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PHYSIOLOGICAL FACTORS AFFECTING
THE DIFFERENTIAL UPTAKE AND
ACCUMULATION OF PHOSPHORUS BY
LONG AND SHORT SEASON GENOTYPES
OF MAIZE

THEODORE FRANK BRUETSCH

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PHYSIOLOGICAL FACTORS AFFECTING THE DIFFERENTIAL
UPTAKE AND ACCUMULATION OF PHOSPHORUS BY LONG AND SHORT
SEASON GENOTYPES OF MAIZE

by

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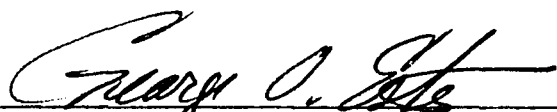
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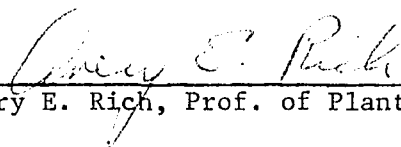
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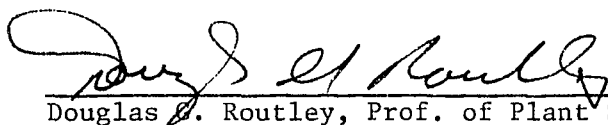
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ABSTRACT

PHYSIOLOGICAL FACTORS AFFECTING THE DIFFERENTIAL UPTAKE AND ACCUMULATION OF PHOSPHORUS BY LONG AND SHORT SEASON GENOTYPES OF MAIZE

by

THEODORE F. BRUETSCH

Genotypes of maize were studied to determine the reasons why long and short season lines exhibit differential uptake of nutrients, especially of P. Four genotypes (Cornell 110, Seneca XX155, Wisconsin 335A, and Agway 590-X) were selected for these investigations on the basis of their economic importance to the Northeast. They are ranked according to maturity, Cornell 110 being the earliest and Agway 590-X being the latest. Experiments were conducted in hydroponic solutions and soil in the greenhouse, as well as in the field.

In the spring under cool soil conditions the early genotypes accumulated significantly more dry matter compared to the later lines. Early lines tended to accumulate more P in both tops and roots. The unique accumulation pattern of P by the early genotypes may afford a degree of protection from the toxic effects of soluble Al in the root zone. The formation of a P-Al complex in or on the root may be responsible. A P-Fe complex may also be occurring at the roots of the early genotypes as shown by an Fe-deficiency symptom. Such a complex would decrease Fe translocation to the plant tops.

Low concentrations of Al in the nutrient solution (0, 2.5, and 5 ppm) stimulated top growth of all genotypes. Aluminum levels of 10 ppm stimulated top growth of early lines but caused dry matter decreases in later lines, indicating sensitivity of the later lines to soluble Al. When P was withheld from the solution and higher Al concentrations were used (0, 10, 25, and 50 ppm), the roots of early genotypes expressed Al toxicity symptoms before those of later lines indicating that P must be present in order to protect the early lines from the harmful effects of soluble Al. Elevated levels of Al in the root environment decreased Mg uptake and appeared to be associated with the maturity rating of the genotype. The early lines contained the most Mg.

In the field, early lines produced more shallow root systems, and these plants were more responsive to surface-applied P. Also, tissue Mg levels increased with applied P, probably due to the inactivation of Al by P which lessens the Al-Mg interaction. Under no-till conditions, the early lines accumulated more P while the later lines accumulated more P under conventional tillage conditions. These results probably reflect the shallow rooting pattern of the early lines as well as the better growth of these lines under cool soil conditions. The early lines removed more Fe, Al, and Mg from the soil under no-till conditions while the later lines removed more under conventional tillage. The choice of variety may well be dictated by the culture system to be used.

INTRODUCTION

Information is needed for the proper selection of maize genotypes with respect to mineral composition, resistance to soil moisture stress, and efficient fertilizer utilization. In the northeastern states, where soil pH frequently limits plant growth, the efficiency of P use is especially relevant. Phosphorus is readily fixed by both Al and Fe in acid soils. The choice of varieties showing superior nutrient efficiency is wise. The physiological factors which contribute to the variation in nutrient use among genotypes are not well understood.

In this investigation a series of studies were designed to determine the effect of root temperature, volume and morphology, root zone Al concentration and pH, and tillage practice on the differential growth and P uptake of early and late season maize genotypes.

REVIEW OF LITERATURE

Characterizations of Root Systems of MaizeVolume

Maize genotypes differ with respect to root volume (Whaley et al. 1950, Andrew and Solanki 1966, Nass and Zuber 1971, and Weihing 1935). The volume of roots in contact with soil or a nutrient solution may well influence the water or nutrient uptake characteristics of that plant. Weihing (1935) studied the differences in root systems of maize varieties that differed materially in aboveground size. He reported that varieties with more massive aboveground portions tended to possess a greater root volume and larger main root diameter. Nass and Zuber (1971) showed that maize genotypes with vigorous young root systems tend to have superior root systems at maturity. Andrew and Solanki (1966) showed root number and root volume to be positively correlated and reported large variation among maize inbreds with respect to the rates of increase of root volume. Their work was done in solution culture in which plants may produce fewer root hairs and have a morphology different from that of soil-grown plants (Warncke and Barber 1974).

Depth

The proportion of roots a maize plant produces in the fertile zones of a soil greatly influences its nutrient uptake, especially during early growth (Mengel and Barber 1974). Shallow rooting may be associated with better early growth and higher

grain yields of maize (Allmaras and Nelson 1971). Leeper et al. (1974) reported much of the variation in maize yield within a field was due to the variation in depth of rooting. Weihing (1935) reported differences among varieties in rooting depth and showed that maize varieties with large aboveground portions tended to have deeper average and maximum penetration than those with smaller aboveground portions.

Differences in depth of rooting among maize hybrids has been suggested by Baker et al. (1970) to be at least partially responsible for differences in P accumulation. This theory was discarded a year later when Baker et al. (1971) concluded that P accumulation in maize is genetically controlled, is associated with the physiological processes within the plant, and is independent of depth of rooting. Jungk and Barber (1974) showed that a large proportion of the maize root must be exposed to a P source in order for the plant to take up an adequate amount of P. If a non-mobile plant nutrient such as P is applied to the surface and not incorporated into the soil as is the case with no-till cultural methods, shallow rooted varieties will be more efficient in the uptake of P than deep rooted varieties. The latter have a smaller portion of their root system exposed to the nutrient. Stryker et al. (1974) noticed a reduction of dry matter accumulation and shoot growth under conditions where only part of the root system of maize was exposed to an external P supply. However, maize plants with shallow spreading root systems have increased susceptibility to a P-induced Fe stress under a no-till culture system. High amounts of P in close proximity to the roots is considered responsible (Estrada and

Cummings 1968). Barber (1971) reported deeper rooting of maize under tilled when compared to no-till conditions. This observation may have been due at least in part to soil temperature and/or moisture conditions.

Mosher and Miller (1972) reported that low soil temperatures tended to cause corn roots to grow laterally while higher temperatures caused them to grow vertically. Onderdonk and Ketcheson (1973) showed maize root growth to be nearly lateral at soil temperatures of 17C; temperatures above or below 17C caused vertical growth.

Extensiveness

Plants with fine roots, a large surface area, and greater length per unit weight should be efficient in nutrient absorption in a large volume of soil (Baylis 1972). Allmaras and Nelson (1971) reported the lateral spread of maize roots to be associated with improved grain yield and early growth. Maize varieties with large tops have been reported to possess roots with a greater maximum spread, more functional main roots, and a greater combined length of main roots per plant when compared to varieties with small tops (Weihsing 1935). Spencer (1940) found that maize lines differed markedly in total length of the main roots. Kiesselbach and Weihsing (1935) reported that inbred lines of maize differed greatly in root characters such as root number per plant, number of branches per unit length, and lateral spread. More recently, Andrew and Solanki (1966) showed differences in the root length of 14 maize inbreds and noted that the rate of growth in root length decreased with

maturity. Maize root length has also been shown to be affected by tillage practice (Barber 1971). Roots tend to be longer under conventional tillage systems when compared to no-till conditions.

Working with maize hybrids selected for high and low P accumulation characteristics, Baker et al. (1970) found that accumulation by the radicle of all hybrids tested was in a zone no more than 4 cm from the root tip. Russell and Sanderson (1967) suggest that the important factors in P uptake are the amount of root elongation, the production of lateral roots, the extent of root hairs produced, and the extent to which different parts of the roots absorb P from the soil.

Biomass

The relationship between root number, length or surface area, and dry weight has been shown by Hackett (1969) to exhibit little variation. Therefore, it was concluded that root dry weight is an adequate method by which to measure a root system. Nass and Zuber (1971) showed maize root volume and weight of greenhouse-grown plants to be significantly correlated with root clump weight in the field. Root growth rate of maize (based on dry weight) was shown to increase exponentially with age to the silking stage at which time it slowed down (Warncke and Barber 1974). They also reported the rate of nutrient uptake for P and Mg to increase rapidly with the age of the plant until silking after which it decreased as the plant changed from vegetative to reproductive growth.

The genotype of maize plays a large role in the type of root system present. Holbert and Koehler (1924) showed differ-

ences among maize inbreds with respect to the size and shape of tracheids and cell wall thickness. Nass and Zuber (1971) reported that a maize genotype with a large root weight in early stages generally would have the most massive root system at maturity. Maize genotypes with large aboveground portions tend to have high root weights (Weihsing 1935). Substantial differences between maize inbred lines were found with respect to the number (Spencer 1940) and dry weight (Spencer 1940, Whaley et al. 1950) of their roots. A close correlation was reported between root dry weight and the number of pounds required to pull the plant from the ground (Spencer 1940).

Andrew and Solanki (1966) compared 14 maize inbreds with respect to top-root ratios. They found that inbreds with high top-root ratios had smaller actual root systems, and vice versa. The relationship between top and root growth of maize was studied by Foth (1962). He found that early development of the maize plant was characterized by rapid growth of both tops and roots. The top weight increased at a greater rate than the root weight, resulting in an increased top-root ratio to the time of formation of brace roots. The production of brace roots tended to decrease the top-root ratio.

Effect of Soil Temperature on Root Growth

Several environmental conditions profoundly affect plant growth. Soil temperature is of special importance in maize production in the Northeastern United States since early plantings into cool soils are common.

