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Response of Wheat Genotypes (*Triticum aestivum* L.) to Acidic and High Aluminum Conditions

by

Joseph Mogire Nyachiro

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IN

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled **Response of Wheat Genotypes (*Triticum aestivum* L.) to Acidic and High Aluminum Conditions** submitted by **Joseph Mogire Nyachiro** in partial fulfilment of the requirements for the degree of **Master of Science** in **Plant Breeding**.

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ABSTRACT

Differential aluminum tolerance exists in wheat (*Triticum aestivum* L.). This study was undertaken to evaluate and determine the response of a cross section of the elite wheat germplasm used in Kenya with respect to aluminum and acidic conditions.

Laboratory nutrient culture solution, greenhouse experiments using media to which aluminum had been added to a toxic level, and liming experiments in the greenhouse were conducted to elucidate the differential tolerance to aluminum and acidic conditions among some Kenyan and other wheat varieties.

Highly significant ($P \leq 0.01$) variety differences were observed on the basis of hematoxylin staining scores, root weight, shoot weight, biological yield, root tolerance index and shoot tolerance index for both the staining and nutrient culture experiments. Significant ($P \leq 0.01$) variety x treatment interactions were observed for biological yield, root length, and root tolerance index in the nutrient culture experiment.

On the basis of varieties grown in artificial media (University of California Mixture) supplemented with aluminum at various concentrations, significant variety differences were observed for all measured variables. Only root tolerance index and shoot tolerance index showed significant variety x treatment interactions.

In liming experiments using Kenyan soils significant variety x treatment interactions were observed for grain yield, harvest index and number of seeds per plot for the Ferralsols (Eldoret soils), but only for 1,000 KWT with the Andosols (Molo soils).

All the measured agronomic characters and determined indices were negatively affected by higher levels of aluminum, although root length and root weight were the most affected. On the basis of determined indices, root tolerance index was the most significantly affected by the change of aluminum concentrations.

Significant correlation coefficients between all measured variables were observed except for root weight and root length in the control treatment of the nutrient culture experiment.

Varieties which showed either tolerance or susceptibility in the nutrient screening experiment showed similar and consistent performance in the subsequent experiments with using high levels of aluminum in the media; and in the liming experiment.

A genetic study was conducted to examine the inheritance of tolerance to aluminum toxicity. Twelve different crosses produced F2 with different segregation ratios of tolerant and susceptible seedlings. The F2 progenies exhibited a wide range of segregation ratios that suggested, that aluminum tolerance in this group of parents is conditioned by more than two genes. Only three out of the twelve crosses showed segregation patterns that would fit a two gene model, and none fitted a single gene model.

The chi-square of homogeneity (x^2) performed on the F2 seedling test results revealed that the tolerant parents Romany, PF7748, K. Kongoni and K. Tembo have different genes with respect to aluminum tolerance. The results of the progenies obtained from the crosses K. Fahari (susceptible) x Siete Cerros (susceptible), and K. Swara (susceptible) x Siete Cerros (susceptible) indicated that aluminum susceptibility is conditioned by recessive genes. No F2 segregants fitted a 3:1 ratio (i.e no single gene difference), but the crosses K. Tembo x Siete Cerros, and K. Swara x Romany fitted a 9:7 ratio (i.e 2 gene difference) suggesting the presence of dominant genes controlling aluminum tolerance. F2 test results indicated that effective levels of aluminum tolerance could be incorporated into some of the Kenyan wheat varieties, but also that the variety Romany is equal in tolerance and in effectiveness as a donor parent to the best aluminum tolerant lines previously reported in the literature.

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Table of Contents

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List of Tables

Page

List of Figures

Page

1. INTRODUCTION

Wheat (*Triticum aestivum* L.) is an important cereal crop in Kenya grown on approximately 119,000 hectares with a national average yield of 2.5 tonne/ha. The national average wheat production per annum is a creditable figure of 250,000 tonnes, depending on the weather conditions and on the rate of decline of hectareage due to sub-division of traditional wheat lands to accommodate other farming activities. The growth rate of wheat yield per annum is now approximately 3.7 percent, coupled with a 3.5 percent per year growth rate in total production in recent years. Despite the fact that these indices show such promising trends, Kenya has been a net importer of wheat in the last decade or so due to difficulty in satisfying ever increasing domestic demands.

In 1981 net wheat imports were approximately 159,000 tonnes. The net imports in 1981, as percent of the 1978-1981 average was 300%. The net import wheat grain per capita in 1961-1965 was -3 kg/yr (indicating that Kenya was exporting wheat) compared to 5 kg/yr in the 1979-1981 period. Imports of wheat grain as percent of total food grain imports in 1961-1965 were zero, compared to 47% in the 1978-1980 period. (CIMMYT,1983).

It is evident that Kenya needs to develop new wheat production technologies in order to satisfy her domestic demands. Such technologies will include, among others, development of:

(i) high yielding cultivars for areas of "high yield potential", and

(ii) high yielding cultivars for areas of "low yield potential", such as the "semi-arid" and mineral stress areas. Mineral stress regions will include areas of acidic soils and those with high levels of aluminum in the soil. Research relevant to these regions should play a major role in development of the wheat crop.

1.1 Overview of the problem and objectives

Aluminum toxicity in wheat is frequently quite severe in soils with a pH of 5.5 or less. Research in development of wheat varieties with tolerance to soluble aluminum was initiated by Brazilian breeders and over the past five decades, has resulted in the identification of large numbers of tolerant cultivars (CIMMYT, 1981).

Liming is usually advocated as an amendment for increased crop production in acidic and high aluminum soils. Some investigators have attributed the benefits of liming to the corresponding increase in pH and reduction in the concentration of exchangeable Al^{3+} and H^{+} (Kato and Haza, 1977).

The effects of aluminum on plant growth have been studied by other workers (Foy, 1974; Camargo, 1981), and various methods have been established to screen for aluminum tolerance (Foy, 1976; Moore *et al.*, 1976; Polle *et al.*, 1978).

Breeding wheat for aluminum and /or acid tolerance in Kenya is relatively recent compared to breeding for rust resistance. Little is known about the level of tolerance to aluminum in most commercially grown wheat varieties. There is inadequate Kenyan information from which sound and practical breeding programs can be designed with respect to aluminum tolerance. Specifically, little is known about the level of tolerance, the number of genes conferring resistance, their mode of inheritance, the lime response of various varieties and, more importantly, the desired choice of parents for crossing in order to incorporate genes that carry resistance to aluminum toxicity without altering the good agronomic characters of the best Kenyan wheats. This study was designed to investigate:

1) the growth response of a range of wheat genotypes to varying aluminum concentrations in both nutrient solutions and artificial media containing different levels of aluminum
2) the inheritance of aluminum tolerance in crosses involving Kenyan and other cultivars.
3) the response of several wheat genotypes to lime, using two acidic Kenyan soils under greenhouse conditions.

1.2 Rationale for this study

To date the mechanisms of aluminum toxicity have not been fully explained nor have the genes for aluminum tolerance been clearly mapped on their respective chromosomes. However, it has been determined that tolerance to aluminum toxicity is a heritable trait. A number of genes ranging from single dominant, oligogenic and polygenic have been cited to control the trait (Camargo, 1981; Lafever and Campbell, 1978).

In order to assess the effects of aluminum on wheat genotypes, it is important to know which plant characters are affected by aluminum. The present study was conducted in an attempt to contribute fundamental knowledge on these subjects; focusing on the implications of genotype-aluminum interaction in Kenyan wheat varieties. Genetic studies involving Kenya wheats, some of which are known to have tolerance to soil acidity and cultivars known to have aluminum tolerance, will give information about the usefulness, or otherwise, of incorporating aluminum tolerance into the Kenyan wheat breeding programs.

2. LITERATURE REVIEW

2.1 Background

Plant performance is influenced by the interaction of many environmental factors and is often limited by individual components such as soil moisture, temperature and mineral stress. Mineral stress in plants can be caused by either nutritional deficiences or toxicities (Duval, 1976). Deficiences of one or more essential plant nutrients are widespread in the soils of developing countries, resulting in low productivity in vast areas of nutritionally depleted soils. There are large areas of the world , an estimated 2.9 billion hectares representing 22.5 percent of the world land area, that are adversely affected by mineral toxicities and/or deficiencies (Duval, 1976).

Among these problem soils are the highly leached Oxisols and Ultisols, which are characterized by toxic levels of soluble aluminum and manganese (Van Wambeke, 1976). Currently, these areas are either undeveloped for agriculture, or where cultivated, are of very low productivity. Aluminum and manganese toxicities are among the most important factors limiting the growth of crop plants in many acidic soils of the world (Da Silva, 1976; Foy, 1973, 1974; Kamprath and Foy, 1971; McLean, 1976; Olmos and Camargo, 1976).

In Kenya it is estimated that about 30 percent of the total wheat growing area, particularly that comprising Plinthic Ferralsol soils, is acidic, of pH 4.3-5.0 (Mulamula, 1983). The distribution of acidic soils in Kenya has not been clearly illustrated. However, soil analyses from the National Agricultural Laboratories (Nairobi) and Maps from Kenya Soil Survey, (pers. comm.)[1] indicate that areas of Mau Narok, Molo, and Eldoret are characterized by low pH levels in the range of 4.3 to 5.6.

To meet a rapidly growing demand for food during the next four decades, these problem soils must be developed and improved in productivity. This can be done by a combination of crop improvement by breeding, and by improving management practices.

[1]Kenya Soil Survey, Nairobi, Kenya.

2.2 Aluminum and pH relationship

In strongly acidic soils, (those with pH below 5.5), aluminum toxicity is a primary suspect as a growth-limiting factor. However, not even water-soluble aluminum is a reliable guide in predicting the toxicity in a given soil. For instance, Adams and Lund (1966), found that the toxicity of a given level of soluble aluminum in displaced soil solutions is influenced by the total nutrient concentration in a given soil. Similarly, the toxicity of aluminum in various soils is more closely related to its molar activity than to its solubility (Bohn *et al.*, 1979).

Over a large portion of the world, rainfall exceeds evapotranspiration for much of the year, and soil leaching results. Leaching removes the basic cations like calcium and magnesium, thence leaving the upper and sub-soil parts acidic. Local, highly acidic soils can result from exposure to air or mine spoils that contain such compounds as iron pyrites (FeS_2) or other sulphides. In the process of oxidation iron pyrites can form the products sulphuric acid and iron hydroxide ($Fe(OH)_3$), which are acidifying (Bohn *et al.*, 1976; Tisdale *et al.*, 1985).

Crop fertilization can also lead to substantial acidification. Continued use of ammonia or ammonium-based fertilizers can lead to soil acidity. This is a microbially mediated reaction as illustrated in the following equation:

$$NH_4^+ + 2O_2 ========== NO_3^- + 2H^+ + H_2O$$

The hydrogen ions generated from this reaction reduce the soil pH. Less acidity is generated from (mono-ammonium fertilizers, for example) NH_4NO_3, as compared to (diammonium fertilizers like) $(NH_4)_2SO_4$, because only one-half of the nitrogen in mono-ammonium fertilizers can be further oxidized. Similarly, the $H_2PO_4^-$ ion which is released by dissolving phosphate fertilizer granules can lead to acidity near the granules as low as pH 1.5. The $H_2PO_4^-$ ion is rapidly neutralized by soils, but the acidic reaction products may remain to influence overall soil properties (Bohn *et al.*,1979; Tisdale *et al.*, 1985). Plant residues or wastes decomposing into organic acids can also cause soil acidity.

The aluminum ions (Al^{3+}) predominate below pH 4.7 (Bohn *et al.*, 1979). The relationship between extractable soil aluminum and soil acidity has been documented (McLean, 1976). Exchangeable aluminum increases exponentially at low pH values below 5.5 (Lee *et al.*, 1970). It is quite possible to simultaneously have toxic concentrations of aluminum and manganese in acidic soils (Lierop *et al.*, 1982). Aluminum toxicity has been implicated as a contributing factor in the poor yields observed in acid soils for some time (Burgess and Pember, 1923; Vlamis, 1953; Foy, 1974), though only recently has it been suggested as a criterion for determining liming requirements of leached soils (Kamprath, 1971; Reeve and Sumner, 1971). Reduction of calcium, magnesium, potassium and phosphorus availability to the plant is another characteristic of aluminum injury at low pH (Fleming, 1983).

Aluminum and hydroxyaluminum cations are present in most acidic soils, and in some, are the dominant cations on the exchange sites. The formation of "exchangeable" aluminum in soils and clays under relative strongly acid conditions has been widely studied (Chernov, 1959; Coleman, 1961; Davis *et al.*, 1962).

High levels of soluble and exchangeable aluminum are among the major causes of soil infertility of strongly leached mineral soils in the tropics (Juo, 1977). The acidity of soils containing exchangeable aluminum is due to the hydrolysis of aluminum in the soil solution and production of hydrogen ions (Dalal, 1975). However, it has been reported that aluminum toxicity can occur in soils with pH values of as high as 5.5 or more (Adams and Lund, 1966; Hester, 1935).

2.3 Aluminum as related to other elements in soils of low pH

Aluminum does not influence soil pH in isolation, rather, pH is governed in a complex manner due to interaction involving other ions, molecules and groups of compounds. For instance, Lindsay and Moreno (1960), developed a solubility diagram for phosphorus in a system containing variscite ($Al(OH)_2H_2PO_4$) and strengite ($Fe(OH)_2H_2PO_4$). At low pH both strengite and variscite persist. These compounds are sparingly soluble and they render phosphorus unavailable to plants. This is why most acidic soils have high phosphorus deficiencies, because phosphorus is "locked" in an unavailable form. (Bohn *et al.*, 1979).

There is a general relationship between solubility of various ions and change of pH in the soil. As the pH decreases, hydrogen (H^{+}), iron (Fe^{2+}), manganese (Mn^{2+}), and aluminum (Al^{3+}) ions become abundant. On the other hand, as pH increases, calcium (Ca^{2+}), magnesium (Mg^{2+}), potassium (K^{+}), sodium (Na^{+}), and molybdate (MoO_4^{2-}) become abundant in the soil. (Bohn *et al.*, 1979). Therefore, it is likely that low soil pH is associated with many other toxicities and deficiencies other than aluminum.

2.4 Development of aluminum tolerant wheat genotypes

Brazilian wheat breeders pioneered the breeding of wheat varieties resistant to aluminum toxicity. This work was initiated in 1925 (Beckman, 1976), and over the past five decades has resulted in a large number of resistant cultivars. Initially, the Brazilian lines had poor agronomic characteristics, but were later crossed with CIMMYT derived lines which were at the time susceptible to aluminum toxicity, but possessing superior agronomic characters. Consequently, great achievements have been made through the shuttle breeding program between Brazil and CIMMYT resulting in lines which combine resistance to aluminum toxicity, good agrononmic characteristics, broad spectrum of disease resistance and high yield potential (CIMMYT, 1980; 1981).

Against this background, major advances are being made in incorporating aluminum tolerance as a specific method of breeding tolerance to acidic soils. Most of the effective genetic sources originated from Brazil (Rajaram *et al.*, 1981). Incorporation of tolerance by backcrossing and field testing on extremely acidic soils (pH 4.0 to 4.6) has been effective in Zambia in producing tolerant varieties, notably PF7748 ("Whydah") and PF72640, which may yield 1.8 tons/ha as compared to 0.4 tons/ha on these soils with varieties lacking tolerance. (Little, pers. comm., 1985). [2] CIMMYT has played a major role in sending aluminum tolerant screening nurseries to regions with soil acidity problems, and the same good sources

[2]Mt. Makulu Research Station, Private Bag 7, Chilanga, Lusaka. Zambia.

of tolerance as in Zambia were independently identified on soils of pH 4.6 in Kenya in 1981 (Briggs, Kenya/Canada CIDA Wheat Project, 1982 Annual Report), where the non-tolerant wheats were killed by the acidic soil.

2.5 Differential aluminum tolerance of wheat varieties and plants

Differential tolerance of wheat varieties to aluminum in the soil nutrient solution is closely associated with the ability of plants to absorb and use phosphorus in the presence of excess aluminum (Foy and Brown, 1964). Varieties differ widely in their tolerance to aluminum in nutrient solution and to acid soils containing high levels of soluble or exchangeable aluminum (Burgess and Pember, 1923; Hartwell and Pember, 1918). Aluminum injury has been associated with decreases in the uptake and utilization of phosphorus reportedly due to decreased permeability of the plant roots (Burgess and Pember, 1923; Foy and Brown, 1964; Jones, 1961; Wright and Donahue, 1952), and calcium (Hortenstine and Fiskell, 1961; Rees and Sidrak, 1961).

Numerous reports indicate success in selection for aluminum tolerance in breeding programs (Beckman, 1976; Campbell and Lafever, 1976; Da Silva, 1976; Mugwira *et al.*, 1981; Rajaram *et al.*,1981). Nyachiro and Briggs (1983, unpublished) studied a range of Kenyan wheat cultivars using pot tests to compare relative growth in two soils of different acidity levels in the greenhouse. Cultivars showed a wide range of tolerance to the acidic soils. Among the cultivars that showed good tolerance to acidic soils were, 'Romany' and 'Kenya Kongoni', while 'Kenya Swara' and 'Bounty' showed poor tolerance. The nature of this differential tolerance to acidity has not been clarified, partly because the mechanism of acidity/aluminum toxicity is ~~still~~ not fully understood.

Differential response of wheat (*T. aestivum* L.) to high aluminum content of some acidic soils has been documented by several investigators. In the 1960's, it was suggested that the adaptability of certain cultivars to strongly acidic conditions was due to their ability to tolerate high levels of free aluminum (Foy *et al.*, 1965; Neenan, 1960). Using response to increasing levels of aluminum as a criterion for tolerance, it is possible to separate cultivars into several response groups (Aniol, 1983; Kerridge *et al.*, 1971; Lafever *et al.*, 1977). Other workers have also found that aluminum is differentially toxic to different cultivars within a species (Camargo and Oliveira, 1981; Foy *et al.*, 1967).

2.6 How aluminum affects plants

As was indicated earlier, high aluminum levels can interact with other macro- and micro-elements to create a nutrient imbalance. Unfavourable aluminum-phosphorus interactions can cause plants to stunt, when aluminum concentration exceeds phosphorus concentration. Aluminum tolerance of plant species is closely related to the abilities of cultivars to absorb and utilize phosphorus in the presence of excess aluminum (Foy and Brown, 1964).

However, the sensitive wheat cultivars may have a higher absolute internal requirement for calcium or phosphorus (Salinas and Sanchez, 1976). Alternatively, a given concentration of aluminum within the plant may interfere to a greater degree in the metabolism of these elements in the sensitive cultivars. Clarkson (1969) found that aluminum inhibits sugar phosphorylation in cultivars of barley.

Retardation of root growth is one of the major ways aluminum affects plants (Kamprath and Foy, 1971; McKenzie, 1973; Mugwira, 1979; Mugwira *et al.*, 1981; Penney, 1973). Aluminum damages both the lateral and primary root tips. Other researchers have found that, apart from stunting root growth, high aluminum concentrations cause thickening of roots, inhibition of cell division, and abnormal undifferentiated tumor-like tissue (Clarkson, 1965; Hartwell and Pember, 1918; Rees and Sidrak, 1961; Rorison, 1958).

It has been demonstrated that aluminum can alter the type of the DNA (deoxyribonucleic acid) produced in barley roots (Sampson *et al.*, 1965). Recently Wallace and Anderson (1984), documented some evidence on the effects of short-term exposure of wheat (*T. aestivum* L.) to various aluminum concentrations. From their experiment, they found that aluminum inhibits the uptake of thymidine, a vital component in the synthesis of the DNA molecule.

