = mean of 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F.	S.S.	M.S.	v-ratio	
Total	23	4799.4			
Replication	1	95.9	95.9	0.815	NS
Genotype (G)	2	78.6	39.3	0.334	NS
pH	1	1643.6	1643.6	13.964	**
CuZn	1	1253.8	1253.8	10.653	**
G-pH	2	68.1	34.0	0.289	NS
G-CuZn	2	92.7	46.4	0.394	NS
pH-CuZn	1	103.4	103.4	0.878	NS
G-pH-CuZn	2	168.7	84.4	0.717	NS
Residual	11	1294.7	117.7		

** = $P < 0.01$; NS = not significant

APPENDIX 90

Experiment 3

(a) Copper content of the grain per plant (µg)[1]

Treatment			Soil pH			
			5.0		8.8	
	Cu added per pot (mg)	Replicate Zn added per pot (mg)	1	2	1	2
Genotype						
Wheat cv. Halberd	0	0	-	-	-	0.06
	4	4	2.70	3.12	16.17	11.67
Triticale	0	0	-	-	0.64	0.13
	4	4	6.79	8.72	18.67	17.25
Rye	0	0	-	-	1.08	3.99
	4	4	11.39	8.60	20.43	28.34

[1] = mean of 3 plants/pot

(b) Analysis of Variance

Source of variance	D.F. (MV)	S.S.	M.S.	v-ratio	
Total	16	2928.01			
Replication	1	1.12	1.12	0.144	NS
Genotype (G)	2	94.49	47.24	6.071	*
pH	1	824.48	824.48	105.947	***
CuZn	1	1876.56	1876.56	241.141	***
G-pH	2	18.92	9.46	1.215	NS
G-CuZn	2	57.64	28.82	3.703	NS
pH-CuZn	0 (1)	0.33			
G-pH-CuZn	0 (2)	0.01			
Residual	7 (4)	54.47	7.78		

* = P < 0.05; *** = P < 0.001; NS = not significant

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