Growth Response

Low soil temperatures early in the growing season can have a detrimental effect on the growth of crops planted (Knoll et al. 1964, Walker 1969, Willis et al. 1957, Alessi and Power 1971, Beauchamp and Lathwell 1966, Beauchamp and Lathwell 1966a, Power et al. 1963, Nielsen et al. 1961, Jones and Mederski 1963, MacLean and Donovan 1973). Walker (1969), working with maize seedlings found that one degree differences in soil temperature ranging from 12C to 35C produced changes in growth and nutritional behavior amounting to as much as 40% per degree change. For each degree rise in soil temperature between 17C and 26C, seedling dry weight increased an average of 20% over each previous soil temperature. Beauchamp and Lathwell (1966, 1967, 1967a) reported that maize plants grown at higher root zone temperatures were lower in percent dry weight at similar leaf stages when compared to plants grown at lower root zone temperatures. They reported the rate of morphological development increased with increasing root zone temperatures. High root zone temperatures have also been shown to increase the rate of cell elongation (Beauchamp and Lathwell 1966a). At lower temperatures the reverse was observed along with a delay in root maturation. Young roots would be more active in water and nutrient uptake than older roots, a condition which may tend to compensate for the effects of low temperatures in the restriction of these processes.

Willis et al. (1957) showed with greenhouse-grown maize

that as the soil temperature increased between 16C and 24C, growth rate and dry matter production increased. In a field experiment, they showed that increased soil temperatures hastened seed emergence, increased growth rate, and promoted earliness. These investigators reported the minimum soil temperature for maize seed germination as 10C, the optimum soil temperature for germination as 34C, and the optimum soil temperature for maize growth in central Iowa as 24C. Richards et al. (1952) reported 29C as the optimum soil or root temperature for maize growth. Alessi and Power (1971) related maize seedling emergence to soil temperature and seeding depth. They found that soil temperature had a much greater effect on maize than seeding depth. They stated that maize planted in a seedbed below 10C will have little or no chance for germination. Jones and Mederski (1963) showed differential response of six maize inbreds to increased soil temperatures. They reported that increased soil temperatures reduced the days to silking in all inbreds tested, but to different extents. The detrimental effect of low root zone temperature was not as great in the early maturing maize cultivars (MacLean and Donovan 1973). These researchers grew six maize hybrids of various heat unit requirements at 10C and 16C and reported increased growth responses to the higher soil temperature in hybrids with a low heat unit requirement. Similarly, Cal and Obendorf (1972) studied the growth of four maize hybrids at three different root zone temperatures. The hybrid with the lowest degree day requirement was the least sensitive to cold root zone temperatures. Conversely, the hybrid with the greatest degree day requirement showed the highest sensitivity to low root zone temper-

ature. There was no significant difference between the hybrids with respect to percent survival and leaf number, but dry matter accumulation differed at the low temperatures. At the high root zone temperatures the differential growth of the hybrids was less evident. These data support field observations that maize varieties with high degree day requirements are more sensitive to cold soil temperatures and grow more slowly in early spring than do varieties with low degree day requirements.

Of interest in regard to temperature influences on root growth is that the direction and growth rate of maize roots is influenced by the temperature of the soil in which they are growing (Mosher and Miller 1972, Onderdonk and Ketcheson 1973). Such changes therefore could indirectly influence the type and rate of nutrient absorption by the plant. Mosher and Miller (1972) showed that at low soil temperatures, radicle growth tended to be horizontal and at high soil temperatures they tended to grow straight down. They found the angle of the radicle from the horizontal was increased from 30 degrees at 18C to 61 degrees at 36C. Onderdonk and Ketcheson (1973) reported the angle of root growth relative to the horizontal to be minimal at a constant root temperature of 17C. Above or below this temperature maize roots tend to grow in a more vertical direction.

Nutritional Response

Phosphorus availability has been implicated in the restriction of growth under low root zone temperatures. Increased plant uptake of P has been shown in warm soils (MacLean and Donovan 1973, Nielsen et al. 1961, Jones and Mederski 1963, Knoll

et al. 1964). Much of the increased total accumulation of nutrients has been attributed to increased yields at higher root zone temperatures (Nielsen et al. 1961, Knoll et al. 1964, Patterson et al. 1972).

Knoll et al. (1964) conducted a greenhouse study to determine effect of soil temperature on the growth and P content of maize. They reported a positive correlation between soil temperature and plant dry weight, as well as P uptake. They also reported that under no circumstances did the addition of fertilizer P completely overcome the harmful effects of low soil temperatures. These results agree with those of Patterson et al. (1972) and Knoll et al. (1964). Nielsen et al. (1961) reported that favorable root zone temperatures will not compensate for a lack of plant nutrients, and the addition of nutrients will not reverse the inhibitory effects of low root zone temperatures. Ketcheson (1957) reported that P applications to maize growing at 13°C soil temperature partially counteracted the low temperature effect. Unlike the above investigators, Knoll et al. (1964) found that P uptake was influenced very little by the root zone temperature and depended almost entirely upon the P level of the nutrient solution. They explained any reduction in P uptake at low root zone temperatures as due to reduced root growth at the low temperature. They also stated that low root zone temperature stimulates the synthesis of anthocyanin and that purpling of maize leaves early in the season is not necessarily indicative of a P deficiency.

Working with barley, Power et al. (1963) found that by increasing the available P supply, the soil temperature range

over which the nearly maximum growth occurred was greatly increased. They reported growth responses to P fertilization to be more dependent on soil temperature when the soil was low in available P than when P was more available. Such results support the practice of using starter-P fertilizers when planting maize in the cool northern areas of the U.S.

Development of Maize Under Minimum Tillage and Conventional Culture Systems

Soil Conditions

The no-till culture system for maize production is being widely practiced in the U.S. due primarily to reduced energy and labor costs, better soil and water conservation, and reported higher yields than obtained with conventional tillage methods (Estes 1972). Minimum tillage practices for producing maize create unique problems with respect to soil nutrients, especially P. These practices may also cause stress conditions with regard to trace elements (Estes 1972).

Phosphorus is relatively immobile in soil, and its movement is retarded in two ways (Bielecki 1973). First, fine soil particles increase the length of the diffusion path, a phenomenon called tortuosity. Secondly, P movement is retarded by a reversible surface interaction between P and soil particle surfaces. Vijayachandran and Harter (1975) studied the P-absorption characteristics of a large number of soils from various locations. They found Al and organic matter to be primarily responsible for P adsorption in most of the soils investigated. Shapiro et al.

(1960) showed the existence of a 1-2 mm wide P depletion zone in the soil around roots suggesting that plants may absorb P faster than it can be supplied by the soil. Such depletion may be a significant problem on farmland in the Northeast U.S. where soils are naturally low in pH and soluble Al content is high.

Due to the slow diffusion of P in the soil (Bielecki 1973), the question of the fate of surface applied P fertilizers must be investigated. This is especially important under no-till conditions where fertilizer is surface-applied and not incorporated into the soil. Without tillage, layers of nutrient concentration and/or depletion may develop over a period of years. Consequently, highly acidic conditions in the lower soil horizons may develop from such stratification creating high soluble Al levels (Estes 1972). Maize varieties with deep, penetrating root systems may be exposed to this higher soluble Al under such conditions and Al toxicity may be the result.

Shear and Moschler (1969) did a six year comparison of no-till and conventional tillage methods for maize production. They reported a stratification of P under no-till conditions with significantly more available P near the surface where it was applied. Moschler et al. (1975) reported more P recovered from soil in the surface 20 cm after no-till conditions than after conventional tillage. These results reflect the immobile nature of P in the soil.

Glycerophosphate, a relatively new product, is being investigated with respect to its value as a P fertilizer. It has been shown to be mobile and will move through the soil via

rain or irrigation water (Rolston et al. 1974). This product may someday prove well suited to no-till maize operations where fertilizer is applied to the surface and not plowed under.

Belcher and Ragland (1972) investigated P absorption by maize grown in Kentucky under no-till conditions from surface applied P fertilizers. They reported that P does not have to be incorporated into the soil in order to obtain high yields. These researchers measured dry matter and P uptake at various stages of plant growth and showed that P fertilizer applied to the surface under no-till conditions was available to the plants throughout the entire growth period. These results were explained on the basis that a dead sod mulch would result in higher soil moisture conditions which would increase shallow rooting and P uptake near the soil surface. Mulch conditions have also been observed to help retain soil moisture by other researchers (Jones et al. 1969, Moody et al. 1963, Moody et al. 1961). At low soil moisture levels, P diffusion is very low and affects the amount of P available to a plant root (Mahteb et al. 1972). Plants growing in soils with low moisture do not respond to added P while plants adequately supplied with moisture do show a more favorable P response (Olsen et al. 1961).

Soil temperatures under a mulch tillage system have been shown to be reduced (Willis et al. 1957, van Wijk et al. 1959, Moody et al. 1963) and may be a major reason for the poor early growth and lower yields of maize that commonly occur under such a system in the northern states. van Wijk et al. (1959) tried to explain why mulch tillage in northern states produced maize yields inferior to those reported by southern

states using similar tillage practices. Data collected from southern states showed soil temperatures early in the growing season to be near optimum for the growth of maize. Conversely, soil temperatures early in the growing period in northern states were far below optimum, and growth rate was low. Mulch conditions in northern areas tended to lower both soil temperatures and growth rate. In warmer regions, a reduction in soil temperature during the summer months may favor growth (Chaudhary and Prihar 1974).

Growth Responses

Many researchers (Jones et al. 1969, Moschler and Martens 1975, Moody et al. 1963, Chaudhary and Prihar 1974, Estes 1972, Shear and Moschler 1969, Jones et al. 1968) reported increased yields under minimum tillage conditions while others (van Wijk et al. 1959, Willis et al. 1957) report yield decreases, especially in the cooler northern areas. Estes (1972) reported a yield increase with no-till over conventional tillage culture during a relatively dry season in New Hampshire in spite of a reduction in plant population. Moody et al. (1963) reported early season growth reduction of mulched maize in Virginia and associated it with low soil temperatures. These researchers attribute increased yields under mulched conditions to favorable moisture conditions later in the season.

The tillage practice employed has been shown to have a definite influence on maize rooting characteristics. Barber (1971) took soil core samples to study the root distribution and morphology of maize grown under various tillage practices.