The toxic effect of aluminum is manifested as a drastic inhibition of root growth and is caused by aluminum binding to DNA in root meristematic cells, with consequent inhibition of mitotic cell division and cell elongation (Clarkson, 1969; Matsumoto *et al.*,1976; Morimura and Matsumoto, 1980; Toogood, 1981). In tolerant genotypes, therefore, the existence of some sort of protective mechanism is postulated, which either prevents aluminum entry into the cytoplasm and/or nucleus of meristematic root cells, or influences the aluminum-binding to the DNA. At the same time, it is not known whether the observed influence of aluminum is a direct response or an indirect effect of disturbed DNA transcription (Clarkson, 1965; Klimashevskii, 1975).

2.7 Mechanisms of tolerance to aluminum toxicity

Wheat tolerance to aluminum toxicity is a relative rather than an absolute characteristic, depending on nutrient availability (Carmago *et al.*, 1981).

Fleming (1983) indicated that tolerant wheat cultivars absorbed nutrients more efficiently and induced a higher pH in the root zone than aluminum sensitive cultivars. He also suggested that the differences in NH_4^+-N (ammonium-nitrogen) uptake and utilization may be responsible for other differences between aluminum-tolerant and aluminum-sensitive wheat cultivars. The depressive effect of NH_4^+ -N uptake on the pH of the soil and NO_3^- -N may be useful indicators of aluminum sensitivity. Specific differences in N metabolism may also be important determinants of aluminum tolerance in wheat (Fleming, 1983).

There is supportive evidence that aluminum-sensitive cultivars maintain a lower pH in nutrient solutions than tolerant cultivars (Dodge and Hiatt, 1972; Foy *et al.*, 1965; Otsuka, 1968; Taylor and Foy, 1985). Dodge and Hiatt (1972) found that such cultivar differences in ability to change pH coincided with differential anion-cation uptake. The abilities of certain cultivars to produce or prevent this pH decline could explain higher aluminum tolerance on the basis of reduced aluminum solubility in the root zone of soils with high aluminum content. Conversely, the ability of certain aluminum-sensitive cultivars to reduce the pH of their root zones could cause yield reductions in soils that would not normally be aluminum toxic (pH 5.5), because aluminum solubility and toxicity increases with a low pH.

The concept of the plant itself conditioning the pH of the nutrient solution has been supported by several reports (Fleming, 1983; Taylor and Foy, 1985; Mugwira and Patel, 1977)

Other suggestions have been made, that aluminum tolerance among cultivars of wheat, barley and soyabeans appears to be closely related to the abilities of plants to absorb and transport calcium in the presence of excess aluminum. Sensitive cultivars accumulate lower concentrations of calcium than tolerant varieties when both are under aluminum stress, but in the absence of aluminum the situation is often reversed (Foy *et al.*, 1972).

Greater aluminum tolerance in wheat has also been suggested to be due to a higher internal tolerance to aluminum levels (Ikeda *et al.*, 1965; Neenan, 1960).

Ouellette and Dessureaux (1958) found that aluminum tolerant alfalfa clones contained lower concentrations of aluminum in their tops and higher concentrations of aluminum and calcium in their roots than did the aluminum sensitive clones. It was suspected that the rate of calcium uptake was one of the factors determining aluminum tolerance. Calcium was believed to act in two ways to reduce the toxicity of aluminum: firstly by reducing the uptake of aluminum; and secondly by immobilizing part of the absorbed aluminum in the roots, thus preventing its translocation to plant tops.These investigators, however, did not indicate whether the differential aluminum tolerance among alfalfa clones could also be due to aluminum-phosphorus interactions.

Several investigators have associated aluminum toxicity with reduced gross accumulations of phosphorus and calcium accompanied by increased aluminum concentrations by plant tops grown in nutrient solutions containing aluminum (Clarkson, 1969; Rorison, 1958). However, it is still not exactly known to what extent the uptake, transport and utilization of these elements are involved in the actual mechanism of aluminum injury and how plants avoid the injury.

Some physiological mechanisms have been identified as being associated with tolerance or sensitivity to aluminum among or within species, but none has been found to apply in all cases. In a review of the subject, the following different mechanisms have been suggested by

Foy (1974):

1) Due to differences in root morphology, some aluminum tolerant varieties may keep developing with no injury to the root tips and lateral roots in acidic soils.
2) Changes in pH of the root rhizosphere. Some aluminum tolerant varieties increased the pH of the growth medium, whereas sensitive ones decreased it. Such changes are believed to be as a result of differential cation-anion uptake, secretion of organic acids, carbon dioxide and bicarbonate.
3) Aluminum in the roots does not inhibit the uptake and translocation of calcium, magnesium and potassium in tolerant varieties, whereas it does so in sensitive varieties. Varietal tolerance to aluminum is related to calcium uptake in soyabeans, wheat and barley, to potassium translocation in sorghum, and to magnesium and potassium translocation in potatoes.
4) High plant silicon content has been associated with aluminum tolerance in certain rice varieties.
5) Lower translocation of aluminum to plant tops. Several tolerant plant species and varieties accumulate aluminum in the roots, but translocate it to the tops at a lower rate than the sensitive varieties.
6) Aluminum-tolerant varieties do not inhibit phosphorus uptake and translocation as much as susceptible varieties or species. Also aluminum-tolerant species or varieties are tolerant to low phosphorus levels.

Varietal tolerance both to high exchangeable aluminum and to low available phosphorus levels are related and depend on the plant's ability to translocate phosphorus from the roots to the shoot in the presence of high levels of aluminum solution. This effect is found in rice, maize, wheat, sorghum, and bean. (North Carolina State University, 1974; Salinas and Sanchez, 1976).

2.8 Response of wheat and other crops to lime application in acidic soils with high aluminum

Liming of acidic soils is an amendment process of trying to raise soil pH to a desirable point where free aluminum toxicity is eliminated or reduced to a low scale. In doing this, different amounts of lime can be used depending on the quality of lime, the calculated lime requirement and the target pH after liming (Adams, 1984; Bohn *et al.*, 1979).

In view of the known differential tolerance to aluminum among wheat genotypes and in other species, it should be expected that there will be differential response to lime application among genotypes.

Hoyt *et al.* (1967) found that liming soils when no phosphorus was added, instead of giving any significant yield increase of barley, contributed to several significant yield decreases. However, when phosphorus was added, liming resulted in significant yield increases in the field. Field and greenhouse experimental results were highly correlated. In another experiment Hoyt *et al.* (1982), found that liming soils of pH 5.0 and lower gave a 50 percent yield response in red clover, compared to 4 percent yield response on liming soils from pH 5.6 to 6.0 using the same crop. In alfalfa the yield response was 300 percent on the soils of pH 5.0 and 45 percent on the soils of pH 5.6 to 6.0. Alfalfa is more susceptible to aluminum toxicity than red clover.

On the basis of such data, one may predict that the genotypes which are most affected by aluminum toxicity might show a greater response to liming, compared to the tolerant genotypes. However, the degree of response would also depend on the pH before liming and the final pH after liming.

Liming increases yield by correcting manganese, calcium and phosphorus levels (Kunishi, 1982). Broadly speaking, lime increases solution phosphorus and hence corrects a growth-limiting condition, coupled with an amelioration of aluminum toxicity in the soil. Lim and Shen (1978) working on maize found that grain yield responded positively and significantly to a 100 kg per hectare phosphorus application even for the sixth continous crop after liming. Liming increased soil pH from 4.3 to 4.5 and decreased exchangeable aluminum and percentage of aluminum saturation from 1.9 to 0.3 meq and 67 to 7 percent respectively.

A strong negative relationship existed between grain yield and exchangeable aluminum which accounted for the 74 percent of the yield variations. Leaf magnesium concentration was also increased from 0.14 to 0.4 percent with lime application in the Lim and Shen (1978) study.

Lierop *et al.* (1982) reported that by liming soils of pH (H_2O) ranging from 4.6 to 5.0 they obtained a 40 percent yield increase of potato tubers. No significant yield increases were obtained from soils which had pH values higher than 4.9 (H_2O). From their study, they found that yields were generally not increased by liming when the concentration of exchangeable soil aluminum was less than 0.9 meq/100g soil.

Mugwira *et al.* (1981) demonstrated significant yield increases in different wheat cultivars afte[illegible]en soil they studied was limed from an initial pH of 4.5 to a pH of 5.8. From this expe[illegible]ey found that liming the Bladen soil increased the top growth of aluminum-sensitive wheats. Foy *et al.* (1965; 1967) also found that liming Bladen soil to pH 5.8 reduced or eliminated the differential growth of wheat cultivars possessing different tolerances to aluminum. Lafever *et al.* (1977) showed ratios of yields on unlimed plots to those on limed plots ranging from 0.98 to 0.16. Significant yield differences in wheat have also been reported by Foy *et al.* (1974) and are described in Alberta Agriculture Publication (1982).

Response of wheat genotypes and other crops to liming depends upon the degree of soil acidity, the type of crop and management practices in a particular area. The purpose of liming is primarily to reduce the exchangeable aluminum. This is normally accomplished by raising the pH to 5.5, below which aluminum effects on wheat start to be expressed. One factor to consider when liming is the amount of lime needed to decrease the percentage aluminum saturation to a level at which a given genotype or crop can grow well.

2.9 Heritability of aluminum tolerance in wheat

Hartl (1980) defines heritability as the ratio of additive genetic variance to phenotypic variance. The additive portion is capable of being genetically fixed. The plant breeder's interest in heritability arises from his having to use the phenotypic value of the character as a guide in selecting individuals for further breeding purposes. The breeding value of the individual, however, can only be established by determining the mean value of its progeny, as expressed in a heritability value.

According to Hartl (1980) if a breeder chooses individuals to be parents according to their phenotypic values, his success in changing the characteristics of the population can be predicted only from a knowledge of the degree of correspondence between phenotypic values and breeding values.

Heritability estimates can be calculated in several different ways:

$$\text{(i)}\ h^2 = Va / Vp$$

where h^2 is the heritability value, Va is the additive variance component, and Vp is the phenotypic variance.

$$\text{(ii)}\ h^2 = Bop$$

where Bop is the regression of the offspring on the parent(s).

High heritabilty does not imply that a trait is relatively insensitive to environmental change. It may be wrongly assumed that high heritabilities for the same quantitative trait in two different populations imply that any difference in the means of the two populations is hereditary or largely hereditary (Hartl, 1980). The high heritabilities only imply that, within each population much of the phenotypic variance is attributable to genetic differences among individuals. By themselves, the high heritabilities are meaningless in comparing two populations grown under different environmental conditions. Therefore, studying heritability of aluminum tolerance becomes a demanding procedure, with respect to controlling environments. Aluminum tolerance in wheat has been shown to be a heritable trait (Camargo, 1981; Lafever and Campbell, 1981). Dominant, partial and additive (polygenic) gene actions have all been postulated to confer aluminum tolerance in different populations of wheat (Camargo, 1978; lorczeski, 1977; Lafever and Campbell, 1978). Campbell and Lafever (1981) estimated the heritabilities of 48-F1 wheat lines to be 0.51 and 0.91 based on male and female parents, respectively. These high heritabilities indicated that selection would be effective in isolating aluminum-tolerant lines.

2.10 Justification of breeding for aluminum tolerance

There is a possibility of breeding for aluminum tolerance since this is a heritable trait (Camargo, 1981; Campbell and Lafever, 1981; Kerridge *et al.*, 1971).

In Kenya, wheat cultivars which perform well in areas characterized by low pH have been demonstrated (Briggs, Kenya/Canada CIDA Project, 1982 Annual Report). The role of aluminum tolerance in these cultivars has not been investigated. It is known that there exists a wide range of tolerance to aluminum toxicity, and the possibilities for breeding for aluminum tolerance seem worth investigating.

The conventional methods of raising pH by liming are costly and do not provide permanent solutions to aluminum toxicity. Bolton (1977) reported that annual lime losses from Rothamsted and Woburn in England amount to 467 and 536 kg/ha. respectively. In Canadian work Hoyt and Henning (1982) found a similar trend for lime loss. They measured the loss of lime over an 8-year period in six soils that had been limed with calcium hydroxide ($Ca(OH)_2$) to pH 6.5 -7.0. The average loss of lime from the soils was equivalent to 495 kg calcium carbonate ($CaCO_3$) per hectare annually. This was accompanied by a decline in pH of 0.48 units in the 8-year period.

One may argue that the lime that is lost goes into liming the sub-soil region thus providing a long term benefit to subsoil root growth. While this may be true, it is also possible that the loss of lime from the surface soil leaves the top soil more acidic such that plant root growth will be negatively affected before the sub-soil region is penetrated.

An hypothetical liming program has been suggested by Alberta Agriculture (Agdex 834-2, 1982). In this program if a soil of pH 5.0 is limed to pH 6.5, after 2 years the pH will start to decline, eventually reaching a minimum of pH 6.0 after 12 years. This decline could be even greater depending on the cropping and fertilization practices used (Perl *et al.*, 1982). The economic merit of liming is still a debatable issue. Hoyt *et al.* (1982) showed that there are large net returns on investments that accrue over the years from the application of lime.

In Kenya some of the wheat growing areas like Molo, Olenguruone, Elgeyo Border, Moiben, Kaptagat, and other places in Uasin Gishu have acidic soils. These areas are far distant from available lime sources. Transportation costs for this bulk commodity make liming uneconomical. Possible use of other products such as calcium oxide (CaO -quicklime), and calcium hydroxide ($Ca(OH)_2$ -slaked lime) is also uneconomical since they are even more costly than dolomitic lime. This places breeding for aluminum tolerance among the high priorities in breeding programs for such soil regions.

Liming Kenya soils from pH 5.5 to 6.5 may require 5.0 tons of lime per hectare (National Plant Breeding Station, 1985, pers. comm.).[3] At the cost of KSh. 250/= per ton of lime, this will cost a farmer KSh. 1150/= per hectare excluding transportation, and lime application costs.[4]. In 1986 values this is equivalent to approximately 475 kg of wheat grain. It may be argued that yield increases realized due to liming may offset the cost of liming. However, if the cost of liming can be partly avoided through use of acid soil tolerant varieties then the farmer can allocate his resources to farming activities other than liming. This subject area requires a separate study to determine the economics of liming versus use of tolerant varieties. Perhaps for the longterm agronomic practices combining both approaches will be needed in Kenya (Nyachiro and Briggs, 1985).

In some case liming can result in development of other undesirable conditions. Lierop *et al.* (1982) reported that liming soils to a pH above 4.6 in a potato field can increase the development of common scab on tubers and thereby reduce their market value. A report in the literature (Tisdale *et al.*, 1985) has indicated that take-all disease of wheat increases when soils are limed. However, the economic yield losses due to take-all after liming as compared to yield increases associated with liming need to be determined.

The feasibility of deep lime incorporation largely depends on soil structural properties and available equipment. It appears reasonable to assume that this would be possible in sandy soils and highly aggregated Oxisols and Andepts, but less possible in Ultisols and clayey argillic horizons.

Reducing aluminum toxicity in the subsoil is a major and most difficult management objective in many areas of the tropics (Pearson, 1975). When deeper lime incorporation is not

[3]National Plant Breeding Station, P.O. Njoro, Kenya. (East Africa).
[4]1 KSh = $ 0.0862 Canadian, 1986.

feasible, other ways must be sought. The use of aluminum tolerant varieties is one of the alternatives.

In some cases there is no positive response to liming. Kamprath (1971) reviewed the reasons for lack of positive lime responses when highly leached soils are limed to neutrality. The consequences of overliming are yield reduction, soil structure deterioration and decreased availability of phosphorus, zinc, boron and manganese (Adams, 1984). Overliming can be defined as liming at higher rates than necessary to neutralize the exchangeable aluminum or eliminate manganese toxicity. These problems associated with soil amendments using lime make breeding for aluminum tolerance a reasonable alternative, since there is a good range of known genetic tolerance available.

The mechanisms leading to the yield advantage of tolerant varieties are not known, but it is suspected that improved subsoil root penetration by aluminum tolerant varieties may be one factor (Toogood, 1981), and more efficient utilization of available phosphorus may be another, at least in East African soils.

Toogood (1981) and Little (1983) have suggested that there are some advantages of root penetration into acidic subsoil by aluminum tolerant genotypes even when top soil is ameliorated. One of the suggestion is that aluminum tolerant varieties are able to develop deeper rooting systems in acidic subsoils than do susceptible varieties. Aluminum tolerant varieties should therefore offer better tolerance to drought stress than susceptible varieties due to their deeper root systems.

2.11 Techniques of screening for aluminum tolerance

Various screening techniques have been used to identify aluminum tolerant wheat cultivars. Nutrient culture and field screening techniques seem to give acceptable results (Foy *et al.*, 1972; 1973; Kerridge *et al.*, 1971; Lafever *et al.*, 1977; Polle *et al.*, 1978).

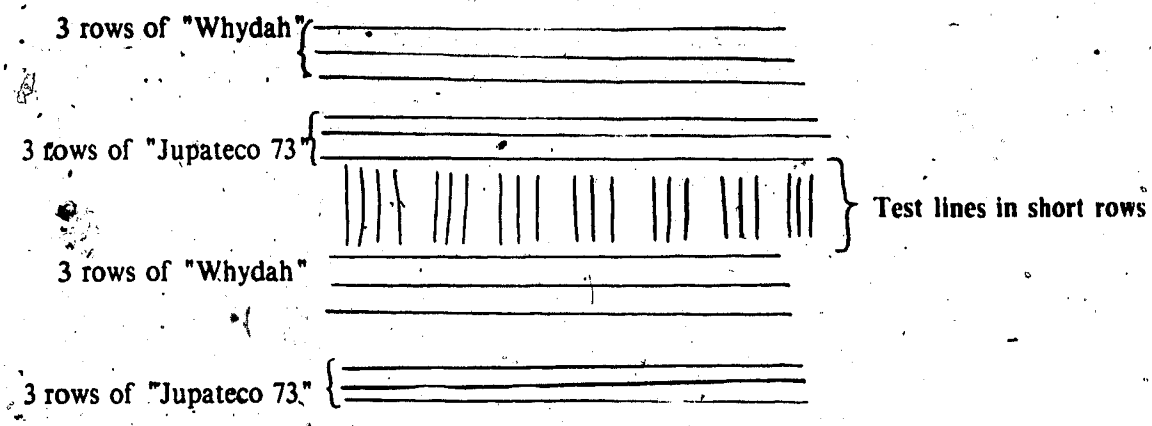
The screening procedure adopted by many workers for detecting tolerance to soluble aluminum in wheat is based upon the visual estimation of the extent of hematoxylin staining of seedling roots following exposure to several levels of aluminum concentration (Polle *et al.*, 1978). CIMMYT uses a modified method adopted from Polle *et al.* (1978) to screen wheat for aluminum tolerance (CIMMYT, 1985, pers. comm.) This method is quick when used to separate very tolerant and susceptible varieties. However, the method does not provide any quantitative data. At the same time the scoring procedure of rating varieties on a 1-9 scale may be subjective depending on prior knowledge of certain varieties, although this bias can be eliminated by coding varieties prior to assay.

According to Foy (1974) one of the mechanisms for aluminum tolerance is that, although aluminum tolerant varieties do accumulate aluminum in their roots, they translocate it to the tops at a lower rate than do sensitive varieties. If this is true, then by using the Polle *et al.* (1978) method alone, it is possible to assign a tolerant variety to a group of susceptible varieties in error due to the different mechanisms in effect. The Polle *et al.* (1978) method should normally be used in conjuction with other methods to determine a complete picture of tolerance levels.

Nutrient culture solutions have been used to screen aluminum tolerant cultivars (McNeilly, 1982; Mesdag and Slootmaker, 1969). Acidic soil techniques combined with nutrient culture techniques have been used to screen for aluminum tolerant cultivars (Foy *et al.*, 1972; 1973). Other investigators have used field plots located on acidic soils with high aluminum levels (Lafever *et al.*, 1977; Little, 1983; McKenzie,1973).

In Mbala, Zambia, a field method is used to screen for aluminum tolerance. In this method materials are screened in a field with pH 4.2 to 4.7 (H_2O). This field is kept lime-free. Two control varieties are used namely "Jupateco 73" (susceptible) and "Whydah" formerly "PF7748" (tolerant). Three rows of each control varietyare planted across the field and the test lines planted at right angles to the controls. This procedure eliminates the scoring bias that can arise due to variabilty of acidity levels or aluminum concentrations across the field. Also control varieties may be included amongst the test lines at frequent intervals

This arrangement is illustrated as follows:



Field vigour is the criterion of scoring (1- excellent, 9- poor). This method is very reliable when test lines are replicated across the field, and it represents the actual response of a cultivar in a given acidic soil under relevant agro-environmental influences.

In Kenya materials for aluminum tolerance screening are planted in Eldoret in nurseries located on soils of known acidity. Test lines are replicated within the nurseries and lines are selected while weak lines get discarded. The concept of using extensive aluminum tolerant controls has not been adequately ~~used~~ in Kenya as compared to Mbala, Zambia. This method of recording general plant growth and vigourin acidic soils was reported earlier by Salinas and Sanchez (1976).

Root tolerance index (RTI) has been used as a determinant of tolerant wheat cultivars (Taylor and Foy, 1985). The RTI is defined as the weight of roots grown with aluminum divided by the weight of roots grown without aluminum. Varieties showing a high RTI will be classified as tolerant, while tho[illegible] RTI will be classified as susceptible. Using this criterion it should be noted that the level of aluminum concentration will determine the RTI boundaries with respect to the cultivars used in a test. To determine RTI a number of cultivars can be grown at a tim[illegible]ols, in nutrient culture solutions or other media of known aluminum concentration. Results from field plots and greenhouse pot experiments correlate well with nutrient culture experiments (Foy *et al.*, 1965; Kerridge *et al.*, 1971; Lafever *et al.*, 1977; Mugwira *et al*, 1981).

Among the problems that can be encountered when screening for aluminum tolerance by using either nutrient culture solutions or field conditions are: inaccuracy of visual assesment, assaying, small seedlings, amount of staining, plant to plant variability, and adequate control of screening environments. However, these problems can be minimized by calibrating the methods being used with a high frequency of control varieties in every test as suggested by Polle *et al.* (1978).

3. MATERIALS AND METHODS

3.1 General description of the experiments

The experiments for this study were conducted during the years 1984, 1985 and 1986, and were designed to determine the effects of acidic and aluminum conditions in some Kenyan soils and a range of Kenyan wheat varieties.

In the first year of the study (1984) pure seed of selected genotypes was developed by growing seed in the field (University of Alberta Experimental Farm - Department of Plant Science, Michener Field) and roguing any off-types. Seed from this increase was used in all the experiments. Original seed lots were obtained from Mexico, Kenya and the U.S.A. and had been increased in the California winter nursery during the winter of 1983-84.

During the first year of the study, preliminary screening of 17 genotypes was carried out using the method described by Polle *et al.* 1978. The purpose of this study was to determine which genotypes were tolerant or susceptible in order to help in designing a suitable crossing block for the genetic study. In the same year crossing started using 4 genotypes of different genetic backgrounds as female parents and 3 male parents of varied aluminum tolerance levels and of varied genetic backgrounds. Genotypes for the study were chosen on the basis of diversity for their pedigree interrelationship (Appendix 1).

During the second year (1985) experiments using acidic soils from Kenya were conducted in the greenhouse at the University of Alberta to determine the effect of aluminum and liming on various plant characters. Other experiments were carried out using a few selected genotypes grown in artificial media (University of California Mixture, UCM - 1:1, sand:peat ratio), augmented with different levels of aluminum. Studies on nutrient culture solutions containing different levels of aluminum were also carried out on several of the genotypes.

During the third year (1986) F2 populations from 12 crosses were screened using the method used by CIMMYT. A random sample of 90 seedlings per cross were progeny tested for tolerance and susceptibility in UCM that was augmented with 46 ppm concentration of aluminum. These tests were conducted to determine the effect of high aluminum concentrations on different genotypes of wheat, and to determine genetic ratios.

The objectives stated necessitated that five different, but related experiments be conducted. Details of each experiment are presented separately.

3.2 EXPERIMENT 1: Variety classification

The objective of the first experiment was to classify 17 wheat (*T. aestivum* L.) varieties according to their tolerance to aluminum.

Seventeen wheat varieties were tested for aluminum tolerance using the method described by Polle *et al.* (1978). Varieties PF7748, Maringa (tolerant) and Siete Cerros (susceptible) have been classified by CIMMYT (pers. comm.) and were used as the controls. The other varieties included Romany, K.[5] Tembo, K. Fahari, K. Swara, K. Kongoni, Bounty, K. Nungu, K. Kulungu, K. Kima, K. Nyumbu, K. Tumbili, K. Zabadi, K. Popo and Paa representing a crosss section of the elite germplasm of wheat used in Kenya. The pedigrees of the 17 wheat varieties are presented in Appendix 1. The varieties were coded during the experiment to avoid any biases.

50 seeds of each variety were pregerminated in petri dishes at 27 °C in the germinator for one day. After emergence of the radicle and the plumule, sound and uniform seedling were transferred into nutrient culture solution as described by Polle *et al.* 1978. Three aluminum concentration levels were used: 8 (0.3 *m*M), 16 (0.59 *m*M) and 46 (1.72 *m*M) ppm supplied as $AlCl_3.6H_2O$. This experiment was conducted in the laboratory at ambient temperatures of 20 to 22 °C with light of approximately 16,000 m^{-2}.cd.sr provided for 10 hours daily and relative humidity of approximately 70%. Ten seedlings per variety with well developed roots were chosen for scoring for aluminum tolerance after staining with hematoxylin. Scoring was done on a 1 to 5 scale (visual judgement), where 1 was designated as the nonstaining, tolerant characteristic of PF7748 and Maringa, and 5 as the susceptible (heavy staining) characteristic of Siete Cerros. Varieties after scoring were assigned to one of

[5]Stands for Kenya throughout the text

the categories:

1) category I scored 1,
2) category II scored 3,
3) category III scored 5.

The design of the experiment was a complete randomized block with 17 varieties, 4 replicates and 3 aluminum treatments

3.2.1 Statistical analyses

The scores were square root transformed using the formula $\sqrt{Y+0.5}$, where Y represented the raw score and 0.5 a transformation coefficient. The transformed scores were subjected to the analysis of variance (ANOVA). Back-transformed mean score values were determined by squaring the transformed mean score values and subtracting 0.5. The back-transformed mean score values were used to classify varieties into categories of tolerance. The Duncan's Multiple Range Test (DMRT) at $P \leq 0.05$ was used to separate varieties according to their back-transformed mean score values.

The square root transformation was chosen on the basis that:

1) it reduces the amount of heterogeneity over that in the raw data
2) it does not violate the assumptions of the ANOVA as drastically as data requiring a logarithmic transformation
3) the scores were not parametric, so they could not be subjected to the ANOVA before transformation.

3.3 EXPERIMENT 2: Variety response in aluminum nutrient culture solution

The objective of the second experiment was to investigate whether 16 varieties of wheat responded differentially to varying concentrations of aluminum in nutrient culture solution.

The same varieties as those used in the Experiment 1, except PF7748, were used in this experiment along with the same selection criteria. The experimental design was a randomized complete block with 16 varieties, 4 aluminum treatments, and 3 replicates (192 cells). Due to handling constraints, replication was attained in time (external replication). The aluminum treatment levels were 0 (control), 4 (0.15 *m*M), 16 (0.59 *m*M) and 64 (2.37 *m*M) ppm supplied as $AlCl_3.6H_2O$. A wider range of aluminum concentration Experiment 2 was used to study related responses of wheat genotypes compared to a narrower range of aluminum concentration in Experiment 1. The nutrient culture techniques used were similar to those described by CIMMYT (1985, pers. comm.) with some modifications. Fifty seeds were pregerminated in the petri dishes for 1 day at 27 °C germinator temperature after which the germinated seeds were placed in the nutrient solution as described by Polle *et al.* (1978). After two days the nutrient solution was changed and different levels of aluminum treatments were augmented in the respective trays. After two days the roots of seedling were washed with distilled water and stained with hematoxylin. The seedling were then washed to remove excess hematoxylin before they were placed in fresh nutrient culture solution without aluminum for another two days. Finally, the seedling were removed from the nutrient culture solution and their roots were rinsed with distilled water. Seedlings were then placed in a cold room between -4 and -7 °C for one day to arrest growth before measurements were made. The longest root of each seedling was measured. Twenty seedlings of each variety were sampled at random and oven dried at 60 °C for 48 hours and root weight, shoot weight and biological yield in mg were determined.

Root tolerance index (RTI), shoot tolerance index (STI) and biological yield tolerance index (BYTI) were computed by dividing the seedling weights of the roots, shoots and biological yields grown in aluminum by those grown without aluminum, respectively.

The experiment was conducted in the laboratory at ambient temperatures of 20 to 23 °C with artificial light of approximately 16,000 m^{-2}.cd.sr provided for 10 hours daily and a relative humidity of approximately 70%.

3.3.1 Statistical analyses

Data were analysed by the SPSS-X Release 2.1 Statistical Package of the University of Alberta. All sets of data for the 4 agronomic characters root weight, shoot weight, biological yield and the three indices RTI, STI and BYTI were subjected to ANOVA using a linear additive random model as outlined in Steel and Torrie (1980):

$$Y_{ijkl} = \mu + R_i + T_j + V_k + (TV)_{jk} + e_{ijkl}$$

where Y_{ijkl} is the response of the k^{th} variety in the i^{th} replicate in the j^{th} treatment in the l^{th} macro-enviroment; μ is the experimental mean; R_i is the effect of i_{th} replicate; T_j is the effect of j^{th} treatment; V_k is the effect of the k^{th} variety; $(TV)_{jk}$ is the interaction between j^{th} treatment and k^{th} variety; and ϵ_{ijkl} is an error associated with an individual plot.

The expected mean squares for each variable were estimated as follows:

Source of variation	d.f.†	Expected Mean Squares (EMS)
Replicates	R-1	$\delta^2_e + \delta^2_{TV} + \delta^2_R$
Treatments	T-1	$\delta^2_e + \delta^2_{TV} + \delta^2_T$
Varieties	V-1	$\delta^2_e + \delta^2_{TV} + \delta^2_V$
Treatment x Variety	(T-1)(V-1)	$\delta^2_e + \delta^2_{TV}$ ←
Error	{(TxV)-1}(R-1)	δ^2_e ←
Total	(TxVxR)-1	

† degrees of freedom

←.... indicates the appropriate error term for testing.

Mean values for all the measured characters and determined indices among the three aluminum treatments were compared using standard errors (SE); and DMRT at $P \leq 0.05$ was used to separate the variety mean values for the 4 agronomic characters and 3 indices.

Stepwise multiple regression analyses were used to estimate the magnitude of the characters and indices contributing to variation in the biological yield and BYTI, respectively. A brief outline of the regression models (Cochran and Cox, 1957) that were adopted for these analyses are presented here:

$$(1)\ Y_u = \phi (X_{1_u}, X_{2_u}, \ldots\ldots, X_{ku} + \epsilon_u$$

where Y_u was the biological yield response as a function of the levels of aluminum treatments; u =1, 2, 3, ... N represented the number of observations in the experiment; X_{iu} represented the level of the i_{th} factor (aluminum treatment) in the u_{th} observation. ϕ represented the response surface, e_u measured the experimental error of the observation. Fitting of the multiple linear regression of Y_u on the k variables X_{iu} (i = 1, 2, ..., k; u = 1, 2, ..., N) was done using the following equation:

$$(2)\ Y_u = \beta_0 + \beta_1 X_{1_u} + \beta_2 X_{2_u} + \ldots\ldots + \beta_k X_{ku} + \epsilon_u$$

To explain the relationship between Y_u and the X_{iu}, a dummy variable of +1 for every observation in the sample was introduced in the equation (2) to give the equation (3):

$$(3)\ Y_u = \beta_0 X_{0_u} + \beta_1 X_{1_u} + \beta_1 X_{2_u} + \ldots\ldots\ldots + \beta_k X_{ku} + \epsilon_u$$

which was used throughout the analyses. Using this equation (3) both biological yield and BYTI were separately each regressed on variables X_1, ..., X_k with various combinations of these being taken to obtain a possible minimun of residual variance in terms of the smallest number of independent varriables. This was done by dropping any potential independent variable that did not remove a significant independent portion of the variation as explained in Steel and Torrie (1980) and Cochran and Cox (1957). The R^2 values (multiple regression coefficients of determination) giving the indication of the amount of variation accounted for by the equation were also determined.

3.4 EXPERIMENT 3: Variety response in the University of California Mixture (UCM) augmented with aluminum

The objective of the third experiment was to determine if 8 wheat varieties responded differentially in artificial medium (University of Calfornia Mixture - UCM) augmented with different levels of aluminum concentrations.

Eight wheat varieties Romany, K. Tembo, K. Fahari, K. Swara, K. Kongoni, PF7748, Siete Cerros and Bounty were used in the experiment. PF7748 and Siete Cerros were used as the tolerant and susceptible controls, respectively. The other varieties Romany and K. Swara were representatives of germplasm previously widely grown in Kenya and believed to have some tolerance and susceptibility to acidic soils, respectively. The varieties K. Tembo, K. Fahari, K. Kongoni and Bounty were included in the study to represent a general cross section of the popular Kenyan wheats.

The experimental design was a randomized complete block with 3 replicates, 8 varieties and 3 aluminum treatments. Aluminum treatment levels were 0 (control), 8 (0.30 *m*M) and 16 (0.59 *m*M) ppm supplied as $AlCl_3.6H_2O$.

40 kg of air -dry UCM (1:1, peat:sand ratio) were weighed. To this 20 g KNO_3, 20 g K_2SO_4, 168 g $Ca(H_2PO_4)_2$, 200 g $CaMg(CO_3)_2$ and 168 g ground hoof and horn were added. The contents were thoroughly mixed in a sand mixing machine. After mixing, a sample of the mixture was taken for chemical analysis (Appendix 3). 900 g of this mixture were weighed into 1 litre non- draining plastic containers. Ten seeds were planted per pot and later thinned to five per pot shortly after emergence.

The plants were grown in the greenhouse at the University of Alberta in August 1985. Environmental conditions in the greenhouse were controlled with average temperatures of 24 °C (day) and 18 °C (night), 18 hours of light using 492 $m^2.kg.s^{-3}$ sodium light bulbs, and 70% relative humidity. Plants were harvested after 30 days growing time. During the growing period, four doses of 100 ml solutions containing 8 ppm or 16 ppm of aluminum concentrations were applied to each pot as appropriate for each treatment. The first dose was applied on the planting day followed by three more doses at weekly intervals. Pots were watered to field capacity using distilled water and no additional nutrients were supplied during the experiment.

Data were collected on a plot basis (where a pot represented a plot), as follows: plant height was measured in cm from the base of the plant to tip of the tallest leaf, and the number of tillers per pot were recorded one day prior to harvesting. During harvest, the entire plants were recovered. The roots were washed and whole plants were partitioned into roots and shoots. The samples were oven dried at 60 °C for 48 hours before determining root weight and shoot weight. Biological yield was estimated from the sum of root weight and shoot weight. RTI, STI and BYTI were computed using the same principle employed in Experiment 2.

3.4.1 Statistical analyses

All sets of data for the measured characters and computed indices were subjected to the ANOVA using a random linear additive model similar to that which was used in Experiment 2. Expected mean squares for each measured character were also estimated as described in Experiment 2.

DMRT at $P \leq 0.05$ was used to separate treatment mean values and variety mean values for all the measured characters and the 3 computed indices. Stepwise multiple regression analyses as described in Experiment 2 were used to determine the magnitude of dependence of biological yield on the variables plant height, shoot weight, root weight and number of tillers. The magnitude of dependence of BYTI on the independent variables RTI and STI was also determined using the same regression models.

3.5 EXPERIMENT 4: Inheritance of aluminum tolerance

The objective of the fourth experiment was to determine the nature of the inheritance of aluminum tolerance using single crosses and by examining segregation ratios in the F2 generations. F2 plants were compared with their respective parents.

K. Kongoni, K. Tembo, K. Fahari and K. Swara were the female parents in crosses with the following 3 male parents: Romany, PF7748 and Siete Cerros. The females were general representatives of the germplasm of the Kenyan wheats as was explained in Experiment 1. In the spring of 1984 a number of varieties were grown at the University of Alberta, Department of Plant Science Research Farm (Michener Field) for seed purification.

Plots were thoroughly rogued for any off-types. Seed from plants of visually verified identity from these plots was used in this study. Female parents were chosen on the basis of the preliminary results that were obtained in Experiment 1. The male parents were selected on the basis of good tolerance which was determined in Experiment 1. (Romany), while PF7748 (tolerant) and Siete Cerros (susceptible) were selected on the basis of their earlier reported responses to aluminum (Camargo *et al.*, 1981)

The sequence that was followed in handling the the crosses is illustrated as follows:

SEED PURIFICATION

1) The seed was purified in a winter increase nursery in California in 1983/84 and again in the field at Edmonton 1984.

CROSS MADE

1) U of A, 1985. The crosses were made in the greenhouse.

F1 U of A, 1985. The F1 plants were grown as individually in root trainers in the greenhouse for seed increase. Insufficient F1 seed was obtained to allow it use in the genetic analysis.

F2 1) U of A, 1985. F2 seedling were tested for aluminum tolerance, visual separation of F2 tolerant and susceptible seedlings, and recording of individuals in each category above. Random selection of individuals from each category above, for transplanting in the greenhouse.

TOLERANT SUSCEPTIBLE

F2 POPULATIONS PROGENY TESTED

1) U of A, 1985-86. 90 plants of each cross were grown in UCM augmented with high aluminum concentrations (46 ppm), and mature F2 plants were assessed as

described in the text.

During crossing precautions were taken to avoid selfing. After emasculation, the emasculated heads were left for 4 days for the ovary to mature. Before fertilization was done on the fourth day, all the emasculated ears were checked for any seed-set. If any had seed-set they were discarded. The red chaff colour of the variety Romany was used as a marker for those crosses that involved this variety. Parents were also grown alongside the F2 segregating populations as an added means of checking any selfings that were suspected.

Assessment of the aluminum tolerance of the seedlings was carried out as explained in Experiment 1 with some slight modifications. Seeds were pregerminated in petri dishes in a germinator set at a temperature of 27 °C for one day. Germinated seeds were placed on appropriate racks on the surface of the nutrient solution trays. Each tray contained 12 litres of nutrient solution that was made with 240 ml of nutrient stock solution and distilled water as described by Polle *et al.*, (1978). The solution pH was adjusted to 4.0 with 0.25 M HCl solution. After 48 hours in nutrient solution, racks with seedlings were transferred to a new nutrient solution that contained 46 (1.72 *m*M) ppm of aluminum for 17 hours (overnight). Thereafter, roots were washed with distilled water to eliminate excess aluminum before staining with 0.2% hematoxylin solution for 15 minutes. Excess hematoxylin was washed off the roots with distilled water and seedling were then suspended in trays with distilled water for 40 minutes. After this stage, racks with seedlings were transferred into nutrient solution for 48 hours, before scoring for individual seedlings was done by comparing with control varieties PF7748 (tolerant) and Siete Cerros (susceptible). Seedlings were scored tolerant if root regrowth after staining was greater than or equal to the tolerant control (PF7748); and susceptible if no noticeable regrowth occurred compared to the susceptible control (Siete Cerros). The seedling assesments were done in the laboratory at a room temperature of 21 °C, with normal daylight and constant forced aeration. The large number of seedlings that were screened before transplanting depended on the number of seeds that were available in the F2 generation from each of each cross.