He showed that annual plowing resulted in maize roots that were deeper, finer, longer, and more extensive than were maize roots produced under minimum or no-till systems. Belcher and Ragland (1972) suggest more extensive root development under dead sod mulch was the result of increased soil moisture.

Mengel and Barber (1974) showed early growth of the maize plant to be strongly influenced by the amount of roots the seedling has in a fertile zone. Shallow rooted maize varieties should show increased efficiency in the uptake of P applied to the soil surface. Singh et al. (1966) reported young maize plants grown under no-till conditions contain higher P relative to conventionally tilled maize while Moschler and Martens (1975) found P concentrations in maize unaffected by tillage system.

Stryker et al. (1974) reported that maize plants showed maximum dry matter accumulation only when the entire root system was exposed to an external P supply. Shoot growth decreased nearly 20% when only part of the root system was exposed to P. Since mulch systems change soil temperature, they will also influence the depth and distribution of roots growing under mulch. This rooting behavior should be predicted and appropriately managed when one is contemplating using a culture system other than conventional tillage.

Nutritional Differences Among Genotypes of Maize

Nutrient Accumulation Patterns of Maize Genotypes

Phosphorus uptake by maize is believed to be an active

process requiring the expenditure of energy. The rate of P uptake will therefore be dependent upon temperature, genotype, and the amount of other ions present in the root zone. Clark and Brown (1974) tested P uptake efficiency of two maize inbreds by varying the amount of P in solution and also by adding various amounts of Al to the nutrient solution. The inbreds varied greatly in their accumulation of P under the P-stress conditions. Phillips et al. (1971a) reported a 1.6 fold difference in P accumulation between maize genotypes, and in related work Phillips et al. (1971b) suggested genetic differences in the mechanism of absorption as an explanation. Differences in rooting depth rather than differences in absorption mechanisms of the genotypes is proposed by Baker et al. (1970) to explain the above variation. In a later study, Baker et al. (1971) reported P accumulation in maize is genetically controlled and is associated with physiological processes within the plant and is independent of rooting depth.

Root zone temperature has also been implicated as affecting P uptake. A significant interaction between maize hybrid and root zone temperature was obtained by MacLean and Donovan (1973) who reported significant yield increases at low root zone temperatures as a response to added P.

Phosphorus accumulation by maize may also be affected by a greenhouse environment. Baker and Woodruff (1963) showed that young maize plants grown in a greenhouse may not reflect the relative P accumulation characteristics of different hybrids when grown to maturity in the field. Much higher fertility levels, especially P, were required by maize plants grown in

containers where the volume of soil in contact with the roots was less than under field conditions. Baker et al. (1964) stated that differential accumulation of P by maize genotypes will be relative whether the plants are grown in the greenhouse or field, although greenhouse-grown plants will contain less P. These researchers concluded that field uptake patterns can be predicted from greenhouse results. Also, P concentration between hybrids has been shown to exhibit a dilution effect and decrease markedly with increasing yields (Terman et al. 1975). Thus, the concentration of nutrients in maize hybrids may need to be evaluated in other terms such as dry matter or maturity ratings, especially during early growth.

Nutritional Interactions

A. Phosphorus-aluminum interactions Plant species or genotypes exhibit differential tolerances to high soluble Al levels in the growth media. A possible explanation is the ability of the plant to complex Al with organic molecules (Barber 1967). Wallihan (1948) reported that Al precipitation is most likely to occur on the root, but Wright and Donahue (1953) concluded that Al was precipitated internally as a phosphate. Latshaw and Miller (1924) reported 0.98, 0.07 and 0.13% Al in the roots, leaves, and stems respectively of maize indicating accumulation in the roots and very little translocation to aerial portions. Adding Al to a nutrient solution has been shown to increase root Al content but has little or no effect on shoot Al content (Foy and Brown 1963). McCormick and Borden (1974) showed that an Al-P interaction does occur in plant roots resulting in the

formation of an Al-P precipitate. They reported that the precipitate occurs in the intercellular and intracellular material of the root cap. Jones (1961) suggested that cell walls or cytoplasm may contain substances which complex Al and allow resistant plants to tolerate high Al levels and still maintain normal P levels in the foliage. Aluminum-induced P accumulation in the growing parts of perennial ryegrass roots was shown to be inhibited by cyanide treatments, indicating metabolic processes may be involved (Jones 1961). In contrast, the results of Clarkson (1966) indicate that increased P accumulation by barley seedlings in nutrient solutions containing Al was due only to adsorption and precipitation reactions and did not involve metabolic activity.

The most detrimental effect of Al toxicity to aboveground portions of a plant is a lack of P due to decreased translocation of P from the roots (Barber 1967). Phosphorus deficiency symptoms and P concentration in plant tops may be used to determine Al toxicity conditions in maize since no Al is translocated to the leaves and a P deficiency is a common symptom of Al toxicity (Foy and Brown 1964). Jones (1961) and Foy and Brown (1964) presented evidence that differential Al tolerance by plant genotypes is related to their ability to absorb and utilize P in the presence of high amounts of Al.

Foy et al. (1974) found a purple pigmentation indicative of a P deficiency in wheat plants grown on unlimed soils or in nutrient solutions containing Al. The plants however, still contained an adequate level of total P. The incorporation of this P into metabolic activities within the plant was apparently

hindered by precipitation with Al. Liming the soil to decrease soluble Al and increase P availability or omitting Al from the nutrient solution reduced or prevented the symptoms.

Clark and Brown (1974) reported that under an Al-induced P stress condition, maize inbreds efficient in P uptake produce increased growth. This indicates an increased efficiency in these plants in competing for P. Using alfalfa, Foy (1964) reported that P applications to acid soils increased growth and decreased Al content in half of the soils used. Recently, Foy et al. (1974) reported that yields of various wheat cultivars were not significantly influenced by Al until the P level in the nutrient solution was reduced to two parts per million. At this low P concentration, the cultivars differed substantially in both top and root growth. While these data are interesting, it should be recognized that the mean P concentration of soils (using Bray 1 extractant) is 25.8 ppm in Pennsylvania soils (Baker and Hall 1967). At these higher P concentrations, P-Al interactions in the plant may differ significantly.

Low levels of Al (5 ppm) in solution culture increased the content and concentration of P in both shoots and roots of eight week old perennial ryegrass while high Al levels (50 ppm) depressed P content but increased P concentration due to a general reduction in growth (Randall and Vose 1963). Estrada and Cummings (1968) investigated the effect of lime and P treatments on the growth and nutrient composition of maize grown in an acid loamy sand under greenhouse conditions. Their results indicated that raising soil pH to 6.7 was not as effective as a P application in decreasing Al uptake by plants. Furthermore,

they suggested that the increased growth resulting from P additions was the result of decreased Al rather than increased P uptake.

Hartwell and Pember (1918) were among the early investigators to recognize a stunting and thickening of barley and rye shoots to be the result of high Al concentrations. Aluminum damage may also be due to the inability of the plant to develop an adequate root system resulting in decreased uptake of other nutrients (Barber 1967). This is especially true during the early stages of growth because sensitivity to Al decreases with age. Such a response may relate to meristematic activity and growth rate since root hairs are especially sensitive to Al (Hatch 1973).

Fleming and Foy (1968) investigated the morphological effects of Al on the roots of wheat. They found that the roots of an Al-sensitive variety ceased to elongate after 24 hours exposure to Al whereas the Al-tolerant variety continued root elongation throughout the duration of the experiment. The Al-sensitive variety showed root tip injury characterized by a disorganization of the root cap, root apex, and vascular elements.

Symptoms of Al toxicity to tops resemble a severe P deficiency symptom (Hewitt 1948). The leaves become small with thick, shortened internodes resulting in a stunted plant. The foliage becomes dark green, and sometimes a purple coloration may appear. Foy (1964) reported that Al toxicity symptoms in alfalfa also include necrotic old leaves and small dark green young leaves.

Lee (1972) has shown that Al reduces Mg uptake in potato roots at solution concentrations of 5 and 10 ppm Al but did not

reduce Mg uptake in the tops until a 10 ppm Al concentration was reached. Clark (1975) states that Al toxicity in maize may be closely related to Mg absorption and translocation. He selected maize inbreds which varied in tolerance to Al. Magnesium uptake decreased significantly in all inbreds at Al concentrations greater than 5 ppm.

B. Phosphorus-iron interactions In many instances, the chemical behavior of Fe in both plants and soils is similar to that of Al. Excessive P in the growth medium frequently decreases Fe absorption (Adriano et al. 1971, Brown and Ambler 1970, Brown and Bell 1969, Estes and Bruetsch 1973, Lee 1972, Odurukwe and Maynard 1969). Iron chlorosis is associated with an increased P concentration in the tops of the plants. Plants exhibiting what appears to be Fe-deficiency symptoms can contain as much Fe as green plants if the concentration of P in the growth medium is high (Brown and Bell 1969). Estes and Bruetsch (1973) showed varietal variation in maize to P-induced Fe stress. The variety susceptible to P-induced Fe stress frequently contained high levels of Fe in the foliage. They related this to reduced Fe translocation within the plant due to high P concentrations. Brown et al. (1972) reported similar results and showed that an Fe-efficient maize genotype is able to compete with P in the growth medium for the Fe present. Odurukwe and Maynard (1969) reported that a Fe-efficient maize inbred was more susceptible to Fe chlorosis because of its low Fe:P and Fe:Mn ratios and consequently lower amounts of available Fe. They state that normal plants have a Fe:P ratio greater than 0.020 while ratios less than this produced chlorotic plants. As the relative P

content of the tissue increases, more Fe is tied up in phosphate combinations resulting in less Fe available for reactions leading to the formation of chlorophyll (Odurukwe and Maynard 1969).

C. pH-nutrient interactions It is an accepted fact that pH plays a major role in soil and plant nutrient reactions. Clark and Brown (1974) adjusted nutrient solution pH to 4.6 when doing Al toxicity studies because, at a pH above 5.0-5.5, the effects of Al on plant growth is minimal. Walker et al. (1975) found that raising soil pH to 5.2 or above decreased the tissue concentration of Al in sorghum. The ability of some genotypes to change the pH of their root environments in the presence of Al is a possible explanation for the differential uptake by high and low P accumulating types (Brown et al. 1972, Clark and Brown 1974, Foy 1975). Foy et al. (1965) mentioned that changing the H^+ of a solution by a factor of 10 (pH 5 to 4) will change the active Al by a substantial amount.