The UCM was used as the growing medium in Experiment 3. 2 kg of this mixture was weighed into 'McConkey' 18 cm diameter non-draining plastic pots. A representative sample of 90 F2 seedlings from each cross was transplanted and 9 seedlings were planted in each pot in an octagonal pattern with the ninth plant in the centre. With this pattern it was possible to collect data on an individual plant basis. The pots were watered to field capacity using ordinary tap water as was predetermined before the start of the experiment. One week after transplanting, 100 ml of solution containing 46 (1.72 *m*M) ppm of Al^{3+} was applied to each pot. This was followed by 3 similar applications at one week intervals. Additional nutrient solution containing 4 *m*M $CaCl_2$, 6.5 *m*M KNO_3, 2.5 *m*M $MgCl_2.6H_2O$, 0.1 *m*M $(NH_4)_2SO_4$ and 0.4 *m*M NH_4NO_3 (Polle *et al.*, 1978), was applied twice at the rate of 80 ml per pot on each application.

The F2 population test plants were grown in the greenhouse at the University of Alberta during November, 1985 to February, 1986. Greenhouse growing conditions were kept at average temperatures of 24 °C (day) and 20° (night), with 18 hours of light using 492 $m^2.kg.s^{-3}$ sodium light bulbs, and an average relative humidity of 75%.

Data were collected on an individual plant basis. At maturity, plant height (PHT) in cm was measured for the main tiller of each plant. The number of kernels per head was recorded on each main tiller. Whole plants were harvested and oven-dried at 60 °C for two days. The seeds produced by each plant were weighed and counted and the 1000 kernel weight (KWT) g was estimated from these determinations. Biological yield (g) was determined and harvest index (HI)% was calculated from these determinations.

3.5.1 Statistical analyses

A chi-square of homogeneity (χ^2) was used to determine the significance of the seedling segregation ratios using the hypotheses of 3:1, and 9:7 (tolerant:susceptible)model.

All sets of data for the parents and F2 progeny were subjected to the ANOVA. Each cross was handled separately. The F2 mean values (Y_1) and variances (s^2_1) were compared to mid-parent mean values ($\overline{Y_2}$) and variances (s^2_2), respectively.

A *t*-test was used to compare the mid-parent mean and F2 progeny mean values. The *t*-test values were derived for each pair of samples in each cross for every measured agronomic character.

In computing the t-test values, weighted averages of the sample variances s^2 were calculated using the equations as indicated in Steel and Torrie (1980). A summary of the equations that were adopted is shown here:

(1) $s^2 = (n_1 - 1)s^2_1 + (n_2 - 1) s^2_2/(n_1 - 1) + (n_2 - 1)$

where s^2 respresen ts the weighted average variance , and n_1 and n_2 represent the sample size of the F2 progeny individuals, respectively. The $s_1{}^2$ and $s_2{}^2$ represent the variances of the F2 progeny individuals and the mid-parent individuals, respectively.

Due to $n_1 \neq n_2$, the appropriate standard deviations were calculated using the equation:

(2) $s_{\bar{Y}^1 - \bar{Y}^2} = \sqrt{s^2[1/n_1 + 1/n_2]} = \sqrt{s^2 [n_1 + n_2]/ (n_1)(n_2)}$

Finally, the appropriate t-test values were determined by dividing the differences of mid-parent and F2 progeny sample mean values by the appropriate standard deviations as follows:

(3) $t = (\bar{Y}_1 - \bar{Y}_2) / s_{\bar{Y}^1 - \bar{Y}^2}$

where $s_{\bar{Y}^1 - \bar{Y}^2}$ represents the appropriate standard deviation; $\bar{Y}_1$, $\bar{Y}_2$ represents the mean values of F2 progeny and mid-parent individuals, respectively.

The weighted average of the sample variances was selected for use on the basis of superiority to the arithmetic average, which gives equal weight to the sample variances. Pooled degrees of freedom were used in each separate cross to determine the critical t values.

3.6 EXPERIMENT 5 : Variety response to lime treatment

The objective of the fifth experiment was to determine if 7 wheat varieties of different aluminum tolerance levels responded differently to lime treatment when grown under greenhouse conditions in two Kenyan soils from the Eldoret and Molo regions. Various plant characters were measured to provide evidence for the responses to lime treatment.

3.6.1 Soils

Two groups of widely differing acidic Kenyan soils were used for the study in the greenhouse. The soils were air-dried and ground so as to pass through a 2 mm screen. The physical and chemical properties of the soils that were used in the study are presented in Appendix 3.

The aluminum and manganese concentrations in these soils were not known at the time this study was started but soils were known to be significantly acidic (Appendix 3). All soils samples were obtained from the 0-22 cm top layer from fields which were previously cultivated with wheat. The Eldoret and Molo soils belonged to the Plinthic Ferralsols and Mollic Andosols taxonomic classes, respectively. The soils, the Plinthic Ferralsols (Eldoret soils) and the Mollic Andosols (Molo soil) are referred to throughout the text as Ferralsols and Andosols, respectively.

The two groups of sôils that were used in the study were obtained by combining and thoroughly mixing the pretested samples from each region to make a composite sample. Each bulk was then handled independently during the experiments. A small sample from each composite sample was taken for detailed laboratory analyses.

3.6.2 Analytical methods

A list of the soil characteristics of the two composite soils is given in Appendix 3. Soil pH was determined on a 1:5 (soil:water) suspension; and 0.01 M $CaCl_2$ using a glass electrode and a shaking time of 1 hour.

Lime requirement (LR) was determined by the addition of measured volumes of 0.02 M $Ca(OH)_2$ to 20 g sample of soil, adjusting the volume to 100 ml with distilled water and determining the pH after a 4 day equilibration period. The pH values that were obtained by varying the amount of 0.02 M $Ca(OH)_2$ were regressed against the respective amounts of 0.02 M $Ca(OH)_2$ that were added. The following regression equations were obtained and used to predict the amount of lime that was required for liming the soils to a target pH of 6.5 for the two soils:

(Equation 1) For Ferralsols: $Y = -0.273 + 0.047X$

(Equation 2) For Andosols: $Y = -0.352 + 0.062X$

where Y is the amount of lime $Ca(OH)_2$ (g) added per 20 g of soil, and X is the resultant pH (H_2O) value of soil.

Exchangeable sodium, potassium, calcium and magnesium were determined by the atomic absorption spectrophotometry method (David, 1960) after leaching 10 g of soil with 200 ml of 1 M NH_4Cl_2. Exchangeable aluminum, manganese and hydrogen were determined by leaching with 1 M KCl according to the procedure described by McLean (1975).

3.6.3 Greenhouse experiment

The greenhouse pot experiment examined the response of the 7 wheat varieties (*T. aestivum* L.) to lime treatment for both Ferralsols and Andosols. The experiment was conducted in a temperature controlled greenhouse at the University of Alberta with average day and night temperatures of 23 and 17 °C, respectively. The experiment was conducted under plant quarantine regulations as required and supervised by the Department of Plant Products, Agriculture Canada, since the experiment involved foreign (Kenya) soils. All used soil and plant materials were incinerated at the end of the experiments.

Two lime treatments were used, lime added and no lime added. The lime treatment involved the addition of pure grade $Ca(OH)_2$ into the soils in amounts sufficient to raise the pH to a targeted pH of 6.5 as estimated from Equation 1 and 2. The lime was thoroughly mixed with 1.4 kg of air-dry soil which was then placed in non-draining plastic pots 15 cm diameter by 15.5 cm deep. The mixture was allowed to incubate at field capacity for 14 days before the seeds were planted.

Ten seeds were planted per pot and were thinned to six seedlings per pot shortly after emergence. The pots were watered to field moisture capacity daily or more frequently during periods of high water demand. Pot position on the bench was rotated on a three day basis within a replication, whilst each replicate was rotated every fifth day.

During the experiment, additional nutrients (N, P, K and S) were added at the following rates in kg/ha: 80 N, 100 P, 50 K and 20 S. They were supplied as NH_4NO_3, $NH_4H_2PO_4$, KCl and $(NH_4)_2SO_4$.

The experimental design was a randomized complete block with 3 replicates, 2 lime treatments and 7 varieties of wheat. Varieties Romany, K. Tembo, K. Fahari, K. Swara and K. Kongoni of Kenyan origin were selected for use in this study on the basis of the results of the preliminary study that was done in Kenya (Appendices 4, 5 and 6 , Nyachiro and Briggs, unpublished data). PF7748 and Siete Cerros were selected on the same criterion as the one mentioned in the previous experiments (Experiments 1, 3, and 4).

Plants were harvested at maturity. Plant heights in cm were measured immediately before harvesting. Whole plants were harvested, and oven dried at 60 °C for 24 hours. Dry mass of biological yield was defined as the total dry weight above the soil level. Harvest index (HI)% was computed by dividing grain yield by biological yield times 100. The number of seeds per head (S/HD) and the number of seeds per plot (S/PT) were determined and were used to estimate the 1000 kernel weights (KWT) g values.

3.6.4 Statistical analyses

ANOVA was conducted for all sets of data using a random linear additive model similar to that used in Experiment 2. DMRT at $P \leq 0.05$ was used to determine significant variety and treatment mean differences. Stepwise multiple regression analyses were conducted to determine the best predictors of grain yield using a similar regression model to that used in Experiment 2.

4. RESULTS AND DISCUSSIONS

4.1 Variety classification

4.1.1 Categories, ANOVA and tolerance mean score values

On the basis of the tolerance mean score values, varieties were classified into three categories (Table.1.1.) in Experiment 1. The categories were:

(I) tolerant

(II) medium tolerant

(III) susceptible.

Category I included the varieties Romany, K. Tembo, K. Kulungu, K. Popo, K. Nyumbu, K. Kongoni, K. Kima, PF7748 and Maringa. These varieties showed incomplete or no staining at all for all three of the aluminum treatments. Category II included three varieties K. Zabadi, K. Nungu and Paa. These varieties showed complete staining with the 0.59 *m*M and the 1.72 *m*M of aluminum treatments but only partial staining in the 0.30 *m*M aluminum treatment. Category III included five varieties K. Fahari, K. Swara, K. Tumbili, Bounty and Siete Cerros. These varieties showed heavy staining in all the three aluminum treatments.

The ANOVA (Table 1.2) indicated that there were significant ($P \leq 0.05$) differences in the staining reaction of varieties. Treatment effect was also significant at $P \leq 0.01$.

Differences in tolerance on the basis of tolerance mean score values (Table 1.3) were observed among the 17 wheat varieties tested. PF7748 and Maringa (tolerant controls) showed consistence in tolerance, while Siete Cerros (susceptible control) showed consistence in susceptibility reactions among the aluminum treatments. K. Kongoni, K. Popo, K. Kulungu and K. Kima were the most tolerant test varieties at the highest (1.72 *m*M) aluminum treatment. Bounty and K. Swara were the most susceptible test varieties in all the aluminum treatments.

The coding of the varieties prior to the start of the experiment was a good precaution against any biases that would have occured in scoring due to the prior knowledge of the

Table 1.1. Tolerance of the 17 wheat varieties to aluminum toxicity: results of hematoxylin staining test.

Origin	Category of tolerance†		
	Very tolerant (I)	Medium tolerant (II)	Susceptible (III)
Kenya	Romany		
	K. Tembo		
	K. Kulungu		
	K. Popo		
	K. Nyumbu		
	K. Kongoni		
	K. Kima	K. Zabadi	
		K. Nungu	
		Paa	K. Fahari
			K. Tumbili
			Bounty
			K. Swara
CIMMYT			Siete Cerros
	PF7748		
	Maringa		

† Tolerance based on hematoxylin staining scores, I - tolerant and III - susceptible.

Table 1.2. Analysis of variance for tolerance score values of 17 wheat varieties. Raw data were square-root transformed..

Source of Variation	d.f†	Mean sum of squares, Square-root transformed scores
Replicates	3	0.18 NS
Treatments	2	3.40 **
Varieties	16	0.97 **
Treatment x Varieties	32	0.14 NS
Error	150	0.12
Total	230	

† degrees of freedom

NS indicates not significant at $P \leq 0.05$

** significant at $P \leq 0.01$

Table 1.3 Mean tolerance scores for 17 wheat varieties after back transformation.

Variety	Overall Mean Scores†	Aluminum concentration (mM) 0.30	0.59	1.72
Romany	2.6 de‡	1.9 de	1.9 c	4.6 a
K. Tembo	2.6 de	1.4 e	1.9 c	4.9 a
K. Fahari	4.5 ab	3.5 b	4.9 a	4.9 a
K. Zabadi	3.2 bcd	2.4 cd	3.0 b	4.6 a
K. Swara	4.9 a	4.9 a	4.9 a	4.9 a
K. Nungu	3.1 bcde	2.7 c	1.9 c	4.9 a
K. Kulungu	2.5 def	2.7 c	1.9 c	2.8 d
K. Popo	2.0 ef	1.8 de	1.4 d	2.8 d
K. Nyumbu	2.9 de	2.7 c	1.9 c	4.6 a
K. Kongoni	2.5 def	2.7 c	1.9 c	2.8 d
K. Kima	2.8 de	2.7 c	1.9 c	3.9 b
K. Tumbili	4.2 bcd	3.3 b	4.6 a	4.9 a
Paa	3.0 cde	1.9 de	2.8 b	4.6 a
Bounty	4.9 a	4.9 a	4.9 a	4.9 a
PF7748	2.0 ef	1.0 f	1.9 c	3.3 c
Siete Cerros	4.[illegible] a	4.6 a	4.9 a	4.9 a
Maringa	1.5 f	1.0 f	1.0 e	2.8 d

† Scores 1 and 5 represent tolerant and susceptible, respectively.
‡Mean score values within a column followed by the same letter are not significantly different according to Duncan's Multiple Range Test at $P \leq 0.05$.

tolerance levels of some control varieties.

The variety Maringa (tolerant control) was the most tolerant in all the aluminum treatments. Both K. Popo and PF7748 were the second most tolerant with a tolerance mean score value of 2.0 each. The other varieties that showed a good amount of tolerance with a tolerance mean score value of $\leq$ 2.9 were K. Kima, K. Nyumbu, K. Kulungu, K. Tembo and Romany. Varieties that showed the least amount of tolerance to aluminum, that is, those that had a tolerance mean score value of $\geq$ 4.0 were K. Fahari, K.Swara, K.Tumbili, Bounty and Siete Cerros.

An interesting finding was the significant tolerance difference between the varieties K. Kima and K. Tumbili which have the same parentage (Appendix 1), except that they are derived from different individual single plants.

4.2 Variety response in aluminum nutrient culture solution

The ANOVA (Table 2.1) in Experiment 2 indicated that there were highly significant ($P \leq 0.01$) treatment differences. Variety differences were highly significant for the 4 agronomic characters root weight, shoot weight, biological yield and root length, and for RTI and BYTI. STI was not significant at $P \leq 0.05$. This indicated that the average performance of all varieties across all the aluminum treatments was similar on the basis of STI (Table 2.2). The variety x treatment interaction was highly significant for one agronomic character root length, and one index, RTI.

4.2.1 Mean values and ranges

In Experiment 2, wheat test varieties and control varieties differed in their response to aluminum treatments (Table 2.2). On the basis of root weight, varieties K. Kongoni, K. Nungu, K. Popo, K. Zabadi, K. Kulungu, K. Nyumbu, Romany and Maringa were the most tolerant to aluminum toxicity. Bounty, K. Fahari and K. Tembo were moderately tolerant, while K. Swara, K. Kima, Paa, Siete Cerros and K. Tumbili were susceptible to aluminum toxicity. These results agree well with those obtained in Experiment 1, except for K. Fahari.

Table 2.1. Analysis of variance of 4 agronomic characters and 3 indices in 16 wheat varieties.

		Mean sum of squares							
		Agronomic characters					Indices		
Source of variation	d.f.†	Root weight (mg)	Shoot weight (mg)	Biological yield (mg)	Root length (cm)	d.f.	RTI‡	STI††	BYTI♭
Replicates	2	427.1	4069.3	6254.0	43.1	2	0.74	0.47	0.58
Treatments	3	13876.5 **	1236.9 **	51675.4 **	188.3 **	5	0.71 **	0.29 **	0.59 **
Varieties	15	985.5 **	5832.5 **	10457.9 **	7.4 **	15	0.08 **	0.05 ns	0.04 **
Treatment x Varieties	45	133.8 ns	179.6 ns	362.5 **	1.3 **	75	0.03 **	0.02 ns	0.01 ns
Error	126	109.1	463.5	851.2	0.7	190	0.02	0.03	0.02
Total	191					287			

† degrees of freedom
ns -not significant at $P \leq 0.05$
**, significant at $P \leq 0.01$.
‡ Root tolerance index
†† Shoot tolerance index
♭ Biological yield tolerance index

The varieties K. Kongoni, Bounty, Romany and K. Popo ranked top in shoot weight. This was consistent with the hematoxylin staining in Experiment 1, except for the variety Bounty. The varieties K. Tumbili, K. Tembo, Paa, K. Kima and Siete Cerros ranked low in shoot weight, and this was consistent with the staining results in Experiment 1, except for the variety K. Tembo.

On the basis of biological yield (Table 2.2) varieties were separated into many as categories as those on the basis of shoot weight, although these categories were not very distinct according to DMRT at $P \leq 0.05$. The varieties K. Kongoni, Bounty, Romany, K. Popo, K. Zabadi and K. Nungu were the highest ranking in biological yield. The severely affected varieties were K. Tembo, K. Swara, Paa, Siete Cerros and K. Tumbili. The difference in mean values of root lengths between Maringa (tolerant control) and Siete Cerros (susceptible control) was 21.3%. No [illegible] variety was more tolerant than Maringa on the basis of root length. On the other hand K. Tumbili was significantly more susceptible than Siete Cerros. The least affected varieties on the basis of root length were K. Popo, K. Nungu, K. Kongoni, Romany, K. Kulungu, K. Tembo and K. Nyumbu.

The striking differences in root length between some of the varieties among the aluminum treatments are shown in Figure 1. Most of the varieties tested did not show considerable root length differences at the 4 ppm of the aluminum treament. At the 16 ppm aluminum treatment the tested varieties differed considerably in root length, and at the 64 ppm of aluminum treatment root lengths in all varieties were considerably reduced relative to the similar varieties grown in the lower aluminum concentrations.

4.2.2 Tolerance indices

There were significant variations in tolerance indices RTI, STI, and BYTI (Table 2.2) between varieties. According to DMRT at $P \leq 0.05$, there were more variety differences on the basis of RTI than on the basis of STI or BYTI. The RTI values were relatively lower compared to STI and BYTI mean values. This indicated that the roots were more affected than to the shoots and biological yield. For example, the RTI mean value for K. Swara wasin

Table 2.2.Mean values for 4 agronomical characters and 3 indices for 16 wheat varieties.