Lutz et al. (1971) grew inbred lines and single crosses of maize on acid soils (pH 3.9) and on the same soil treated with various amounts of dolomitic limestone to raise the soil pH. They showed that there were significant differences among the inbreds and single crosses with respect to dry weight and plant height. Acid soils of the eastern U.S. may create Al toxicities in plants due to increased solubility at low soil pH (Brown et al. 1972). Ragland and Coleman (1959) reported the growth of roots into unlimed subsoils was inversely related to the amount of exchangeable Al in the subsoil. However, roots grew well into these subsoils when lime was applied to them.

Since liming of surface soils does not raise the pH of acid

subsoils, Al toxicity in these subsoils may limit root penetration and therefore reduce drought tolerance and the utilization of subsoil nutrients (Brown et al. 1972). Maize genotypes that are better able to tolerate high acid soil conditions would be desirable where it is impossible or impractical to correct such soil acidity. Such a situation would exist under no-till culture where the soil is not mixed, or on rocky soils where subsoil acidity is significant.

MATERIALS AND METHODS

Four maize genotypes were selected on the basis of their relative maturity for use in these investigations. They were ranked according to the percent dry matter (%DM) of the plant tops after 115 days of growth in the field. A lower %DM after 115 days indicated a less mature genotype and vice versa. The genotypes matured in the following order from early to late: Cornell 110; Seneca XX155; Wisconsin 335A; Agway 590-X. These genotypes were used in all the greenhouse, laboratory, and field investigations. Greenhouse studies were conducted in the Plant Science research facilities at Durham, New Hampshire. Field studies were conducted at the University of New Hampshire Agronomy Research Farm, Madbury, New Hampshire.

Greenhouse Investigations

Root Temperature Studies

Two greenhouse studies were initiated in an attempt to relate the temperature of the root zone to the plant dry weight and to nutrient uptake and accumulation.

Study 1. Seeds from the four maize genotypes were planted on October 19, 1973 approximately 3 cm deep in plastic trays filled with vermiculite. The trays were watered with distilled water for 11 days at which time the seedlings were at the two leaf stage. The seedlings were removed from the trays and the vermiculite washed from the roots with distilled water. The seed piece was removed with a razor blade.

The seedlings were moved to water-jacketed crocks containing 2.2 l of a nutrient solution of the following concentration: 0.001M KCl, 720 μ M Ca(H₂PO₄)₂·H₂O, 0.005M KNO₃, 0.005M Ca(NO₃)₂·4H₂O, 0.002M MgSO₄·7H₂O, 38 μ M H₃BO₃, 9.2 μ M MnCl₂·4H₂O, 0.5 μ M H₂MoO₄·H₂O, 10 μ M CuSO₄·5H₂O, 1 μ M sequestrene Na₂Zn (15.5% Zn) and 172 μ M sequestrene NaFe (12% Fe). The nutrient solutions were aerated with a slow stream of bubbles from a Pasteur pipette. The crocks were completely randomized on a greenhouse bench with four maize genotypes, two root temperatures, and three replications. One-half of the crocks had cool water running through the jackets to maintain the temperature of the nutrient solution at 15.5 \pm 1.5C. The remaining crocks were left at ambient greenhouse temperature which maintained a nutrient solution temperature of 24.4 \pm 3.5C. This variation was due to problems with the greenhouse heating system.

The plants were allowed to grow for 19 days under these conditions with a fresh nutrient solution employed after 11 days. After 19 days the plant tops and roots were harvested and dried in an oven at 70C for one week. After dry weight measurements were taken the tissue was ground in a Wiley mill to pass a 20 mesh screen. A sample was ashed for 4 hours at 500C in a muffle furnace. The ash was dissolved in acid according to Jones and Weaver (1970) and analyzed for P by the ammonium molybdate-stannous chloride colorimetric method. Iron was determined with a Jarrel-Ash atomic absorption spectrophotometer.

Study 2. A second greenhouse study was initiated on November 19, 1973 because variation was relatively high in the first study.

The treatments, experimental design, and analyses were identical to those of the first study.

Phosphorus-32 Absorption

A greenhouse investigation was initiated to characterize the P uptake of four maize genotypes. Seeds of the four genotypes were grown in vermiculite for 11 days. Roots were then washed with distilled water, the seed piece excised, and the seedlings placed in stone crocks containing the nutrient solution. The crocks were set up in a randomized complete block design with 4 blocks containing 12 experimental units each. There were 3 replications of each of the 4 genotypes within each block. The solutions were aerated using aeration stones.

After growing the plants for 14 days, the nutrient solution was replaced. Three days later (28 days from seed) all 12 crocks in the first block were spiked with 20 microcuries (uCi) of phosphorus-32 (^{32}P). The ^{32}P activity of the center of each leaf was measured with a GM scaler (Tracerlab Model 16U) with an efficiency of 3.9%. The distance between the GM tube and the leaf was standardized to minimize variation. A piece of cardboard approximately 1 mm thick was placed on a ringstand and the leaf placed on the cardboard. A sheet of lead approximately 1 mm thick with a 15 mm diameter round hole was positioned over the leaf so that the center of the leaf was directly beneath the hole and 1.76 cm² of leaf surface was exposed. A 4 mm thick rubber washer was glued to the top of the lead sheet to encircle the hole. The GM tube was placed on top of the rubber washer and all measurements were made with identical sample geometry. Radio-

activity measurements were made on all the leaves of the plants from the first 12 crocks (Block 1) 7, 17, 28, 52, and 96 hours after spiking with ^{32}P . Following these measurements, the tops of the plants in the first block were harvested, dried in an oven at 70C for 7 days, and weighed.

After 24 days in nutrient solution (35 days from seed) crocks 13 through 24 (Block 2) were spiked with $20\mu\text{Ci } ^{32}\text{P}$. The radioactivity in the leaves of these plants was measured after 6, 26.5, 51, 76.5, and 102 hours and dry weights determined.

The nutrient solution in the remaining 24 crocks was changed for the second time, and three days later (31 days in solution or 42 days from seed) crocks 25 through 36 (Block 3) were spiked with $20\mu\text{Ci } ^{32}\text{P}$ and the radioactivity measured after 6.5, 29.5, 53, 76.5, and 101 hours and dry weights determined.

The nutrient solutions for the remaining 12 plants (Block 4) were renewed 10 days after the second change. Solutions were spiked with $20\mu\text{Ci } ^{32}\text{P}$ after a total of 38 days growth in solution (49 days from seed). The activity of ^{32}P in the leaves was measured 5.5, 29.5, 54, 76.5, and 103 hours after spiking and dry weights determined.

Radioactivity measurements were made on each fully expanded leaf. The total counts per plant were divided by the number of leaves to calculate the mean counts per minute (cpm) for each plant. These counts were converted to absolute activity (dpm) after correcting for decay. The dpm's for each genotype in each block of plants were plotted and a line was fitted to the data points by means of a second degree polynomial regression equation.

Root Volume

Solution grown maize plants may exhibit different root morphology and have fewer root hairs than soil-grown plants (Warncke and Barber 1974). To determine if differences in nutrient uptake of the four maize genotypes were affected by rooting habit, root volume was determined. The plants were grown with their roots in nutrient mist instead of nutrient solution. Plants grown in mist systems have been shown to have root volumes comparable to plants grown in sand culture (Martin and Hendrix 1967) but significantly different from those in nutrient solutions. The roots of mist-grown plants can be measured without breakage and inevitable root loss.

A mist chamber was constructed to accommodate 12 plants (Fig. 1). Seedlings of the four genotypes were grown to the two leaf stage (13 days from seed) in vermiculite. After excising the seed piece, the plants were positioned to permit the roots to hang down into the mist chamber. The experimental design consisted of a randomized complete block design with 3 replications of each of the four genotypes. An electric humidifier was placed in the base of the mist chamber, and all the root systems were arranged to be equidistant from it. The humidifier was timed to mist the roots with the nutrient solution used previously for a 3 minute duration spaced 3 minutes apart. Approximately 12 liters of solution were used in 24 hours. The temperature inside the mist chamber remained approximately 21°C throughout the experiment.

Root volumes were measured 8, 16, 23, 30, and 36 days after placing in the mist chamber (21, 29, 36, 43, and 49 days

from seed, respectively). These measurements were made by water displacement (Fig. 2) using the method of Pinkas et al. (1964). The longest root was also measured after 36 days in the mist chamber. At this time the tops and roots were separated, dried at 70C for 7 days, and weighed.

Soil pH

A greenhouse experiment was conducted to test the response of genotypes to soil acidity. A split-plot design was utilized with 5 replications; applied lime served as main plots and genotype as subplots. Each unit consisted of a stone crock lined with a polyethylene bag into which 3500 g of air dried soil was placed.

Chemical analyses were conducted on the soil prior to planting. Soil Fe and Zn concentrations were measured by the DTPA-TEA extraction method of Lindsay and Norvall (1969). Phosphorus was extracted with a Bray 1 extracting solution (0.025N HCl + 0.30N NH_4F) (Bray and Kurtz 1945) and determined with the molybdenum-blue reduction method of Jackson (1958). Cation exchange capacity (CEC) was determined by adding 25 ml of 1N ammonium acetate (pH 7.0) to 5 g of soil. After 30 minutes agitation, the mixture was filtered through Whatman 2 filter paper and the residue washed with 70% ethanol to remove excess ammonium acetate. A Kjeldahl distillation was performed on the soil to determine the CEC. The filtrate was analyzed for Ca, Na, and K using flame emission and Mg using atomic absorption spectrophotometry. A Jarrel-Ash atomic absorption spectrophotometer was used in the above analyses. The milliequivalents of individual

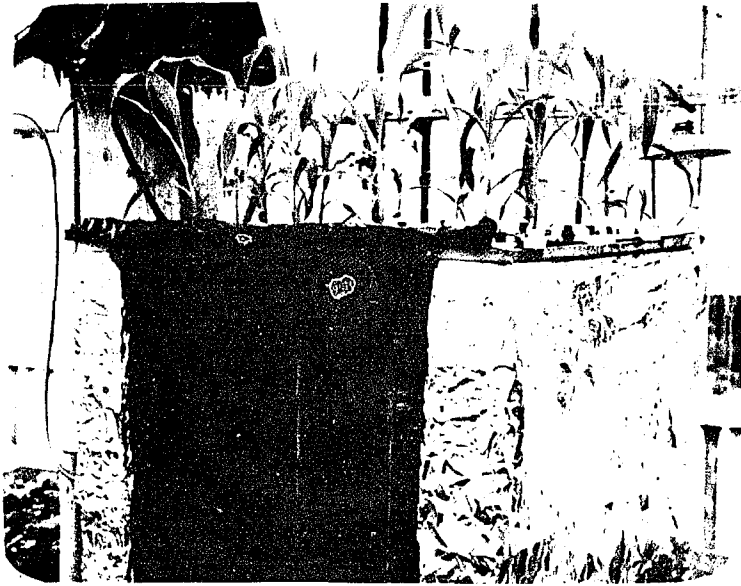


Figure 1. Mist chamber used for growing corn plants in the greenhouse root-volume experiment.