	Agronomic characters				Indices†		
Variety£	Root weight (mg)	Shoot weight (mg)	Biological yield (mg)	Root length (cm)	RTI‡	STI††	BYTI♭
K. Kongoni	66.9 aÞ	140.8 a	207.8 a	6.3 bcde	0.67 bcde	0.91 a	0.84 b
K. Nungu	64.5 ab	130.8 abcd	195.3 abc	7.0 ab	0.66 cde	0.88 a	0.80 bc
K. Popo	63.8 ab	140.0 ab	203.8 ab	6.8 abc	0.69 bcd	0.88 a	0.81 bc
K. Zabadi	62.9 ab	137.5 abc	200.4 ab	6.1 defg	0.70 bcd	0.89 a	0.83 b
K. Kulungu	62.6 ab	119.2 cd	181.8 bcd	6.3 bcde	0.63 de	0.81 ab	0.74 bcd
K. Nyumbu	61.7 abc	119.2 cd	181.2 bcd	5.9 efg	0.78 ab	0.84 ab	0.81 bc
Romany	60.9 abc	140.0 ab	201.8 ab	6.7 bcd	0.74 abc	0.91 a	0.85 a
Maringa	58.9 abc	122.5 bcd	181.4 bcd	7.5 a	0.85 a	0.86 a	0.83 b
Bounty	57.7 bc	150.0 a	207.7 a	5.1 i	0.67 bcde	0.86 a	0.81 bc
K. Fahari	57.3 bc	131.7 abcd	188.9 abc	6.1 defg	0.62 de	0.88 a	0.80 bc
K. Tembo	52.3 cd	98.3 e	150.6 e	6.2 cdefg	0.67 bcde	0.86 a	0.78 bcd
K. Swara	47.3 d	122.5 bcd	170.6 cde	5.5 fghi	0.58 e	0.78 ab	0.72 cd
K. Kima	46.1a	70.0 f	116.1 g	5.2 hi	0.63 de	0.71 b	0.68 d
Paa	46.0 d	115.8 de	161.0 de	5.5 fghi	0.69 bcd	0.80 ab	0.77 bcd
Siete Cerros	45.0 d	111.7 de	156.7 de	5.9 efg	0.63 de	0.81 ab	0.75 bcd
K. Tumbili	35.7 e	80.8 f	116.5 f	4.4 j	0.66 cde	0.87 a	0.80 bc

† *ad hoc* values, estimated by dividing parameter values in greater aluminum concentrations by those in lesser or no aluminum concentrations

£ Varieties are listed in order of root weight for easier reading and referencing.

Þ Means within a column followed by the same letter are not significantly different in the Duncan's Multiple Range Test at $P \leq 0.05$.

‡ Root tolerance index

†† Shoot tolerance index

♭ Biological yield tolerance index

the magnitude of 58% while that for Maringa was 85%. This would mean that Maringa was relatively more tolerant than K. Swara by 27 percent on the basis of root weight. The highest RTI mean values were determined in the varieties Maringa, K. Nyumbu, Romany, K. Nungu and K. Zabadi while the lowest RTI mean values were determined in the varieties K. Swara, K. Fahari and Siete Cerros. The STI mean values ranged from 71 % for K. Kima to 91% for both K. Kongoni and Romany. Both Romany and K. Kongoni were the top ranking varieties for STI mean values, while Paa and K. Kima were the lowest ranking. The BYTI mean values ranged from 68% for K. Kima to 85% for Romany. The top ranking varieties for the BYTI mean values were Romany, Maringa and K. Kongoni whereas the lowest ranking were K. Kima, K. Swara and Siete Cerros.

Aluminum treatments (Table 2.3) affected the perfomances of the varieties significantly as evidenced from the four agronomic characters root weight, shoot weight, biological yield and root length. There was consistent decline in the mean values for the four characters as the aluminum concentration increased. An increase of aluminum treatment from 0 to 64 ppm was associated with a range in decline of 44.2 to 53.7% for the root weight, 25.7 to 28.1% for the shoot weight, 35.2 to 37.3% for the biological yield, and 41.9 to 44.9% for the root length. It was clear, then, that aluminum affected both the root weight and the root length more than it affected the shoot weight and the biological yield.

An inverse relationship (Table 2.4) between the relative aluminum concentration and the three indices was observed. The RTI decreased from 91 to 46%, STI from 94 to 73% and BYTI from 92 to 63% as the relative aluminum concentration increased from 4 ppm/o ppm to 64 ppm/0 ppm, respectively. The decrease in the mean RTI values were greater than the STI and BYTI mean values as the difference in relative aluminum concentration increased, but in every instance the differences were within one standard error of the estimate. From the present study it was indicated that the RTI mean values were better indicators or predictors of aluminum tolerance than the STI and BYTI mean values.

Table 2.3. Effects of aluminum treatments on 4 agronomic characters for 16 wheat varieties. Data represent the mean values and SE from 4 aluminum treatments; treatments were replicated 4 times.

Aluminum conc. (ppm)	Agronomic character: Root weight (mg)	Shoot weight (mg)	Biological yield (mg)	Root length (cm)
0	70.9 ±1.9	138.1 ±3.9	209.2 ±5.3	7.6 ±0.2
4	64.6 ±2.1	128.1 ±4.3	192.8 ±5.8	7.4 ±0.2
16	54.7 ±2.3	115.4 ±4.3	169.9 ±5.8	5.8 ±0.2
64	32.1 ±1.6	101.0 ±4.5	133.5 ±5.6	3.3 ±0.2

Table 2.4. The indices of tolerance to aluminum concentration in 16 wheat varieties. Data represent the mean tolerance index values and SE of all possible treatment comparisons of aluminum concentrations.

Relative aluminum conc. (ppm)	Indices†		
	RTI‡	STI††	BYTI♭
4 ppm/0 ppm	0.91 ±0.02	0.94 ±0.03	0.92 ±0.02
16 ppm/4 ppm	0.84 ±0.02	0.90 ±0.02	0.88 ±0.01
16 ppm/0 ppm	0.77 ±0.03	0.84 ±0.02	0.81 ±0.02
64 ppm/16 ppm	0.61 ±0.03	0.89 ±0.03	0.78 ±0.02
64 ppm/4 ppm	0.50 ±0.02	0.79 ±0.03	0.69 ±0.02
64 ppm/0 ppm	0.46 ±0.02	0.73 ±0.03	0.63 ±0.02

† Indices were determined by dividing data values in higher aluminum concentrations by those in lower aluminum concentrations for the three agronomic characters.
‡ Root tolerance index
†† Shoot tolerance index
♭ Biological yield tolerance index

4.2.3 Correlations

Stepwise multiple regression analyses (Table 2.5) confirmed the relationships between the four agronomic characters within the four aluminum treatments. The following multiple regression equations and coefficients of determinations were determined within the four aluminum treatments:

(1) 0 ppm : $Y = 0.57X_0 + 0.97X_1 + 1.01X_2$ $\quad R = 0.99$ **

(2) 4 ppm : $Y = 15.93X_0 + 1.38X_2$ $\quad R = 0.95$ **

(3) 16 ppm: $Y = -0.66X_0 + 1.01X_1 + 0.99X_3$ $\quad R = 0.99$ **

(4) 64 ppm : $Y = 0.12X_0 + 0.98X_1 + 1.01X_2$ $\quad R = 0.99$ **

**, significant at $P \leq 0.01$

where Y represents the predicted biological yield, X_0 is the dummy variable of value +1, X_1 and X_2 are root weight and shoot weight, respectively, and R is the coefficient of determination.

Correlations (Table 2.5) between the measured agronomic characters that had coefficients of ≤ 0.50 were three for the 0 ppm, 3 for the 4 ppm, 1 for the 16 ppm, and none for the 64 ppm aluminum treatment. Coefficient of determination values (r^2) of less than 25% were obtained for root length with root weight, root length with shoot weight and root length with biological yield for the 0 ppm and 4 ppm aluminum; root length with shoot weight for the 16 ppm of aluminum treatment. These results may indicate that it is possible to breed for aluminum tolerance using the criterion of those characters which are associated with low correlation coefficients under low aluminum concentrations (0 to 16 ppm). However, the higher aluminum concentration treatments of 64 ppm resulted in high correlation coefficients. This may indicate that high aluminum levels of the magnitude of 64 ppm may not be very useful in the laboratory screening procedures for distinguishing the tolerant varieties from the susceptible ones.

Correlation coefficients (r) for the estimated indices (Table 2.6) were relatively low ranging from 0.18 to 0.60 for the RTI with STI for all the relative aluminum concentrations as compared to the range of 0.58 to 0.95 for the RTI with BYTI, and the STI with BYTI

Table 2.5. Correlation coefficients (r)† between measured agronomic characters of 16 wheat varieties. Correlation coefficients for 0 and 4, 16, 64 ppm are presented, consecutively.

Measured	Measured variables				
0 variables	Root weight (mg)	Shoot weight (mg)	Biological yield (mg)	Root length (cm)	Aluminum conc. (ppm)
Root weight (mg)		0.63	0.81	0.22	0
		0.77	0.89	0.45	4
		0.54	0.79	0.81	16
		0.58	0.75	0.81	64
Shoot weight (mg)			0.96	0.42	0
			0.98	0.37	4
			0.94	0.36	16
			0.97	0.68	64
Biological yield (mg)				0.40	0
				0.42	4
				0.58	16
				0.79	64

† N = 48. Correlation coefficients (r) $\geq$ 0.28, 0.36 significant at $P \leq 0.05$ and 0.01, respectively.

Table 2.6. Correlation coefficients (*r*)† between estimated indices for 16 wheat varieties. Correlation coefficients for relative 4 ppm/ 0 ppm, 16 ppm/ 4 ppm, 16 ppm/ 0 ppm, 64 ppm/16 ppm, 64 ppm/4 ppm, 64 ppm/ 0ppm aluminum are presented, consecutively.

Indices	Indices		Relative aluminum
	STI††	BYTI♭	
RTI	0.27	0.58	4 ppm/0 ppm
	0.18	0.56	16 ppm/4 ppm
	0.25	0.66	16 ppm/0 ppm
	0.48	0.79	64 ppm/16 ppm
	0.60	0.80	64 ppm/4 ppm
	0.51	0.80	64 ppm/0 ppm
STI		0.92	4 ppm/0 ppm
		0.86	16 ppm/4 ppm
		0.87	16 ppm/0 ppm
		0.86	64 ppm/16 ppm
		0.95	64 ppm/4 ppm
		0.91	64 ppm/0 ppm

† N = 48. Correlation coefficients (*r*) $\geq$ 0.28, 0.36 are significant at P $\leq$ 0.05 and 0.01, respectively.
‡ Root tolerance index
†† Shoot tolerance index
♭ Biological yield tolerance index among the relative aluminum concentrations.

The low correlation coefficients between RTI and STI may indicate that it is possible to breed and select varieties that have either a better root or shoot system under high aluminum concentration environment.

4.3 Variety response in UCM augmented with aluminum

In Experiment 3, variety effects were highly significant at $P \leq 0.01$ (Table 3.1) for the characters plant height, shoot weight, root weight, biological yield, number of tillers; and for the indices RTI and STI. The index BYTI was significant at $P \leq 0.05$. The aluminum treatments were highly significant for all the measured characters and indices. Replicate effects were not significant ($P \leq 0.05$) in all cases except for the number of tillers and BYTI at ($P \leq 0.01$).

There were no significant treatment x variety (Table 3.1) interactions for all the measured characters, except for the in[illegible]TI, and STI. Treatment x variety interaction for the index STI was significant at $P \leq 0.05$, whereas that for the index STI was significant at $P \leq 0.01$.

4.3.1 Mean values and ranges

Experiment 3 results (Table 3.2) indicated that there was significant ($P \leq 0.05$) decline in all the measured characters as aluminum increased except for the number of tillers. No significant differences in the treatment mean values for the number of tillers were detected between the 0 ppm and 16 ppm aluminum treatment. The relatively low number of tillers in the 8 ppm aluminum treatment compared to either the 0 ppm or 16 ppm aluminum treatments was unexpected.

In absolute values, (Table 3.2) as the concentration of aluminum was increased from 0 ppm to 8 ppm, and 16 ppm, there was an associated decrease of 23%, and 32% for the root weight; 6.9%, and 18.0% for the shoot weight; 29.0%, and12.0% for the biological yield; and 7.5%, and 2.3% for the plant height. In general, there were decreases in the mean values for all the measured characters, but the decrease in the root weight was of a relatively higher

Table 3.1. Analysis of variance of 8 agronomic characters, and 3 indices in 8 wheat varieties grown in UCM.

		Mean sum of squares							
		Agronomic characters					Indices†		
Source of variation	d.f.Þ	Plant Height (cm)	Shoot Weight (g)	Root Weight (g)	Biological Yield (g)	No. of Tillers	RTI‡	STI††	BYTIþ
Replicates	2	5.7 NS	0.21 NS†	0.50 NSΦ	0.01 NS	13.2 **	0.03 NS	0.43 NSΦ	0.88 **††
Treatments	2	124.3 **	0.68 **	0.41	2.14 **	74.0 **	0.39 **	0.05 **	0.09 **
Varieties	7	164.2 **	0.20 **	0.06 **	0.42 **	53.9 **	0.04 **	0.84 ** Φ	0.60 *†
Treatment x Variety	14	1.3 NS	0.01 NS	0.64 NSΦ	0.02 NS	3.8 NS	0.03 *	0.12 **Φ	0.27 NSΦ
Error	46	1.8	0.82Φ	0.52Φ	0.01	2.5	0.01	0.26Φ	0.23Φ
Total	71								

† $\times 10^{-3}$
Þ degree of freedom
Φ $\times 10^{-2}$
NS Not significant
*, ** significant at $P \leq 0.05$ and 0.01, respectively.
‡ Root tolerance index
†† Shoot tolerance index
þ Biological yield tolerance index

Table 3.2. Treatment mean values for all measured variables for 8 wheat varieties grown in UCM with three aluminum concentrations 0, 8 and 16 ppm.

Trait	Aluminum concentration (ppm) 0	8	16
	Mean values		
Root weight (g)	0.56 a†	0.43 b	0.29 c
Shoot weight (g)	2.18 a	2.03 b	1.85 c
Biological yield (g)	2.74 a	2.45 b	2.14 c
Plant height (cm)	45.17 a	41.79 b	40.83 c
No. of tillers	17.83 a	14.54 b	17.25 a
Indexþ	Relative aluminum concentration		
	8 ppm/0 ppm	16 ppm/0 ppm	16 ppm/8 ppm
RTI‡	0.78 a	0.53 c	0.69 b
STI††	0.93 a	0.84 b	0.90 a
BYTIþ	0.89 a	0.78 b	0.87 a

† Means followed by the same letter within a row are not significantly different at $P \leq 0.05$ according to Duncan's Multiple Range Test

þ *ad hoc* values estimated by dividing character values in greater aluminum concentrations by those in lesser or no aluminum concentrations.

‡ Root tolerance index

†† Shoot tolerance index

þ Biological yield tolerance index

Table 3.3. Mean values for 8 wheat varieties that were grown in 3 aluminum concentrations, for 5 agronomic characters and 3 indices.

	Agronomic characters					Indices		
Cultivar	Root Weight (g)	Shoot Weight (g)	Biological Yield (g)	Plant Height (cm)	No. of Tillers	RTI‡	STI††	BYTI♭
PF7748	0.56 a†	2.09 ab	2.65 a	47.88 a	15.66 de	0.73 ab	0.83 c	0.81 b
K. Konogni	0.49 ab	2.16 a	2.64 a	37.11 e	20.88 a	0.64 bc	0.91 ab	0.85 ab
K. Fahari	0.49 ab	2.13 a	2.61 a	44.11 c	14.88 ef	0.69 abc	0.92 ab	0.86 ab
Romany	0.42 bc	2.03 bc	2.45 b	45.66 b	17.55 c	0.58 c	0.90 ab	0.83 b
Bounty	0.42 bc	1.93 d	2.35 b	47.11 a	16.66 cd	0.66 abc	0.88 ab	0.83 b
Siete Cerros	0.38 cd	1.97 cd	2.35 b	37.01 e	14.01 f	0.67 abc	0.86 bc	0.84 b
K. Swara	0.32 de	2.11 ab	2.44 b	41.55 d	13.88 f	0.77 a	0.92 ab	0.90 a
K. Tembo	0.29 e	1.70 e	2.01 c	40.33 d	18.77 b	0.57 c	0.91 ab	0.85 b

† Means followed by the same letter within a column are not significantly different at $P \leq 0.05$ according to Duncan's Multiple Range Test.
‡ Root tolerance index
†† Shoot tolerance index
♭ Biological yield tolerance index

magnitude compared to the other characters as the concentration of aluminum was increased [illegible] ppm to 16 ppm.

Mean values for RTI, STI and BYTI (Table 3.2) were significantly different according to DMRT ($P \leq 0.05$). The indices decreased significantly as the relative aluminum concentration increased. A relatively greater magnitude of decrease was indicated in the RTI compared to either the STI or the BYTI.

A DMRT performed on variety mean values (Table 3:3) indicated significant ($P \leq 0.05$) differences within the 8 varieties for the agronomic characters and the three indices. The 8 varieties did not separate into distinct classes for the measured characters except for the biological yield and the plant height. The varieties K. Tembo and K. Swara responded contrarily to the findings in Experiments 1 and 2. In this experiment K. Tembo performed worse than expected at higher aluminum concentration, whereas K. Swara performed better than expected. Also Romany did not perform as well as expected in this experiment.

4.3.2. Correlations and multiple regression analyses

Biological yield was significantly ($P \leq 0.01$) correlated (Tables 3.4 and 3.5) with the root and the shoot weight within the aluminum treatments. The correlations between the biological yield and other variables were relatively low. Significant ($P \leq 0.05$) negative correlations, although not high were observed, for instance, between the RTI and root weight $r = -0.45$.

The BYTI was significantly correlated (Tables 3.4 and 3.5) with the RTI and STI within all the aluminum treatments. The correlations for the BYTI with the RTI for the 0 ppm, 8 ppm and 16 ppm aluminum concentration were $r = 0.51$, 0.45 and 0.48, respectively.

The biological yield was significantly ($P \leq 0.01$) correlated (Tables 3.4 and 3.5) with the root and the shoot weight within the aluminum treatments. The correlations between the biological yield and other variables were relatively low. Significant ($P \leq 0.05$) negative correlations, although not high were observed, for instance, between the RTI and root weight $r = -0.45$.

Table 3.4. Correlation coefficients (r)† between measured variables, and indices for 8 wheat varieties. Correlation coefficients for 0 and 8, 16 ppm are presented consecutively for each character.

	Agronomic characters				Indices			
	Shoot Weight (g)	Biological Yield (g)	Plant Height (cm)	No. of Tillers	RTI‡	STI††	BYTI♭	Al^{3+} conc. 0, 8, & 16 (ppm)
Root wt. (g)	0.58	0.85	0.30	0.10	-0.45	-0.33	-0.63	0
	0.35	0.74	0.14	0.03	0.18	-0.09	-0.08	8
	0.42	0.72	0.31	0.19	0.58	-0.03	0.34	16
Shoot wt. (g)		0.92	0.14	-0.22	-0.12	-0.61	-0.58	0
		0.87	0.09	-0.31	0.37	0.18	0.28	8
		0.93	-0.08	-0.17	0.21	0.63	0.72	16
Biological yield (g)			0.25	-0.09	-0.30	-0.55	-0.69	0
			0.12	-0.16	0.37	0.06	0.14	8
			0.07	-0.05	0.39	0.47	0.69	16
Plant height (cm)				-0.33	-0.24	-0.09	-0.25	0
				-0.11	0.03	-0.22	-0.26	8
				-0.06	0.34	-0.34	-0.05	16
No. of tillers					-0.12	-0.07	0.05	0
					-0.50	0.25	-0.06	8
					0.05	-0.23	-0.24	16
RTI‡						0.05	0.51	0
						-0.08	0.45	8
						-0.26	0.48	16
STI††							0.67	0
							0.82	8
							0.68	16

† N = 24. Correlation coefficients (r) $\geq$ 0.40, 0.51 are significant at P $\leq$ 0.05 and 0.01, respectively. ‡ Root tolerance index, †† Shoot tolerance index, ♭ Biological yield tolerance index

Table 3.5. Correlation coefficients (r)† between measured variables, and indices for 8 wheat varieties. Correlation coefficients for 8 and 16 ppm are presented below and above the diagonal, respectively.

	Aluminum concentration 16 ppm							
	Agronomic characters					Indices†		
Aluminum conc. 8 ppm	Root Weight (g)	Shoot Weight (g)	Biological Yield (g)	Plant Height (cm)	No. of Tillers	RTI‡	STI††	BYTI♭
Root Weight (g)		0.42	0.72	0.31	0.19	0.58	-0.03	0.34
Shoot Weight (g)	0.35		0.93	-0.08	-0.17	0.21	0.63	0.72
Biological yield (g)	0.74	0.87		0.07	-0.05	0.39	0.47	0.69
Plant height (cm)	0.14	0.09	0.12		-0.06	0.34	-0.34	-0.05
No. of tillers	0.03	-0.31	-0.16	-0.11		0.52	-0.24	-0.24
RTI	0.18	0.37	0.36	0.03	-0.50		-0.26	0.48
STI	-0.09	0.18	0.06	-0.22	0.25	-0.08		0.68
BYTI	-0.08	0.28	0.14	-0.26	-0.06	0.45	0.82	

†N = 24. Correlation coefficients (r) $\geq$ 0.40, 0.51 are significant at P $\leq$ 0.05 and 0.01, respectively.
‡ Root tolerance index
†† Shoot tolerance index
♭ Biological yield tolerance index

The BYTI was significantly correlated (Tables 3.4 and 3.5) with the RTI and STI within all the aluminum treatments. The correlations for the BYTI with the RTI for the 0 ppm, 8 ppm and 16 ppm aluminum concentration were $r = 0.51$, 0.45 and 0.48, respectively. Comparatively, the correlations for the BYTI with the STI within the three aluminum treatments were $r = 0.67$, 0.82 and 0.68. This indicated a higher magnitude of correlations for the BYTI with the STI than the BYTI with the RTI.

There was a highly significant multiple coefficient of determination ($R^2 = 0.99$) for the biological yield accounted for by the variables shoot weight and root weight. The R^2 values decreased from 0.99 to 0.86 as the concentration of aluminum was increased from 0 ppm to 16 ppm. The variable shoot weight and root weight were entered on the first and second iterations, respectively. However, at the 16 ppm of aluminum treatment the variable root weight did not contribute to the prediction of the biological yield. The decrease of the partial regression coefficients (b) as the amount of aluminum concentration was increased from 0 to 8 ppm was not significant. At the 16 ppm of aluminum treatment, the partial regression coefficient ($b_1 = 1.233$) for the variable shoot weight was of significantly greater magnitude than at the 0 ppm and 8 ppm levels of aluminum treatment.

4.4 Inheritance of aluminum tolerance

Experiment 4 results (Tables 4.1 and 4.2) indicated that no cross fitted a 3:1 ratio, meaning that no single gene differences were determined. For a 9:7 ratio only two crosses fitted (i.e two gene differences). The crosses which fitted a 9:7 ratio were:

1. K. Kongoni/PF7748 (T x T)
2. K. Tembo/Siete Cerros (T x S)
3. K. Fahari/PF7748 (S x T)
4. K. Swara/Romany (S x T)[6]

No case was found where a cross between a susceptible and susceptible gave tolerant F2 seedlings, but 3 crosses involving tolerant and tolerant (K. Kongoni/PF7748, K.

[6] T refers to tolerant, and S refers to susceptible.

Tembo/PF7748, and K. Kongoni/Romany) gave some susceptible F2 seedlings. These results may suggest that the aluminum tolerant varieties PF7748, Romany, K. Tembo, and K. Kongoni have different genes which control aluminum tolerance.

A significantly larger number of tolerant seedlings were recovered from the crosses that involved variety Romany as the male parent than those that involved variety PF7748 as the male parent (Table 4.2). No tolerant F2 seedlings were recovered from the cross K. Swara (S) and PF7748 (T) suggesting a complex mode of genetic control. However, the variety Romany may have homozygous dominant genes for aluminum tolerance based on the segregation ratios of the cross between K. Tembo and Romany, since all the F2 seedlings were tolerant to aluminum.

The attained ratios of the crosses K. Fahari (susceptible) x Siete Cerros (susceptible), and K. Swara (susceptible) x Siete Cerros (Tables 4.1 and 4.2), may suggest that susceptibility to aluminum toxicity is contributed to by recessive genes. Subsequently, segregations observed among F2 seedlings indicated that dominance played some role in aluminum tolerance in some crosses, although several complexities were noticed in the observed ratios. Such complexities involved the cross of the susceptible variety K. Swara (susceptible) with PF7748 (tolerant), from which no tolerant seedlings were obtained. This type of result was in agreement with similar findings by Aniol (1984), using different cultivars of wheat.

Variance (δ^2) measures how closely a set of individual observations are clustered around the mean. In this study δ^2, mean and standard error (SE) values were used to describe the F2 populations.

Tables 4.3 and 4.4 results may suggest that both grain yield and biological yield may not be effective indicators to use for selecting for aluminum tolerance in segregating populations . On the other hand, harvest index, 1,000 KWT, plant height, and number of seeds per head which show relatively high variance levels may form good indicators to use in se[illegible] aluminum tolerance. The variance for F2 populations for harvest index was re[illegible]ow compared to 1,000 KWT, plant height and number of seed per head in most

Table 4.1. Aluminum tolerance of F2 seedlings produced from 4 female crossed to each of the 3 male parents. Tested at 46 ppm aluminum.

Cross/Variety	No. of F2 Seedlings		Homogeneity χ^2	
	Tolerant	Susceptible	3:1	9:7
K. Kongoni/PF7748	290	207	73.5 **	0.9 NS
K. Kongoni/Romany	520	43	90.5 **	230.1 **
K. Kongoni/Siete Cerros	†	†	†	†
K. Fahari/PF7748	250	226	128.3 **	2.7 NS
K. Fahari/Romany	421	93	13.1 **	137.5 **
K. Fahari/Siete Cerros	0	461	153.7 **	358.6 **
K. Tembo/PF7748	255	150	31.3 **	7.4 **
K. Tembo/Romany	760	0	253.3 **	591.1 **
K. Tembo/Siete Cerros	452	326	118.5 **	1.1 NS
K. Swara/PF7748	0	778	259.3 **	605.9 **
K. Swara/Romany	489	368	147.6 **	0.3 NS
K. Swara/Siete Cerros	0	679	226.3 **	10.8 **
K. Kongoni	40	0		
K. Fahari	0	46		
K. Tembo	54	0		
K. Swara	0	49		
PF7748	56	0		
Romany	48	0		
Siete Cerros	0	48		

† Data omitted from discus[illegible] which occurred during the screening
NS Nonsignificant at 95% [illegible] *, ** Significant at 95% and 99% probability levels, respectively.

Table 4.2. Summary of F2 ratios Tolerant (T) : Susceptible (S) that were obtained from 12 crosses of wheat.

		Male parents		
		PF7748	Romany	Siete Cerros
Female parent	Characteristic	(T)	(T)	(S)
K. Kongoni	(T)	290 : 207	520 : 43	†
K. Tembo	(T)	255 : 150	760 : 0	452 : 326
K. Fahari	(S)	250 : 226	421 : 93	0 : 461
K. Swara	(S)	0 : 778	489 :368	0 : 679

T = tolerant
S = susceptible
† = No data due to an error of method during screening.

Table 4.3. Mid-Parent variance values for six agronomic characters for 12 populations of wheat.

Cross	n†	Grain Yield (g)	Biological Yield (g)	Harvest Index (%)	1,000 KWT‡ (g)	Plant Height (cm)	No. of Seeds per Head
K. Kongoni/PF7748	36	0.2	0.9	76.3	83.9	60.3	40.9
K. Kongoni/Romany	35	0.1	2.1	36.7	20.9	145.3	66.5
K. Kongoni/Siete Cerros	35	0.1	0.5	58.2	115.9	74.3	38.1
K. Fahari/PF7748	35	0.5	2.5	71.9	151.2	89.4	69.7
K. Fahari/Romany	34	0.4	2.4	21.5	169.7	84.3	75.9
K. Fahari/Siete Cerros	34	0.6	3.3	19.7	237.6	260.9	104.1
K. Tembo/PF7748	34	0.1	0.6	21.0	198.4	163.3	66.7
K. Tembo/Romany	34	0.1	0.6	26.0	81.4	168.6	42.6
K. Tembo/Siete Cerros	35	0.1	0.6	42.6	89.6	100.6	31.8
K. Swara/PF7748	35	0.2	4.2	100.3	423.7	400.5	30.5
K. Swara/Romany	36	0.2	2.8	53.8	504.7	84.0	44.0
K. Swara/Siete Cerros	36	8.4	4.6	155.4	373.9	68.5	29.5

† Number of mid-parent individuals. ‡ Weight of a thousand kernels in g

Table 4.4 Variance values of six agronomic characters for 12 F2 populations of wheat.

Cross	n†	Grain Yield (g)	Biological Yield (g)	Harvest Index (%)	1,000 KWT‡ (g)	Plant Height (cm)	No. of Seeds per Head
K. Kongoni/PF7748	86	0.1	0.6	21.9	60.9	236.5	70.9
K. Kongoni/Romany	35	0.1	0.8	29.4	46.3	336.2	52.4
K. Kongoni/Siete Cerros	90	0.1	0.4	23.2	32.7	54.7	53.4
K. Fahari/PF7748	87	0.4	1.3	36.1	168.5	113.2	97.9
K. Fahari/Romany	83	0.3	2.5	18.7	157.7	172.2	86.5
K. Fahari/Siete Cerros	89	0.4	1.5	28.3	184.2	74.6	59.2
K. Tembo/PF7748	87	0.2	0.7	115.9	78.5	100.4	61.8
K. Tembo/Romany	80	0.3	1.0	48.7	92.9	137.7	73.7
K. Tembo/Siete Cerros	83	0.3	0.8	19.7	77.9	56.2	69.8
K. Swara/PF7748	89	0.4	1.7	82.9	228.4	73.4	72.9
K. Swara/Romany	89	0.7	2.6	121.4	386.5	104.8	62.8
K. Swara/Siete Cerros	86	0.7	1.9	205.3	536.8	62.0	96.9

† Number of F2 progeny individuals ‡ Weight of a thousand kernels in g

cases.

The comparison of the F2 progeny mean values and the mid-parent mean values (Table 4.5) indicated the complexity of selecting for aluminum tolerance using the various agronomic characters. No specific trends with respect to the six agronomic characters were noticed between the crosses. For instance, in the cross of K. Kongoni (tolerant) x PF7748 (tolerant) highly significant ($P \leq 0.01$) negative differences were shown for biological yield and the number of seeds per head, whereas highly significant positive differences were shown for harvest index and plant height. For the cross K. Kongoni x Romany (tolerant) highly significant positive increase for three agronomic characters grain yield, harvest index, and 1,000 KWT were demonstrated. For the cross K. Swara (susceptible) x PF7748 highly significant positive increases were obtained in the F2 progeny with respect to grain yield, harvest index, and number of seeds per head. For the cross K. Swara x Romany highly significant positive F2 increases were obtained on grain yield, harvest index, plant height, and number of tillers. However, for the cross K. Swara x Siete Cerros highly significant positive F2 increases were were noticed for grain yield, harvest index, and 1,000 KWT. On the other hand, no significant increases were obtained in the F2 progeny for the cross between K. Kongoni x Siete Cerros (susceptible) for any of the six agronomic characters. For the cross K. Swara (susceptible) x PF7748 highly significant positive F2 increases were obtained for grain yield, harvest index and number of seeds per head. For the cross K. Swara x Romany highly significant positive increases were obtained for grain yield, harvest index, plant height and number of tillers. However, for the cross K. Swara x Siete Cerros highly significant poistive increases were obtained in harvest index and plant height, whereas progress for biological yield was highly significantly negative. On the basis of the crosses involving K. Swara (female parent), it may be interpolated that selection for aluminum tolerance may be possible by selecting F2 individuals which show higher grain yield, biological yield, harvest index, plant height, 1,000 KWT, and number of seeds per head.

Table 4.5 Differences† between mid-parents and F2 progeny mean values for 6 agronomic characters in 12 different crosses of wheat grown in UCM with high aluminum (46 ppm) concentrations.

Cross	d.f††	Grain Yield (g)	Biological Yield (g)	Harvest Index (%)	1,000 KWT‡ (g)	Plant Height (cm)	No. of Seeds per Head
K. Kongoni/PF7748	120	- NS	- **	+ **	+ NS	+ **	- **
K. Kongoni/Romany	124	+ **	- NS	+ **	+ **	+ NS	- NS
K. Kongoni/Siete Cerros	123	- NS	- NS	+ NS	- NS	+ NS	- *
K. Fahari/PF7748	120	+ *	+ NS	+ *	+ **	+ *	+ NS
K. Fahari/Romany	115	- *	- NS	- NS	- *	+ **	+ NS
K. Fahari/Siete Cerros	121	+ **	+ **	- NS	+ **	+ **	+ NS
K. Tembo/PF7748	119	+ NS	- *	+ **	- NS	- **	+ *
K. Tembo/Romany	112	+ *	+ NS	+ NS	+ **	- **	- **
K. Tembo/Siete Cerros	122	+ **	+ **	+ NS	+ **	+ **	- NS
K. Swara/PF7748	122	+ **	- NS	+ **	+ NS	+ *	+ **
K. Swara/Romany	123	+ **	- **	+ **	+ *	+ **	+ **
K. Swara/Siete Cerros	120	- NS	- **	+ **	+ NS	+ **	- NS

† Number of F2 progeny mean values - Mid-parent mean values.
†† Effective degrees of freedom
‡ Weight of a thousand kernels in g
+, - Represent positive and negative differences, respectively.
NS Not significant.
*, ** Significant according to the pair-wise t-test value at $P \leq 0.05$ and 0.01, respectively.

4.5 Variety response to lime treatment

In Experiment 5 the ANOVA indicated (Table 5.1 and 5.2) that there were significant ($P \leq 0.05$) treatment effects for all characters for the harvest index and the S/PT for both the Ferralsols and Andosols. Variety effects were significant for the biological yield and the S/HD in the Ferralsols and Andosols, respectively. Variety effects were highly significant ($P \leq 0.01$) for all the other characters in the two soils.

The treatment by variety interaction (Table 5.1 and 5.2) was highly significant ($P \leq 0.01$) for the grain yield, harvest index and S/PT for the Ferralsols; for the KWT and plant height for the Andosols. This indicated that the association between the lime treatment and the varieties was in agreement with the null hypothesis for the characters biological yield, KWT, plant height and S/HD on the Ferralsol soils. On the other hand, the lime x variety interaction was in agreement with the null hypothesis for all the characters except for the KWT and plant height for the Andosols.

4.5.1 Mean values, ranges and standard errors

In Experiment 5 DMRT ($P \leq 0.05$) (Table 5.3 and 5.4) indicated that there were significant differences between the varieties on all the measured characters for both the Ferralsols and Andosols.

Varieties separated into distinct categories for all the measured characters, except for KWT (Table 5.3). The variety Romany ranked first in terms of grain yield, biological yield, S/HD and S/PT, whilst the varieties K.Swara and Siete Cerros ranked last in all the measured characters in the Ferralsols. A wide range in the calculated mean values was indicated between varieties. For example, the mean grain yield difference between Romany (3.7 g) and K. Swara (1.5 g) was 59% in absolute terms.

The results (Table 5.4) from the Andosols indicated relatively higher mean values for all the measured characters compared to those from the Ferralsols (Table 5.3) . The variety Romany ranked first in terms of grain yield, harvest index, S/HD and S/PT. The varieties Siete Cerros and Kenya Swara were consistently low ranking in grain yield, biological yield.

Table 5.1 Analysis of variance for all sets of data for seven varieties of wheat grown in Ferralsols (Eldoret soils).

Source of variation	d.f.†	Mean sum of squares						
		Grain Yield (g)	Biological Yield (g)	Harvest Index (%)	1,000 KWT‡ (g)	Plant Height (cm)	Seed per Head (S/HD)	Seed per Plot (S/PT)
Replicates	2	0.3	4.1	27.6	50.1	78.2	27.6	422.4
Treatments	1	1.4 **	12.1 **	0.4 NSþ	211.7 **	495.1 **	205.9 **	247.7 NS
Varieties	6	3.7 **	6.2 *	304.8 **	210.5 **	387.8 **	401.9 **	5820.4 **
Treatment x Varieties	6	0.4 **	0.4 NS	79.5 **	5.9 NS	11.2 NS	11.2 NS	369.7 **
Error	26	0.1	0.2	22.5	40.7	13.5	5.5	113.48
Total	41							

† degrees of freedom
*, ** Significant at P ≤ 0.05 and 0.01, respectively.
NS Not significant
þ x10 ²
‡ 1,000 kernel weight g

Table 5.2 Analysis of variance for all sets of data for seven varieties of wheat grown in Andosols (Molo soils).

Source of variation	d.f.†	Mean sum of squares: Grain Yield (g)	Biological Yield (g)	Harvest Index (%)	1,000 KWT‡ (g)	Plant Height (cm)	Seed per Head (S/HD)	Seed per Plot (S/PT)
Replicates	2	4.3	27.7	28.0	69.7	23.9	50.3	342.1
Treatments	1	1.7 **	10.8 **	0.3 NSÞ	148.9 *	454.1 **	152.4 *	342.9 NS
Varieties	6	11.4 **	14.3 **	600.9 **	318.5 **	355.5 **	540.6 **	8157.4 **
Treatment x Varieties	6	0.2 NS	0.3 NS	19.9 NS	77.3 *	25.1 *	2.0 NS	179.6 NS
Error	26	0.1	0.7	14.7	30.3	9.6	4.7	99.5
Total	41							

† Degrees of freedom

*, ** Significant at $P \leq 0.05$ and 0.01, respectively.

NS Not significant

Þ $x10^{-29}$

‡ 1,000 Kernel Weight g

Table 5.3 Mean values of seven wheat varieties grown in Ferralsols (Eldoret soils) with respect to eight characters.

Variety	Grain Yield (g)	Biological Yield (g)	Harvest Index (%)	1,000 KWT♭ (g)	Plant Height (cm)	Seed per Head (S/HD)	Seed per Plot (S/PT)
Romany†	3.7 a‡	9.3 a	39.9 a	33.4 bc	59.2 c	32.7 a	111.8 a
K. Fahari	3.3 b	7.6 c	43.3 a	40.9 ab	57.3 c	22.7 b	81.8 b
K. Tembo	3.3 b	7.5 c	43.7 a	34.8 bc	65.1 b	25.2 b	94.8 b
PF7748	3.1 b	8.1 b	37.7 a	36.2 bc	69.6 a	23.2 b	84.7 b
K. Kongoni	2.3 c	7.5 c	30.6 b	46.8 a	52.8 d	17.5 c	52.2 c
Siete Cerros	2.1 c	6.5 d	31.9 b	31.1 c	46.6 e	14.3 d	52.5 c
K. Swara	1.5 d	6.3 d	24.6 c	44.6 a	51.3 d	7.3 e	20.2 d

† Varieties are listed in order of grain yield for easier reading and cross referencing in subsequent table(s).
‡ Means followed by the same letter within a column are not significantly different at $P \leq 0.05$ according to Duncan's Multiple Range Test.
♭ 1,000 Kernel Weight (g).

Table 5.4 Mean values of seven wheat varieties grown in Andosols (Molo soils) with respect to eight characters.

Variety	Grain Yield (g)	Biological Yield (g)	Harvest Index (%)	1,000 KWT♭ (g)	Plant Height (cm)	Seed per Head (S/HD)	Seed per Plot (S/PT)
Romany†	5.8 a‡	12.8 a	45.5 a	38.6 c	67.0 b	40.5 a	150.0 a
K. Fahari	5.1 b	10.6 cd	46.9 a	44.9 bc	66.2 b	29.0 bc	113.7 bc
K. Tembo	4.7 cd	10.4 d	45.2 a	38.5 c	63.9 c	31.2 b	121.5 b
PF7748	5.0 bc	11.7 b	44.6 a	46.8 b	74.2 a	27.7 cd	106.5 cd
K. Kongoni	5.4 b	11.5 bc	47.1 a	56.5 a	58.3 c	25.8 de	96.3 d
Siete Cerros	4.5 d	9.6 d	46.7 a	46.3 b	50.5 d	24.7 e	96.6 d
K. Swara	1.6 e	8.0 e	19.6 b	55.9 a	58.0 c	8.8 e	29.8 e

† Varieties are listed in order used on Table 5.3 for ease cross referencing.
‡ Means followed by the same letter within a column are not significantly different at $P \leq 0.05$ according to Duncan's Multiple Range Test.

plant height, S/HD and S/PT. No significant variations were observed between varieties on the basis of harvest index. A wide range of mean values was observed between Romany (tolerant) and K. Swara (susceptible). For instance, in grain yield, biological yield, harvest index, S/HD and S/PT differences of 72%, 38%, 56%, 78% and 80%, respectively, were observed.