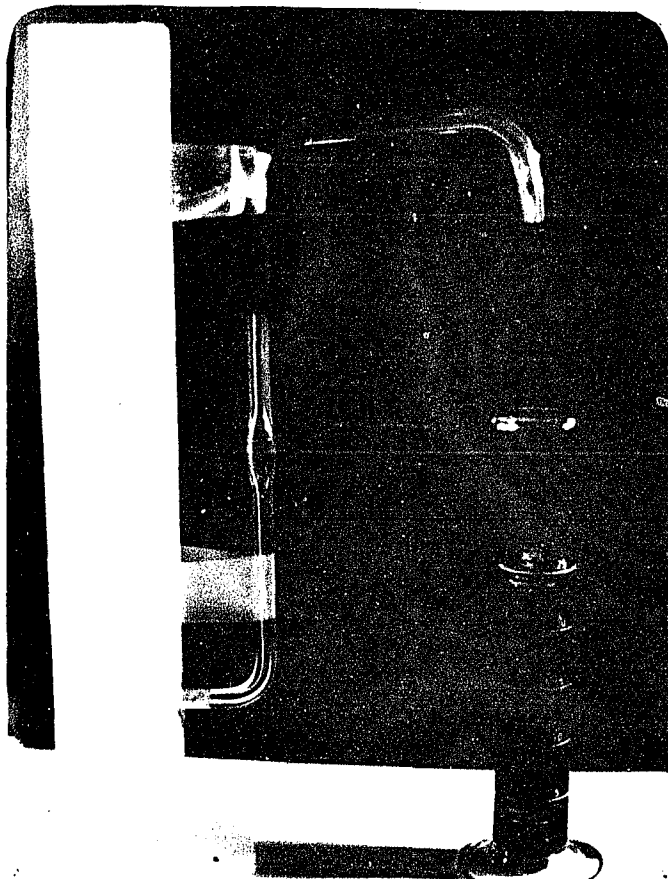


Figure 2. Water displacement device used to measure root volume in the greenhouse-mist experiment.

cations per 100 g of soil and the percent base saturation of these elements were calculated. Soil pH was measured on a 1:1 soil to water slurry using a Model 701 Orion pH meter. Aluminum concentration was determined on the soil prior to the experiment and again after completion. Soil Al was extracted with the procedure of McLean (1965) and analyzed by atomic absorption spectrophotometry.

Twenty days before planting, hydrated lime was thoroughly mixed with the soil in the crocks at a rate equivalent to 0, 3.3, and 6.7 metric ton/ha of calcium carbonate. Soil in each of the 60 crocks received the equivalent of 224 kg/ha N (using NH_4NO_3), P_2O_5 (using KH_2PO_4), and K_2O (using KCl); the fertilizers were thoroughly incorporated with the soil.

Three seeds of the four genotypes were planted approximately 2.5 cm deep in each of the crocks. Six cool white fluorescent lamps were placed approximately 60 cm from the tops of the crocks and timed to give a 14 hour daylength. Six days after planting, two of the three seedlings were removed leaving one representative plant per crock. The plants were kept moist with distilled water and were harvested after 35 days. The tops and roots were separated, washed in distilled water, and dried in an oven for 7 days at 70C. After drying, the plants were weighed, ground to pass a 20 mesh screen, and analyzed for P, Al, Fe, and Zn. Soil pH was measured after harvest.

Hydroponics Studies

Study 1. A greenhouse experiment was run to determine the effect of Al on P uptake and accumulation by the four maize genotypes.

The automatic sub-irrigation hydroponics system described by Estes and Bruetsch (1973) was employed. A split-plot design was utilized with three replications; genotypes served as main plots and Al levels as subplots. The nutrient solution used in this experiment was identical to those described previously. However, in this study, Al from $\text{Al}_2(\text{SO}_4)_3 \cdot 16\text{H}_2\text{O}$ was added to the solutions to give concentrations of 0, 2.5, 5, and 10 ppm Al.

Seeds were planted approximately 3 cm deep in vermiculite. After 11 days the seedlings were removed, the roots washed with distilled water, and the seed piece removed. Seedlings were transplanted into 7.6 liter stone crocks containing sterile quartz sand. The nutrient solution was pumped into the crocks every two hours. Additional light was provided to give a total of 14 hours daily with the aid of Gro-Lux lamps. The lamps were maintained at 60 cm above the tops of the plants throughout the experiment. After 17 days, the nutrient solutions were changed. After an additional 22 days, the plants were harvested. The tops and roots were separated, washed with distilled water, dried in an oven at 70C for 7 days, and weighed.

Study 2. A second study was conducted to determine the effect of high levels of soluble Al on the four genotypes. Methods and materials were identical to those of the previous study except that the levels of Al were 0, 10, 25, and 50 ppm. Also, when the nutrient solutions were changed after 19 days (33 days from seed), P was left out of the solutions in an effort to reduce the P-Al interaction, and to increase the sensitivity of the Al response. Calcium was supplied as CaCl_2 since the removal of P also removed

Ca when $\text{Ca}(\text{H}_2\text{PO}_4)_2 \cdot \text{H}_2\text{O}$ was used.

After 10 days of growth in the P-deficient nutrient solution (43 days from seed) the plants were harvested and prepared as described previously. After weighing, the dried plants were ground to pass a 20 mesh screen and analyzed for P, Al, Fe, and Mg using the procedures described previously.

Laboratory Investigations

Seed Analysis

Seeds of each genotype were analyzed for P, Fe, and dry weight in an effort to relate these parameters to maturity. The seed was ground into coarse pieces approximately 3 mm in diameter. The coarse pieces were dried at 70C for 7 days, weighed, ground to pass a 20 mesh screen, ashed in a muffle furnace at 500C for 5 hours, and analyzed for P and Fe by the procedures described previously.

Field Investigations

Study 1. In 1973, the same four genotypes were grown in a Charlton loam soil under field conditions. A split-plot design was utilized with four replications; applied P_2O_5 served as main plots and genotype as subplots. Each plot measured 6.9 by 4.6 meters. Prior to planting, soil samples were taken at random to a depth of 20 cm and analyzed for CEC, pH, P, Al, Fe, and Mg by the methods described previously.

Nitrogen and K_2O were applied to the field at a rate of 224 kg/ha from urea and muriate of potash respectively. Dolomitic limestone was applied at the rate of 2.24 metric ton/ha. They

were incorporated into the soil by deep disking. The P_2O_5 was supplied from superphosphate (20% P_2O_5) and was applied to the plots at rates of 0, 112, and 224 kg/ha. The superphosphate was applied by hand to the entire surface of each plot so that it remained near the surface

Seed was planted approximately 6 cm deep, 20 cm apart, in rows 76 cm apart. Prior to emergence, the herbicides Atrazine 80W and Lasso 4EC were applied to the soil surface at the rate of 2.2 kg/ha and 0.76 liter/ha respectively.

After 53 days from planting, one representative plant from each plot was harvested, dried at 70C for 7 days, and weighed. The tissue was ground to pass a 20 mesh screen and analyzed for P and Fe by methods previously described.

The plants were harvested and fresh weight taken 127 days after planting. Plant tissue samples were dried at 70C for 7 days, weighed, ground to pass a 20 mesh screen, and analyzed for P, Al, Fe, and Mg by spectrographic methods.

Study 2. In 1974, a field investigation was initiated to compare the effects of no-till and conventional tillage conditions on nutrient uptake. Special attention was paid to the root systems.

In the fall prior to the study, the research area (Charlton loam) was seeded with annual rye as a cover crop. Prior to spring plowing of this field, the rye was killed with Paraquat applied at a rate of 1.1 kg/ha. Strips 6.1 meters wide of the dead sod were plowed and disked so that the field was composed of four sets of no-till and tilled soil. Each culture system measured 6.1 by 48.8 meters. Each plot within a culture system measured

6.1 by 6.1 meters. Between each set of no-till and tilled strips a 6.1 meter wide alley was used for turning machinery.

Soil samples were taken at random from the field and analyzed for CEC, exchangeable cations, P, Al, Fe, and pH by methods previously described. These soil samples were taken at depths of 0 to 10 cm, 10 to 20 cm, 20 to 30 cm, and 30 to 40 cm.

Seed was hand planted approximately 6 cm deep, 20 cm apart, in rows 76 cm apart. Atrazine 80W and Lasso 4EC were applied prior to seedling emergence at a rate of 2.2 kg/ha and 0.76 liter/ha to control weeds.

Plants were harvested from the plots four times during the growing period (37, 62, 93, and 110 days from planting). At each date a representative plant was harvested, dried at 70C for 7 days, and weighed. The dry tissue was ground to pass a 20 mesh screen and analyzed for P, Al, Fe, and Mg as previously described. Also, at each harvest the soil was excavated from one side of the plant to display the roots while the plant was still anchored in the ground. Water under pressure was used to wash the soil away from the roots in an effort to determine visually the root depth, extensiveness, and morphology.

RESULTS AND DISCUSSION

Greenhouse InvestigationsRoot Temperature Studies

Study 1. In this preliminary study, significant differences in dry weight of the four genotypes were observed. Dry weight of tops was always higher at the higher root temperature. Root dry weight of all genotypes except Agway 590-X was higher at 25C.