A paired *t*-test (Table 5.5) between the grand mean values for all the measured characters indicated that the application of lime had a significant ($P \leq 0.01$) increase for the biological yield on the Ferralsols, whilst a significant ($P \leq 0.05$) plant height increase was observed on the Andosols. Generally, there was no significant increase for the grain yield, KWT, plant height, S/HD and S/PT due to the liming of the Ferralsols from the initial pH of 5.5 to the target pH of 6.5 using a lime rate of 3.25 tonne/ha. Both the grain yield and biological yield were characterized by relatively small standard errors. Large standard errors were observed in S/PT. This might have been contributed by the wide variations of seed count between the varieties.

In the Andosols (Table 5.5) it was indicated that the only significant ($P \leq 0.05$) increase due to liming was on the plant height. All the other characters were not significantly affected by liming the soil from the initial pH of 5.4 to the target pH of 6.5 using a lime rate of 5.10 tonne/ha.

The lack of response to the lime in most of the tested characters may be explained by the low aluminum content in the two soils (Appendix 3). Results in Appendix 3 indicate that both the Andosols and the Ferralsols had relatively low concentrations of exchangeable aluminum, therefore, the lack of significant positive response to liming of these soils may be partly explained by this factor.

4.5.2 Correlation coefficients and multiple regression analyses

Experiment 5 results (Table 5.6) indicated that grain yield was significantly ($P \leq 0.01$) correlated to biological yield, harvest index, S/HD and S/PT in both the limed and non-limed Ferralsols. A significant ($P \leq 0.01$) negative correlation ($r = -0.64$) was observed

Table 5.5. Effect of lime treatment on measured variables for seven wheat varieties. Data represents the mean values and SE from two lime treatments on two soils, Ferralsols (Eldoret soils) and Andosols (Molo soils).

Variable	Ferralsols (Eldoret soils)					Andosols (Molo soils)				
	Limed pH 6.5		Unlimed pH 5.5		t-test mean difference	Limed pH 6.5		Unlimed 5.4		t-test mean difference
	Mean	SE	Mean	SE		Mean	SE	Mean	SE	
Grain yield (g)	2.9	0.03	2.6	0.04	NS	4.8	0.08	4.4	0.11	NS
Biological yield (g)	8.1	0.07	7.0	0.06	**	11.2	0.14	10.2	0.25	NS
Harvest index (%)	35.9	2.51	35.9	4.50	NS	42.2	4.08	42.2	5.85	NS
1,000 KWT† (g)	40.5	2.61	36.0	3.24	NS	48.7	3.36	44.9	4.50	NS
Plant height (cm)	60.9	3.21	53.9	[illegible].69	*	65.9	3.38	59.3	2.27	*
Seed per head	22.6	2.64	18.2	3.72	NS	28.7	3.91	24.9	4.37	NS
Seed per plot	73.6	37.99	68.7	59.47	NS	105.0	51.40	99.3	75.44	NS

NS not significantly different
*, ** limed and unlimed mean values significantly different based on the pairwise t-test at at $P \leq 0.05$ and 0.01, respectively.
† 1,000 Kernel Weight (g)

Table 5.6. Correlation coefficients (r)† between all measured variables for 7 wheat varieties. Correlation coefficients for Ferralsols (Eldoret soils), limed and unlimed are presented above and below the diagonal, respectively.

Unlimed pH 5.5	Limed pH 6.5						
	Grain Yield (g)	Biological Yield (g)	Harvest Index (%)	1,000 KWT (g)	Plant Height (cm)	Seed per Head	Seed per Plot
Grain Yield (g)		0.73	0.83	-0.30	[illegible]	0.91	0.87
Biological Yield (g)	0.78		0.24	-0.23	0.49	0.80	0.73
Harvest Index (%)	0.92	0.48		0.25	0.24	0.66	0.65
1,000 KWT‡ (g)	-0.15	-0.16	-0.12		-0.20	0.39	-0.64
Plant Height (cm)	0.62	0.54	0.56	0.05		0.49	0.43
Seed per Head	0.87	0.86	0.69	-0.33	0.55		0.92
Seed per Plot	0.92	0.78	0.80	-0.40	0.63	0.95	

† N = 21. Correlation coefficients $\geq$ 0.43, 0.55 are significant at P $\geq$ 0.05 and 0.01, respectively.
‡ 1,000 Kernel Weight (g)

Table 5.7. Correlation coefficients (r)† between all measured variables for 7 wheat varieties. Correlation coefficients for Andosols (Molo soils), limed and unlimed are presented above and below the diagonal, respectively.

Unlimed pH 5.4	Limed pH 6.5						
	Grain Yield (g)	Biological Yield (g)	Harvest Index (%)	1,000 KWT♭ (g)	Plant Height (cm)	Seed per Head	Seed per Plot
Grain Yield (g)		0.81	0.87	-0.07	0.20	0.86	0.86
Biological Yield (g)	0.85		0.42	-0.09	0.39	0.74	0.66
Harvest Index (%)	0.79	0.39		-0.06	0.02	0.71	0.79
1,000 KWT (g)	-0.44	-0.14	-0.58		-0.39	-0.50	-0.47
Plant Height (cm)	0.40	0.32	0.37	-0.32		0.30	0.25
Seed per Head	0.89	0.75	0.72	-0.65	0.49		0.95
Seed per Plot	0.87	0.68	0.76	-0.69	0.55	0.95	

† N = 21. Correlation coefficients ≥ 0.43, 0.55 are significant at $P \geq 0.05$ and 0.01, respectively.
♭ 1,000 Kernel Weight (g)

between KWT and S/PT on the limed Ferrralsols, but the correlation (r = -0.40) between the same charactcers KWT and S/PT was not significant on the non-limed Ferralsols.

In Experiment 5 the correlation coefficients (Table 5.7) between all the measured variables for the limed and non-limed Andosols were closely related to those of the Ferralsols (Table 5.6) on the basis of general observation. Significant ($P \leq 0.05$) negative correlations (r) of -0.50 and -0.47 between KWT and S/HD; KWT and S/PT, respectively, were observed on the limed Andosols. For the non-limed Andosols a significant negative correlation (r = -0.44) was observed between KWT and grain yield. Highly significant ($P \leq 0.01$) negative correlations were observed between KWT and harvest index (r = -0.58); KWT and S/HD (r = -0.65); and KWT and S/PT (r = -0.69).

Stepwise multiple regression analyses in Experiment 5 indicated that both the biological yield, and harvest index were the best grain yield predictors for both the Ferrralsols and Andosols with lime or no lime. However, no significant differences were obeserved between the coefficients of determinations (R^2) between the limed and the non-limed Andosols and Ferralsols. The partial regression coefficients (b -values) were not significantly different between the limed and the non-limed treatments for both the Andosols and Ferralsols. Both biological yield and harvest index accounted for approximately 99% of the total variations in grain yield in the limed, and non-limed Ferralsols, the limed Andosols; and 96% in the non-limed Andosols.

4.6 DISCUSSION

Results of the studies revealed that there were significant variations amongst Kenyan and other varieties with respect to aluminum tolerance and response to lime treatment. No previous work has been reported on the tolerance to aluminum toxicity of Kenyan wheat varieties.

Polle *et al.* (1978) subjected a number of wheat cultivars to aluminum treatments and thereafter stained the roots of the seedlings with hematoxylin stain. On the basis of staining patterns as the amount of aluminum concentration was varied, they classified cultivars into tolerant and susceptible categories.

In the classification of varieties (Experiment 1) using the hematoxylin method of Polle *et al.* (1978), Kenyan varieties were separated into three categories:

I. tolerant

II. medium tolerant

III. susceptible The varieties Romany, K. Tembo, K. Popo, K. Kuhungu and K. Kongoni were the best tolerant varieties overall. On the other hand K. Swara, K. Fahari, Bounty and K. Tumbili were the most susceptible on the basis of overall back transformed mean scores.

Polle *et al.* (1978), suggested that for routine use of hematoxylin stain procedure, it would be better to screen for tolerance at the highest level of aluminum (0.72 *m*M). The reason for this suggestion was that at low aluminum concentrations it is hard to differentiate tolerant and susceptible varieties, since they may react in a similar way. This concept was verified in the present study, where at 0.30 *m*M aluminum concentration the degree of variation was small amongst the Kenyan varieties compared to when the concentration of aluminum was 0.59 *m*M. On the other hand, when the concentration of aluminum was increased to 1.72 *m*M a trend of low degree of variation, similar to that demonstrated at 0.30 *m*M aluminum concentration, was observed among varieties. This results reconfirms that tolerance to aluminum toxicity is a rather relative than an absolute characteristic as pointed out by Aniol (1984); and Lafever *et al.* (1977).

From the experimental results, perhaps screening at low (0.15 *m*M) levels of aluminum may provide cultivars which have low levels of aluminum tolerance through which a breeding program can be built, especially for regions with low Al levels. On the contrary, screening at high ($\geq$ 0.72 *m*M) aluminum concentrations may be useful to determine tolerant varieties for regions where high aluminum toxicity exists.

In Experiment 2, severe depressions of root weight, shoot weight, root length, and biological yield at $\geq$ 0.15 *m*M ppm of aluminum were similar to those reported by others (Kerridge *et al.* (1971); Taylor and Foy, 1985; Ohki, 1985). However, the present results indicate that root growth is more severely affected by aluminum than shoot growth, and overall biological growth. This result is also in agreement with the previous reports (Campbell and Lafever, 1976; Foy *et al.* 1967; Kerridge *et al.*, 1971; Taylor and Foy, 1985) using different sets of cultivars. Therefore, it was not a suprise that in the ANOVA there were highly significant variety x treatment interactions for root length and RTI.

On the basis of RTI, varieties were classified into aluminum-tolerant and aluminum-susceptible using the test results of Experiment 2. There was close agreement with a number of previous reports (Lafever *et al.*, 1977; Taylor and Foy, 1985), again using different sets of cultivars. The correlations between RTI and STI partly agreed with the report of Taylor and Foy (1985).

The severity of aluminum toxicity symptoms was similar to those previously reported (Foy, 1984; Kerridge *et al.*, 1971; Lafever *et al.*, 1977). Severity of symptoms was noticed to increase as the the concentration of aluminum was increased from 4 (0.15 *m*M) to 64 (2.37 *m*M) ppm. Figure 1 illustrates the effects of aluminum concentrations on different cultivars. Aluminum effect on visually obvious rooting differences were much more than those observable on shoots. This confirmed previous reports (Foy *et al.*, 1967; Foy and Brown; 1964 Lafever *et al.*, 1977; Taylor and Foy, 1985), that roots are the most affected in an environment with aluminum toxicity.

The varietal studies in UCM (Experiment 3) indicated that there were significant differences among varieties in all the agronomic characters. This agree well with previous studies by Kerridge *et al.* (1971); Mesdag and Slootmaker (1969). The significant varietal differences in this study may suggest that considerable "natural selection" has occurred in some the Kenyan wheat varieties for tolerance to acidic and aluminum conditions. Similarly to Experiment 2, the UCM study indicated that roots were the most affected by aluminum and acidic conditions (Figure 2).

According to Haug (1985), the organic fraction of the soil contains metal chelates which diminish the activity of free metal ions. From this concept, it will be postulated that the high organic content in the UCM that was used in the experiment may have masked some

Figure 1. Differential effects of aluminum concentrations on nine wheat varieties grown in nutrient [illegible].

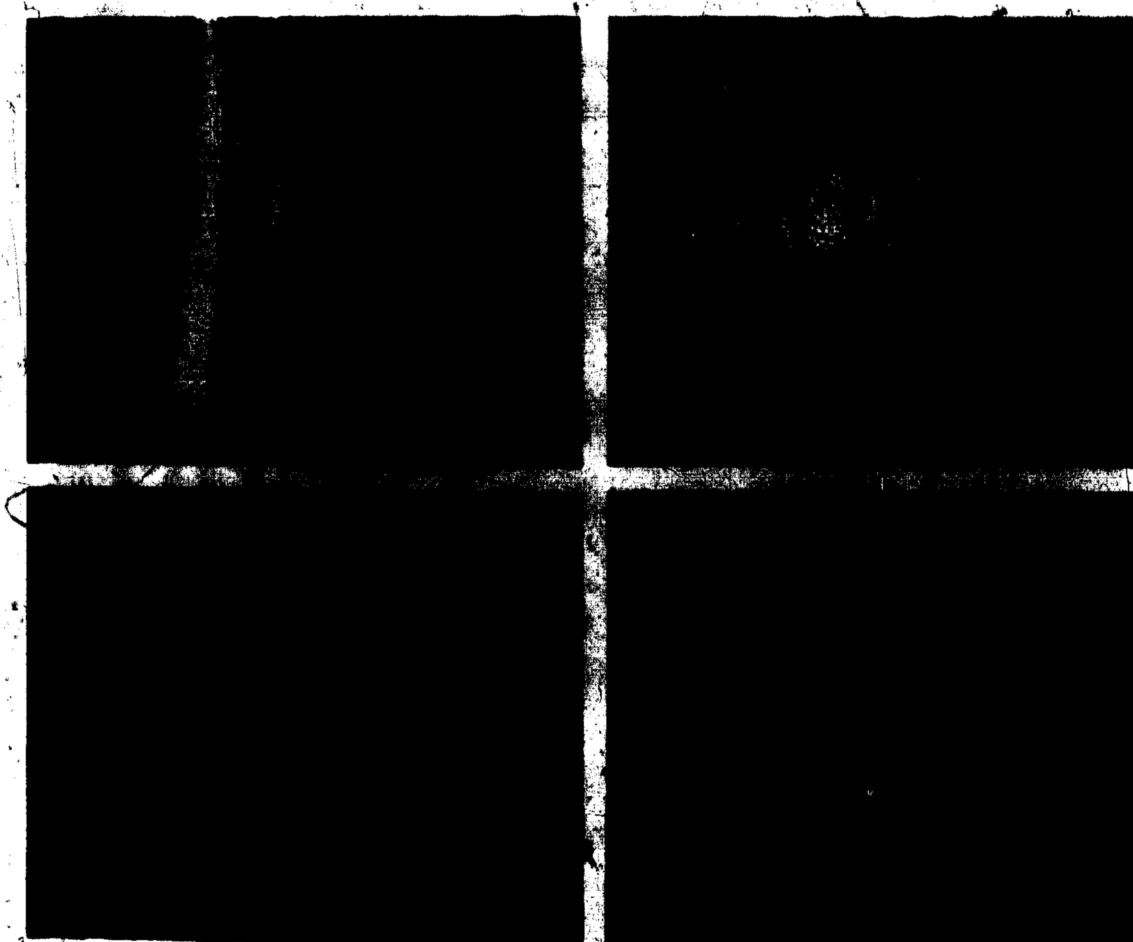
Pictures 1, 2, and 3 represent varieties Maringa, K. Kongoni, and Romany (tolerant), respectively.

Pictures 4, 5, and 6 represent varieties K. Zabadi, K. Nungu, and Paa (medium tolerant), respectively.

Pictures 7, 8, and 9 represent varieties Siete Cerros, K. Swara, and K. Fahari (susceptible), respectively.

Aluminum concentrations increase left to right: 0 (control), 4, 16, and 64 ppm for each set of variety.

Figure 2. The effect of aluminum concentratioin on four wheat varieties grown in UCM . Pictures 1, and 2 represent varieties Romany, and PF7748 (tolerant); 3, and 4 represent varieties K. Swara, and Siete Cerros (susceptible). Aluminum concentrations increase from left to right: 0 (control), 8, and 16 ppm for each set of variety, respectively.



of the aluminum toxicity effects. Therefore, it would be valuable to do field tests to compare results obtained from artificial media such as UCM. Similarily, due to the amount of labour and time requirements for recovering and washing roots, such studies should be limited to testing only a few varieties in breeding programs, perhaps to identify good parents.

Some previous studies (Lafever and Campbell, 1978; Campbell and Lafever, 1981), suggested that aluminum tolerance in wheat was controlled by dominant and additive genes. The present study (Experiment 4), demonstrated that there are different degrees of aluminum tolerance among phenotypically tolerant genotypes as illustrated in the data of Table 4.1. The F2 populations were screened at 46 ppm aluminum level. Therefore, tolerance of the segregants in this case should be interpreted with respect to aluminum level used.

Aniol (1984), suggested that aluminum tolerance in hexaploid wheat is determined by several genes, probably located in different genomes. Our data seem to agree in part with this concept that aluminum tolerance is determined by several genes.

Camargo *et al.*, (1980), indicated that selection in early generations from either plant height or tolerance to aluminum should be effective. This implied that plant height was closely related to aluminum tolerance. There is no a priori reason to believe that aluminum tolerance was related to plant height, but it was noticed that the tolerant F2 plant were both tall and relatively late maturing, compared to the susceptible plants. However, some of the F2 tolerant segregants showed semi-dwarf, and early-maturing characteristics (Figure 3). The results agree with the previous studies (Camargo *et al.*, 1980), which suggested that it is possible to select for plant types which combine both aluminum tolerant, and semi-dwarf characteristics.

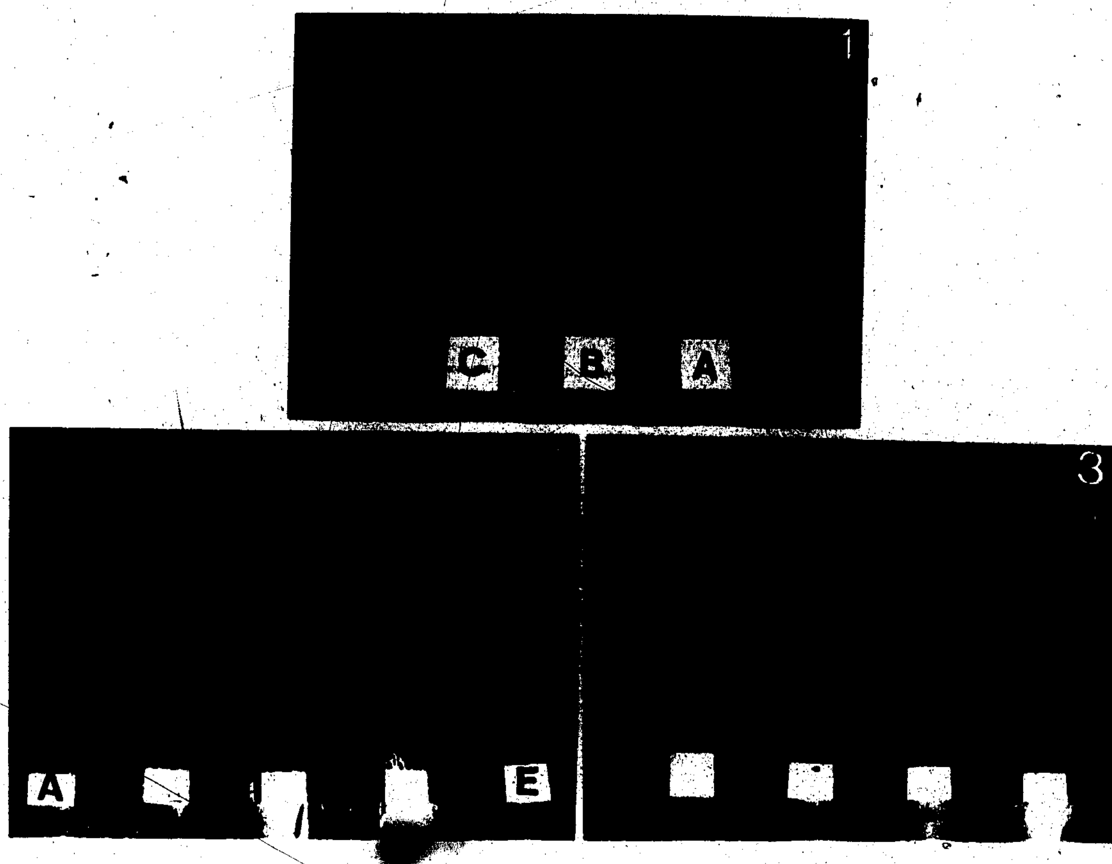
The low variance dispersions for both the mid-parent and F2 progeny on the basis of grain yield suggests that grain yield is not a strong criterion to use for indirect selection for aluminum tolerance. A closely related concept by Camargo *et al.*, (1980) was demonstrated that grain yield can not be effectively used as a criterion to select for aluminum tolerance. Nevertheless, they suggested that selection for aluminum tolerance may be done during the early generations, with delayed selection for yield in later generations within the previously selected tolerant populations.