No significant differences were observed at either root temperature with respect to P and Fe concentration of tops and roots, P and Fe content of tops, and P content of roots. Root Fe content of Agway 590-X was significantly lower than that of the other genotypes under both root zone temperatures. A highly significant negative correlation ($r = -0.60$, 22df) existed between root Fe content of the genotypes and their growing degree day requirement (GDD). The GDD requirement was 1500, 1700, 2000, and 2300 for Cornell 110, Seneca XX155, Wisconsin 335A, and Agway 590-X respectively (Bruetsch and Estes 1976).

Study 2. Because of problems encountered with the greenhouse heating system in Study 1, a second experiment was run in an effort to minimize variation. The results of this study are presented in Tables 1 and 2. Dry weight of tops and roots generally increased when the plants were grown at the higher root temperature (Table 1). The increased dry weight accounted for a significantly higher total accumulation of P in the tops and roots of Seneca XX155 and the tops of Agway 590-X (Table 2). The

Table 1. Dry weight of tops and roots of four maize genotypes grown under hydroponic conditions at two root temperatures. Plants were grown in a greenhouse to 30 days of age (19 days in hydroponic solution). Values represent the mean of three replications.

Genotype	Tops		Roots	
	15.5C	25C	15.5C	25C
Cornell 110	0.34 a*#	0.53 a	0.14 a	0.17 a
Seneca XX155	0.29 a #	0.54 a	0.17 a	0.22 a
Wisconsin 335A	0.24 ab	0.21 b	0.13 ab	0.10 b
Agway 590-X	0.09 b	0.17 b	0.07 b	0.09 b

* Figures within a column followed by the same letter are not significantly different at 5%, according to Duncan's New Multiple Range test.

Indicates a significant difference at 5% with respect to top or root dry weight within a genotype due to the root temperature.

Table 2. Content of iron (Fe) and phosphorus (P) in the tops and roots of four maize genotypes grown under hydroponic conditions at two root temperatures. Plants were grown in a greenhouse to 30 days of age (19 days in hydroponic solution). Values represent the mean of three replications.

Genotype	Tops				Roots			
	15.5C		25C		15.5C		25C	
	Fe	P	Fe	P	Fe	P	Fe	P
	mg							
Cornell 110	0.03 a*	3.23 a	0.05 a	4.10 b	1.98 a	0.91 a	2.60 a	1.29 b
Seneca XX155	0.06 a	4.28 a#	0.06 a	8.05 a	1.99 a	0.64 a#	2.38 a	2.92 a
Wisconsin 335A	0.08 a	2.91 a	0.06 a	1.54 c	2.15 a	1.04 a	1.45 a	1.08 b
Agway 590-X	0.04 a	0.46 b#	0.04 a	2.01 bc	1.07 a	0.53 a	1.44 a	0.20 b

* Figures within a column followed by the same letter are not significantly different at 5%, according to Duncan's New Multiple Range test.

Indicates a significant difference at 5% with respect to Fe or P content of a genotype top or root due to root temperature.

early maturing genotypes accumulated significantly more dry matter when compared to the later lines which indicates a more rapid early growth even under cool root temperatures.

The foliage of two genotypes (Seneca XX155 and Agway 590-X) showed a P content which was significantly lower at 15.5C compared to 25C. The total P content of foliage from the early genotypes was higher than from the late genotypes irrespective of temperature (Table 2).

The above results do show an association between the maturity of the genotypes and their accumulation of P. Early maturing lines tend to contain more P in both tops and roots. The movement of Fe from the roots to the tops appears to be retarded in these genotypes (Table 2). A P-Fe precipitation in or on the root which reduces Fe translocation is a strong possibility (Odurukwe and Maynard 1969).

Phosphorus-32 Absorption

The ^{32}P uptake characteristics of the four genotypes were plotted by means of second degree polynomial regression and are presented in Figures 3, 4, 5, and 6. Because of variation in natural light intensity from day to day, relative comparisons within rather than between figures may only be made. With 28 day old plants, Seneca XX155 was the most and Wisconsin 335A the least efficient in P uptake (Fig. 3). These differential accumulation patterns of P by the genotypes remained unchanged at 35 and 42 days from seed (Fig. 4 and 5). The P-uptake characteristics shown in Figure 6 show that at about seven weeks from seed, Seneca XX155 and Cornell 110 are substantially higher in radioactivity than

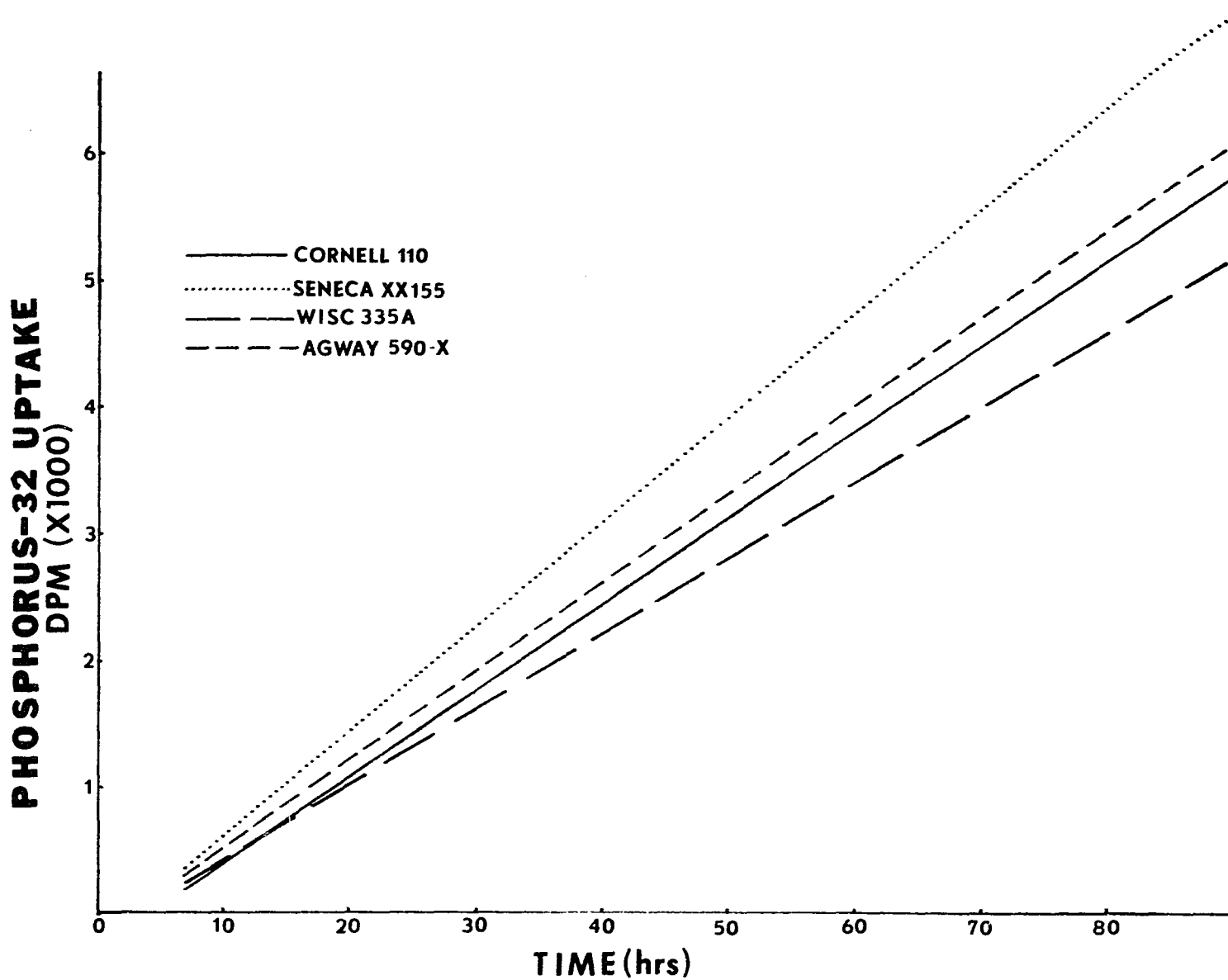


Figure 3. Regression analysis of phosphorus-32 uptake by four maize genotypes grown to 28 days from seed in a hydroponic solution under greenhouse conditions. At time 0, plants were 28 days old.

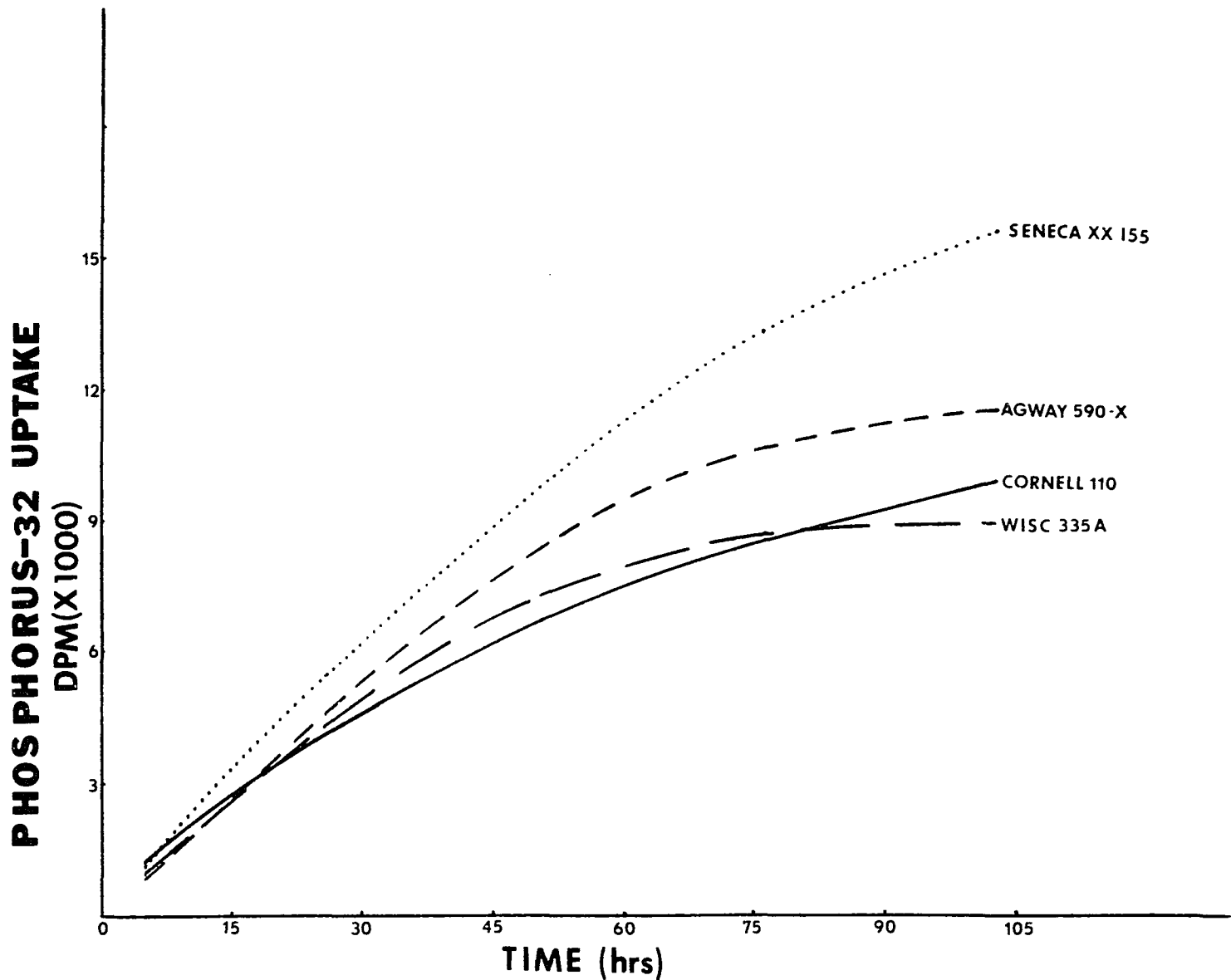


Figure 4. Regression curves of phosphorus-32 uptake by four maize genotypes grown to 35 days from seed in a hydroponic solution under greenhouse conditions. At time 0, plants were 35 days old.

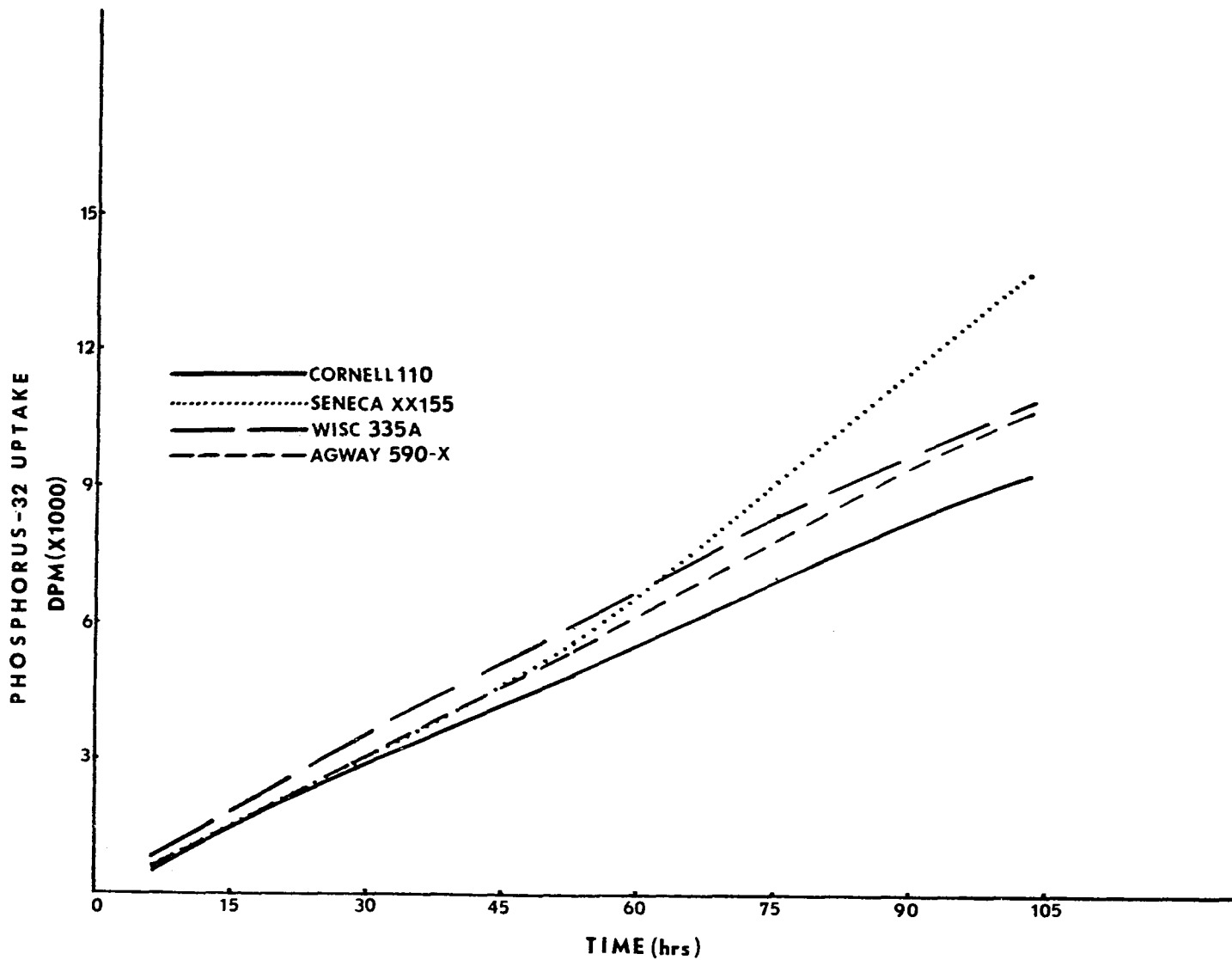


Figure 5. Regression curves of phosphorus-32 uptake by four maize genotypes grown to 42 days from seed in a hydroponic solution under greenhouse conditions. At time 0, plants were 42 days old.

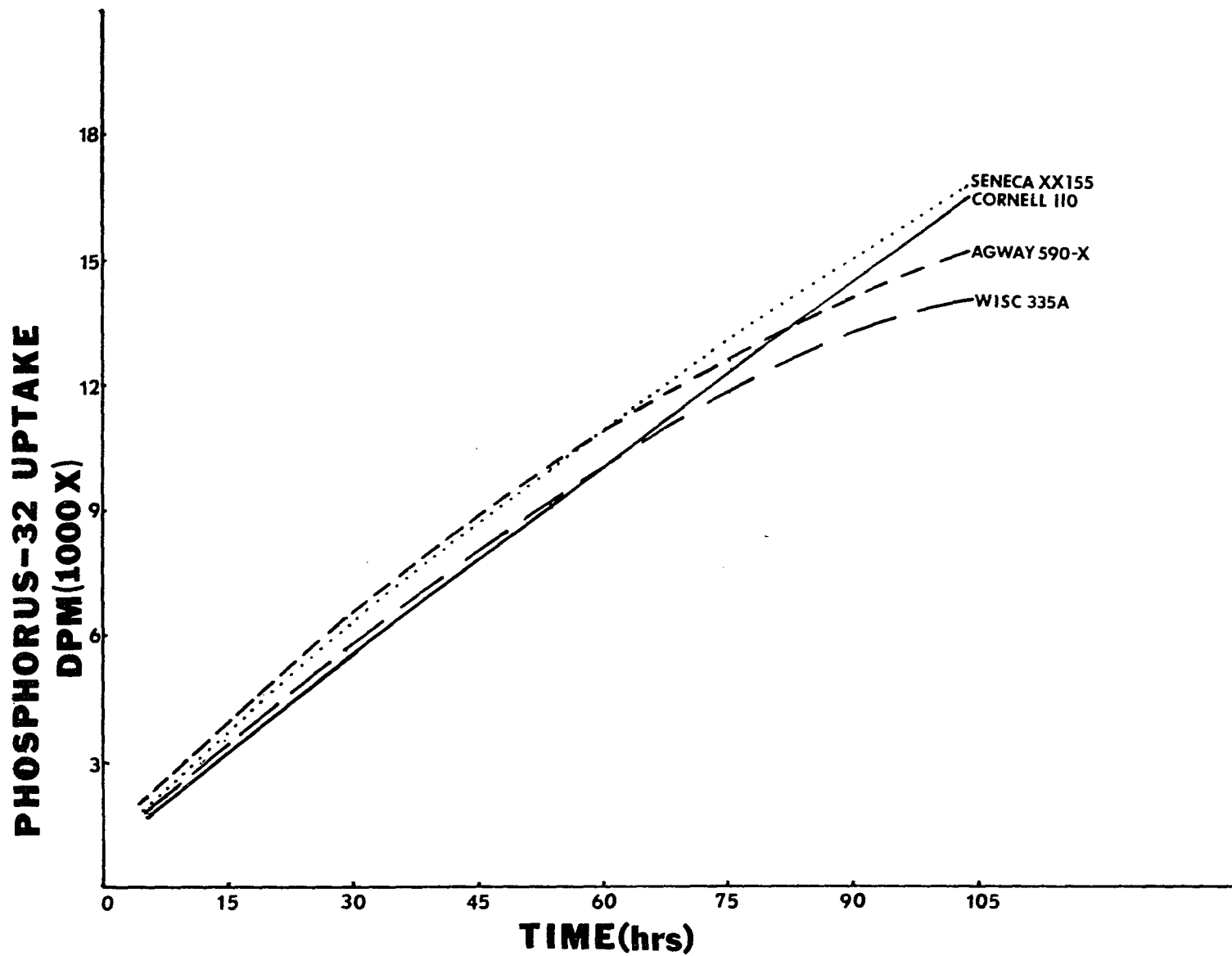


Figure 6. Regression curves of phosphorus-32 uptake by four maize genotypes grown to 49 days from seed in a hydroponic solution under greenhouse conditions. At time 0, plants were 49 days old.

Wisconsin 335A and Agway 590-X. The above results indicate that the earlier genotypes, especially Seneca XX155, exhibit a greater ability to absorb P from solution compared to other genotypes. Furthermore, differences do exist in nutrient absorption rates and, in the case of P, may be easily and quickly determined by the radiotracer technique.

Table 3 shows that in nearly all cases, the dry weight of the early genotypes was greater than the later genotypes at the various stages of development. The absorption of ^{32}P in dpm's is a measurement of isotope concentration. To determine total content of absorbed ^{32}P , plant dry weight was taken into account. When the dpm's are multiplied by the dry weight of the plant tops, an index of total ^{32}P accumulation is obtained; the earlier genotypes were always greater in total accumulation at each harvest except for Cornell 110 after 24 days in the radioactive solution (Table 4). Statistical significance was achieved in all but the third harvest.