Figure 3. F2 wheat plants and some of the wheat parents grown in UCM with high (46 ppm) aluminum concentration.

Picture 1 represent varieties K. Fahari (A), PF7748 (B), and F2 plants (C) obtained from a cross between A and B.

Picture 2 represent varieties K. Fahari (A), Romany (E), and F2 segregants (middle three pots) obtained from a cross between A and E.

Picture 3 represent (left to right) varieties K. Fahari (susceptible), Romany, and PF7748 (tolerant), and Siete Cerros (susceptible).


1
C
B
A
3
A
E

Some of the Kenyan varieties like Romany and K. Kongoni showed good tolerance of equal or better magnitude compared to PF7748 (Brazilian tolerant line). The F2 progenies of Romany and PF7748 in most cases indicated significantly positive performance in aluminum toxic conditions.

In order to obtain effective selection for aluminum tolerance and high yield, large F2 populations will be necessary. However, when selecting for aluminum tolerance the traits used as indicators of tolerance should be interpreted with care, since segregation of these traits may not be directly related to aluminum tolerance.

Acidic soils tend to have amounts of aluminum that are toxic to plants (Kamprath, 1972; Reid *et al.*; 1969). However, the soil test results (Experiment 5), as indicated in Appendix 3, demonstrated that the the concentration of exchangeable aluminum in both soils is relatively low. Consequently, it may be argued that the noticed differential response to lime amongst the test varieties is not solely due to aluminum toxicity, but due to other soil factors. According to the results on Appendix 3, the aluminum concentration in the soils is relatively low compared to manganese. This result was not anticipated at the start of these studies.

In the literature (Foy *et al.*, 1973; Neenan, 1960; Ouellette and Dessureaux, 1958), it has been reported that manganese and aluminum have a confounding effect in a given acid soil-plant situation. Neenan (1960) also concluded that, differential internal Mn tolerance was responsible for different responses of certain wheat varieties to high Mn levels. Based on this criteria, it may be suggested that the differential response to lime noticed in the test varieties may be partly due to the effect of Mn concentration in the soils (Appendix 3). On the other hand Akira *et.al.*, (1984), reported that a combination of low pH and low P in the soil magnifies adverse effects on plants. Similarily, Sanchez and Salinas, (1981) reported that it is possible to select for species or varieties which are tolerant to low pH and/or low phosphorus conditions. On the same subject Akira *et al.*, (1984), reported that response to lime for forage crops was attributed to the addition of Ca, Mg and other nutrients like P. Using these established facts, it may be likely that, the differential response to lime in the test varieties is a result of a myriad of factors. Some of these factors may be related to Ca, Mg, pH and P.

The variety Romany and its backcrosses has been reported (Rakotondramanana and Randriantsalama, 1985; 1986) to perform well in the East African soils which are characterized by low pH, aluminum toxicity and low P.

Results from the present study indicate that Romany and PF7748 have significantly higher acidity tolerance than than K. Swara and Siete Cerros, as measured by any of the tests, including tolerance to aluminum.

The consistently low mean values for the varieties K. Swara and Siete Cerros in most characters measured, compared to the varieties, K. Kongoni, Romany and PF7748, may imply that susceptible varieties to aluminum toxicity may not perform better than aluminum tolerant varieties under a lime management program.

The lack of significant liming response for all measured characters except for biological yield and plant height in the Ferralsols, and plant height in the Andosols, may suggest indirectly that at the initial pH of 5.4 for the soils is not low enough for the soils to contain significant levels of aluminum concentrations in solution (Appendix 3).

When interpreting the liming results it should be borne in mind that greenhouse experiments are not particularly useful in helping to identify critical soil pHs, because they usually test only the A horizon under a demanding growth regime (Lafever *et al.*, 1977). Field experiments, on the other hand, test the combined effects of surface and sub-surface soil horizons on crop yield. Consequently, it will be necessary to carry out field experiments with local varieties in Kenya using lime in the field to confirm the acidity tolerance demonstrated in the present study.

4.7 Interrelationship of study results

Results from the five experiments followed very similar trends. The varieties that were scored as tolerant in the hematoxylin procedure (Experiment 1) consistently exhibited better performance in subsequent experiments, with few exceptions.

The results from the staining procedures of Polle *et al.*, (1978), used in the study agree well with those from nutrient culture, UCM and lime treatment studies. Our results in turn agree with the previous studies done by Lafever *et al.* (1977); Mugwira *et al.*, (1981); Foy and Brown, (1964); Foy *et al.*, (1967) which indicated that nutrient culture techiniques were highly correlated with greenhouse screening techniques using acidic soils with some aluminum toxicity.

Some literature (CIMMYT, 1983; Rajaram *et al.*, 1983) indicate that some varieties like Alondra"s" have superior performance in acidic soils despite lack of aluminum tolerance perhaps partly due to their ability to efficiently extract and utilize phosphorus under lower levels of availability. On the basis of this concept, it may be likely that some of the anomalies that were encountered in the various screening procedures of the present study can be attributed to the interaction between "actual" aluminum tolerance and "indirect" tolerance due to better use and extraction of phosphorus.

Helsel (1985), using oats as the test crop used biomass as a means of selecting for grain yield. In the present study it was found that those varieties that were scored as tolerant in the hematoxylin screening procedure, showed higher biological yield than the susceptible varieties, except for K. Fahari in a few cases. As suggested by Helsel (1985), biological yield is partly controlled by additive gene action. Similarily, Lafever and Campbell, (1978); and Campbell and Lafever, (1981), have indicated that aluminum tolerance is controlled by dominant and additive genes. Combining these two suggetions, it would be possible to select for aluminum tolerance using biological yield as the criterion.

Helsel (1985); and Singh and Stoskopf (1977) reported that selecting indirectly for grain yield through harvest index was the most effective way of improving grain yield in early generations. At the same time they reported that selection for harvest index retained lines that were preferred for plant height and maturity. Using this concept, it may also be possible to select for aluminum tolerant plants by selecting those plants which have a high harvest index in an aluminum toxic environment. It was noticed in the present study that most of the varieties and F2 individuals that were designated as tolerant had characteristics of tallness and late maturity.

Overall in these studies, the responses of individual varieties and F2 progenies observed in the nutrient culture studies were in close agreement with results of UCM and results reported earlier by Foy *et al.*, (1974). Similarily, results of the present studies agree well with the preliminary work carried out at Njoro, Kenya (Nyachiro and Briggs, Appendices 4, 5, 6 - Unpublished data). Also it was noticed in these studies that the large number of characters measured, whilst adding to the complexity of interpretation, emphasized the vast genetic variability available to the plant breeder interested in developing varieties to fit specific production conditions.

5. SUMMARY AND CONCLUSIONS

The objectives of this study were to classify some wheat germplasm commonly used in Kenya using the criterion of response to aluminum toxicity, using different methods to determine the response of the wheats to aluminum toxicity and acidic conditions, and to [illegible] the response of [illegible] to lime treatment. The study was also aimed at determining the inheritance of [illegible] tolerance through simple crosses.

In the study it was demonstrated that the wheat test varieties responded differentially to aluminum toxicity and acidic conditions. Similarily, it was demonstrated that the test varieties responded differentially to lime treatment. Results of aluminum inheritance study showed that, F2 segregation ratios did not agree well with 3:1 Mendelian ratios, although a number of exceptions were noted to agree well with the 9:7 segregation ratio.

In the hematoxylin screening procedure it was shown that the Kenyan wheat varieties used in the study differed significantly in their tolerances to aluminum. It was also shown that "sister varieties" could differ significantly in aluminum tolerance. From the present study, it can be said that some of the Kenyan wheat varieties have beeen previously selected indirectly for aluminum tolerance. However, the present experiment did not provide data on staining reactions as related to aluminum tolerance. Additional studies to compare the staining reactions and the field aluminum tolerance of the Kenyan wheat varieties will need to be conducted to determine this correlation. However, on the basis of hematoxylin staining results, it can be concluded that some genetic differences with respect to aluminum tolerance do exist in the Kenyan wheat varieties that were used in the study. For instance, the variety Romany was determined to be equal in tolerance to Maringa, and PF7748. In all the screening procedures, Romany scored significantly higher values than most Kenyan varieties except on a few cases.

On the basis of variety response in the aluminum nutrient culture solution study, it was again inferred that there was significant differential tolerance to aluminum toxicity within the 16 wheat varieties. Some of the Kenyan varieties like Romany, K. Kongoni, and K. Popo were among the most tolerant, whereas others like K. Swara, K. Kima and Paa were some of the most susceptible.

In the study using UCM that was augmented with varying aluminum concentration (Experiment 3), it was found that there were no significant treatment x variety interactions in the ANOVA for any of the agronomic characters studied, except for the indices RTI and STI. This result confirms previously published results (Taylor and Foy, 1985), that indicated aluminum tolerance effects are expressed most clearly on root development. Nevertheless, indications of wide differences in the mean values of the measured characters and indices were observed between low and high aluminum concentration. There were significant decreases in mean values for the three indices RTI, STI and BYTI as the relative aluminum was increased from 8 ppm Al/0 ppm Al to 16 ppm Al/ 0 ppm Al.

Highly significant correlations were observed between biological yield and root weight, and between biological yield and shoot weight in all the aluminum treatments.

On the basis of the F2 progeny test results, it was indicated that it was possible to transfer aluminum tolerance into some Kenyan wheat varieties. Nevertheless, the complex behaviour of the F2 segregants suggests that more studies need to be carried out to identify the homozygous aluminum tolerant parents which will be used for breeding programs.

In the study, the hypothesis of 3:1 ratio was not demonstrated to hold true for all the crosses that were studied (Tables 4.1 and 4.2), whereas a 9:7 ratio was confirmed in some crosses using a x^2 test. This in turn suggested that 2 dominant genes were responsible for aluminum tolerance with some complexities demonstrated.

On the basis of variety response to lime treatment (Experiment 5), there were highly significant treatment x variety interactions for grain yield, harvest index, and number of seeds per plot for the Ferralsols, whereas this was only found for KWT and plant height for Andosols.

On the basis of the results (Table 5.5) that were obtained from the two soils using wheat varieties as indicators of lime response, it can be said that there were no significant advantages of liming. This study is in agreement with other (Foy, 1974; Lee *et al.*, 1970) studies that aluminum toxicity only becomes a major problem when soil pH is below 5.5. The

Ferralsols and Andosols had pH of 5.5 and 5.4, respectively, before liming. Hence, these soils can be said to be "marginal" for pH. Based on the results of this study, it might be recommended that growing of the varieties that are well adapted and tolerant to acid soils other than liming the study soils will suffice, though this would require confirmation under field conditions in Kenya. Studies should be planned to quantify the yield advantage of liming over that of growing tolerant varieties in acidic Kenyan soils.

Another area of study that should be attended to in the future is on the trend of pH and aluminum changes in these soils due to continuous cropping and management practices over time. Information that will be obtained from such studies can be of help in making decisions whether to lime or not.

In conclusion, results presented in this study have indicated significant aluminum tolerance and acid tolerance differences for a cross section of the elite germplasm of wheats grown in Kenya. In addition to this, it was shown that aluminum tolerance can be transferred into some of the Kenya wheat varieties using other sources of wheat germplasm which are tolerant to aluminum toxicity. Nevertheless, more detailed studies are required to explain the correlations between laboratory and greenhouse screening results and actual field tolerance to aluminum of the Kenyan germplasm. Results from the present study did not demonstrate that aluminum *per se* is necessarily an essential character in Kenyan wheat varieties, since aluminum concentrations were not high in the Kenyan soils sampled for this work.

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6. APPENDICES

Appendix 1. Parentage/Pedigree of cultivars used in the study.

Cultivar	Parentage/Pedigree
Romany	Colotana 262/51 x Yaktana 54A
K. Tembo	Wis245/II-50-17//CI8154/2*Fr/3/2*Tob66 = K6661-53
K. Fahari	Tob66/SRPC 527/CI8154*Fr = K6648-6
K. Zabadi	Son64/450E//Gto/3/Inia 66/4/K4500-2/5/KSW/Tob66 =K6919-1
K. Swara	CI8154/2*Fr/3/2* K//Y59.2.B = K5393.L.23.C.3.MN
K. Nungu	Wis245/II-50-17//CI8154/2*Fr/3/2* Tob66 = K6661-B
K. Kulungu	On/Tr207/3/Cno//Son64/4/K. Tembo"s"
K. Popo	Kl Alt/Tob66/Cno/3/Bb/4/K. Fahari"s"
K. Nyumbu	On/Tr207/3/Cno//Son64/4/K. Nungu"s"
K. Kongoni	CI8154/2*Fr/2/3* Rom/3/Wis245-II-50-17/CI8154 /2/2*Fr = K6928-1
K. Kima	KTB/Giza 155//NRDISN 799/CM-11029-1WY-F = K7207-20
K. Tumbili	KTB/Giza 155//NRDISN 799/CM-11029-1WY-F = K7207-12
Paa	Kavkaz/Cno-Chris/On = Sel.375-125-35-0k-4Ke-λ = R200
Bounty	T. Kenya/2/Bonza
PF7748	ND81/IAS59//IAS58
Siete Cerros	Kalyansona"s"
Maringa†	--------------------------

† Pedigree for Maringa was not available

Appendix 2. Analysis of UCM† used in Experiment 4.

Type of Analysis	Analytical Results‡	Sufficient Range††
Ammonium-N	19.5	0-20
Nitrate-N	39	35-180
Phosphorus-P	65	5-50
Potassium-K	198	35-300
Sodium-Na	20	0-30
Calcium-Ca	277	60-400
Magnesium-Mg	68	30-200
Chloride-Cl	31.3	0-30
Sulphates-S	28	30-60
Nitrites-NO_2	BDL♭	NIL
pH (1:5 H_2O)	4.6	5.5-6.9
Electro-Conductivity	2.1	0.8-3.0

† Refers to University of Calfornia Mixture
‡ All results in Parts Per Million except pH, and EC. EC expressed as $mS\ cm^{-1}$. Analyses conducted by Alberta Soil and Feed Testing Laboratory (ASFTL) O.S. Longman Building, 6909-116 ST., Edmonton, Alberta. T6H 4P2 pH, texture and EC according to Alberta Agriculture Methods.(pers. comm.)
†† Nutrient sufficiency range in growing with water extract acccording to ASFTL greenhouse recommendations
♭ Below detection levels of current analytical methods.

Appendix 3. Some of the characteristics for the soils that were used in Experiment 5.

	Mollic Andosols			Plinthic Ferralsols		
Analysis	32‡	33	Blend 1	36	37	Blend 2
pH (H_2O)	5.5	5.4	5.4	5.5	5.3	5.5
pH ($CaCl_2$)	4.5	4.5	4.5	4.7	4.6	4.6
Na meq/100 g	0.22	0.15	0.15	0.14	0.13	0.14
K ,, ,,	2.28	2.36	2.26	1.67	1.69	1.74
Ca ,, ,,	7.09	5.98	5.70	2.77	3.74	3.46
Mg ,, ,,	2.03	1.58	1.58	1.31	1.58	1.48
Mn ,, ,,	0.19	0.29	0.24	0.28	0.21	0.24
Al ,, ,,	0.03	0.03	0.02	0.01	0.01	0.01
NH_3 ,, ,,	29.34	32.25	30.52	20.66	20.51	20.52
ACe† ,, ,,	16.18	16.81	15.71	12.51	12.78	9.81
NH_4^+-N ppm	3.17	3.08	3.29	1.67	1.61	1.70
NO^{3-}-N	0.97	1.72	1.22	0.13	3.25	2.32
Total P %	0.05	0.05	0.06	0.09	0.09	0.09
,, ,, N %	0.26	0.26	0.26	0.11	0.12	0.12
,, ,, C %	3.85	3.63	3.78	1.36	1.66	1.63
Sand %	30	26	-	30	44	
Clay %	40	42	-	58	46	
Silt %	30	32	-	12	10	

† Exchangeable acidity
‡ Nos. 32 to 37 refer to soil sample number, where 32 and 33 were combined to form blend 1, and 36 and 37 were combined to form blend 2, respectively.

Appendix 4. Analysis of variance for all sets of data for 12 cultivars of wheat grown in two Kenyan soils differing in pH. Study conducted in greenhouse at Njoro, 1983.

		Mean sum of squares	
Source of variation	d.f.†	Biological Yield (g)	Plant Height (cm)
Replicates	3	1.8 **	31.3 **
Soils	1	113.8 **	333.8 **
Varieties	11	1.8 **	8.4 NS
Soils x Varieties	11	1.1 **	4.2 NS
Error	69	0.3	4.8
Total	95		

† degrees of freedom

NS Not significant

*, ** significant at $P \leq 0.05$ and 0.01, respectively.

Appendix 5. Mean values for 12 varieties of wheat cultivars grown in acidic soils (Plinthic Ferralsols from Eldoret) differing in pH.

Cultivar	Biological Yield (g)	Plant Height (cm)
K. Kongoni†	4.2 a‡	44.7 b
R 456	3.6 b	46.5 b
R 455	3.6 b	48.0 b
K. Zabadi	3.5 b	47.2 b
K. Kulungu	3.4 bc	44.5 b
Romany	3.3 bcd	53.1 a
K. Popo	3.3 bcd	44.2 b
K. Fahari	3.2 bcde	43.4 b
K. Swara	2.8 cdef	48.3 b
Paa	2.8 cdef	48.5 b
Bounty	2.7 ef	43.2 b
K. Tembo	2.5 f	46.9 b

† Cultivars listed in the order of biological yield
‡ Mean values within a column followed by the same letter are not significantly different according to the Duncan's Multiple Range Test at $P \leq 0.05$.

Appendix 6. The effect of pH of two acidic soils on 12 wheat cultivars.

	Biological Yield (g)		Plant Height (cm)	
	pH			
Cultivars	4.8	5.6	4.8	5.6
K. Kongoni	3.1 a†	5.4 a	37.5 g	52.1 c
R 456	2.8 bc	4.4 cd	41.9 de	50.8 d
R 455	2.9 ab	4.2 de	43.8 b	52.1 c
K. Zabadi	2.5 d	4.5 c	43.2 cd	52.1 cd
K. Kulungu	2.9 ab	4.0 e	39.4 f	49.5 e
Romany	2.6 cd	4.1 e	49.5 a	56.5 a
K. Popo	2.0 e	4.5 c	41.3 e	46.9 f
K. Fahari	1.4 fg	5.0 b	39.4 f	47.6 f
K. Swara	1.6 f	4.1 b	42.5 de	53.9 b
Paa	1.2 g	4.5 cd	40.0 f	57.2 a
Bounty	1.5 f	4.0 e	43.8 b	47.6 f
K. Tembo	1.5 f	3.5 f	41.9 de	52.1 c

‡ Mean values within a column followed by the same letter are not significantly different according to the Duncan's Multiple Range Test at $P \leq 0.05$.