Elemental analysis of the tissue was not made due to the radioactive nature of the sample. However, visible Fe-deficiency symptoms appeared in the last two harvests (plants older than 35 days from seed). The severity of the Fe-deficiency symptoms were as follows: Cornell 110 = Seneca XX155 > Agway 590-X > Wisconsin 335A. These symptoms may indicate that Fe is being immobilized in the roots of the early genotypes, thus reducing its translocation to the tops. Such immobilization may be the result of a P-Fe complex within or on the root. Such a complex has been postulated by Rasmussen (1968) where an Al-phosphate may be formed; an Fe-phosphate is also a possibility. Similar immobility of Fe

Table 3. Top dry weights from four consecutive harvests of four maize genotypes grown in a greenhouse under hydroponic conditions. The plant tops were harvested 28, 35, 42, and 49 days from seed (17, 24, 31, and 38 days in solution, respectively). Values represent the mean of three replications.

Genotype	Days from seed			
	28	35	42	49
	g			
Cornell 110	0.49 ab*	0.93 bc	2.44 a	5.59 ab
Seneca XX155	0.64 a	1.27 a	2.37 a	7.09 a
Wisconsin 335A	0.42 ab	1.09 ab	1.81 a	5.35 ab
Agway 590-X	0.38 b	0.74 c	1.75 a	3.88 b

* Figures within a column followed by the same letter are not significantly different at 5%, according to Duncan's New Multiple Range test.

Table 4. Phosphorus-32 uptake from four consecutive harvests of four maize genotypes grown in a greenhouse under hydroponic conditions. The plants were measured 28, 35, 42, and 49 days from seed (17, 24, 31, and 38 days in solution, respectively). Values represent the mean of three replications and are the result of the top dry weight multiplied by disintegrations per minute.

Genotype	Days from seed			
	28	35	42	49
Cornell 110	3236 ab*	9402 b	24823 a	93509 ab
Seneca XX155	4642 a	20426 a	32988 a	119939 a
Wisconsin 335A	2443 b	9681 b	20029 a	76676 b
Agway 590-X	2363 b	8605 b	18256 a	59680 b

* Figures within a column followed by the same letter are not significantly different at 5%, according to Duncan's New Multiple Range test.

was observed in the root temperature studies reported earlier in this manuscript.

Root Volume

In addition to root biomass, it is possible that the volume of roots possessed by a genotype may influence the pattern or rate of nutrient accumulation. Plants grown with their roots subjected to a mist rather than submerged in a hydroponic solution produce root systems similar to soil-grown plants (Warncke and Barber 1974). An added advantage of mist culture over soil-grown plants is the fact that the roots can be measured periodically without damage to the root system and with a minimum of shock to the plant.

Root volume was measured by water displacement five times over a period of 49 days (Fig. 7). At the end of 49 days, the plants were harvested and dry weight measurements taken. The results of these analyses are presented in Table 5.

The data gathered in this experiment do not support the hypothesis that root volume plays a major role in the differential uptake or accumulation of P by the maize genotypes. The genotypes did differ with respect to root volume but no trends were apparent to associate those differences with previously observed nutrient absorption characteristics. Root length likewise showed no relationship to nutrient uptake characteristics for any given genotype. At the end of this experiment, the highest dry weight was obtained by Seneca XX155 which agrees with the root temperature experiments discussed earlier. Agway 590-X, the latest genotype, produced not only the lowest biomass of roots but also

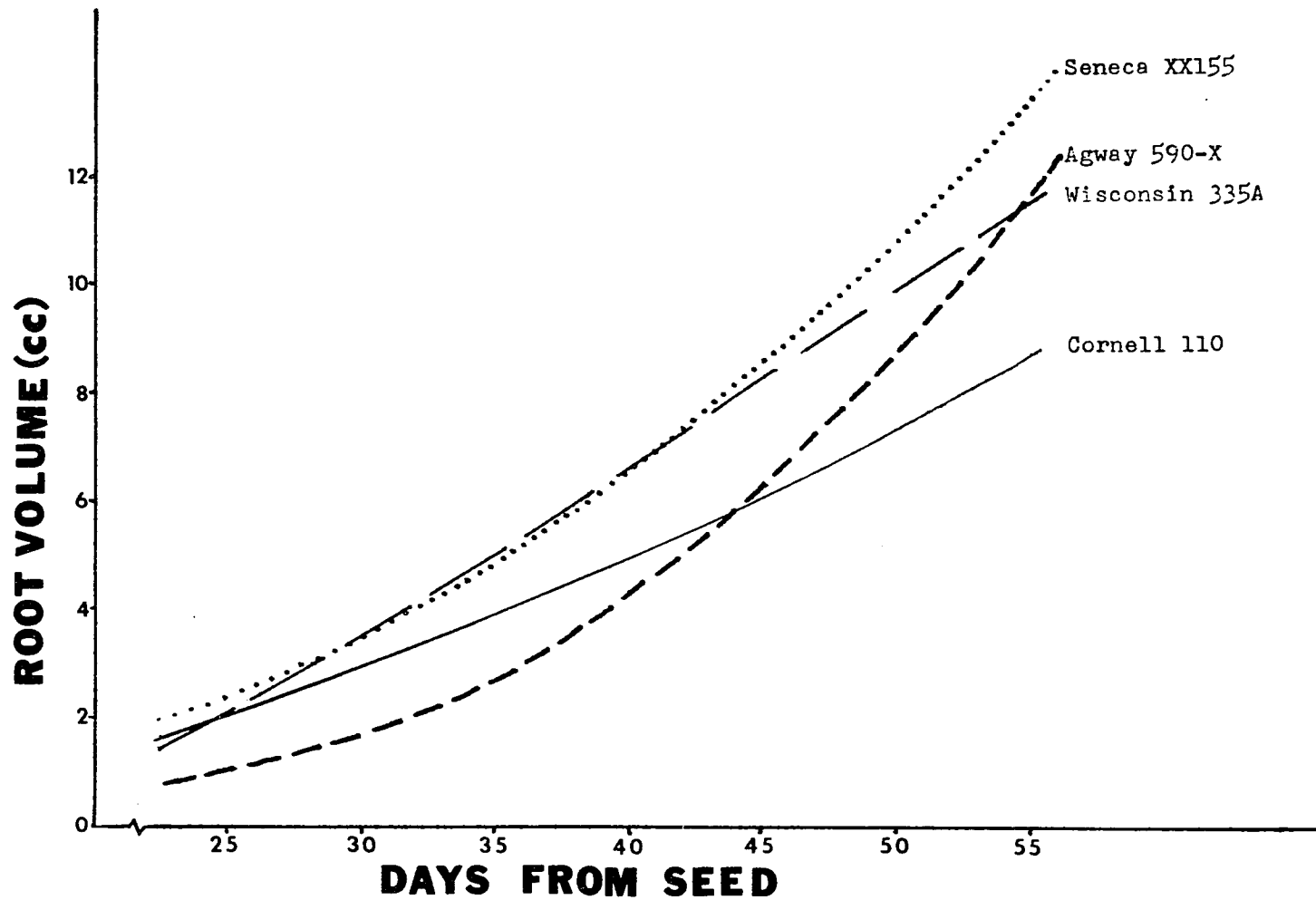


Figure 7. Regression curves for root volume of four maize genotypes grown in a mist culture system. Plants were placed in the mist chamber at 12 days from seeding and grown to 49 days from seeding.

Table 5. Dry weight of tops and roots, top/root ratio, and length of the longest root of four maize genotypes grown in a mist culture system. Values represent the mean of three replications.

Genotype	Dry weight (g)		Top/root ratio	Length of longest root (cm)
	Top	Root		
Cornell 110	0.90 a*	0.50 a	1.82 a	55.8 a
Seneca XX155	1.45 a	0.71 a	2.03 a	81.3 a
Wisconsin 335A	1.24 a	0.65 a	1.85 a	73.1 a
Agway 590-X	0.88 a	0.50 a	1.66 a	56.7 a

* Figures within a column followed by the same letter are not significantly different at 5%, according to Duncan's New Multiple Range test.

had the lowest top/root ratio. This indicates a larger root system in proportion to the tops although the actual root system was smaller compared to the other genotypes at this stage of development. Long term studies with root volumes in a mist chamber could be extremely valuable in providing information on nutrient use throughout the growing season.

The above results help to explain the Fe-deficiency symptoms reported in the ^{32}P uptake study, where the earlier maturing genotypes exhibited the most visible Fe deficiency. The later genotypes had larger root systems in relation to the tops, contained more Fe but less P (absorption at 25C, Table 2), when compared to the early genotypes. The lower levels of Fe in the proportionally smaller root systems of the earlier genotypes may have been saturated by P, and through the formation of a P-Fe precipitate in the root prevented the Fe from being translocated to the tops.

Soil pH

The soil used in this experiment was analyzed before treatment and again after completion of the experiment. Results of the soil analyses are presented in Table 6. The levels of extractable nutrients did change during the 35 days of the experiment. For example, the pH of the untreated soil was 4.58 initially and 4.28 at the conclusion of the experiment. The amount of extractable P, Fe, Zn, and Al in the soil at the completion of the study decreased with increased lime rates. This decrease could be the result of either increased absorption of

Table 6. Analysis of soil used in the greenhouse soil pH study. The soil was analyzed prior to treatment and again after the experiment was completed.

Lime Treatment	Analysis									
	pH	Cation exchange capacity	Na	Ca	K	Mg	P	Fe	Zn	Al
			meq/100g				ppm			
Untreated soil *	4.58	8.19	0.28	3.86	0.52	0.61	4.51	101.7	2.99	15.0
Treated soil** (post harvest)										
0 metric ton/ha	4.28						6.68	99.1	2.68	21.3
3.3 metric ton/ha	5.05						5.60	99.4	2.49	15.0
6.7 metric ton/ha	5.66						3.43	70.8	2.29	12.2

* Values represent the mean of three replications.

** Values represent the mean of two replications.

these elements or a chemical interaction of elements such as Fe-P or Al-P within the soil which renders them insoluble.

Differences in sensitivity of the four genotypes to lime treatments were noted from observing the dry weight of the tops and roots (Table 7). Top and root weight of Seneca XX155 was superior to the other genotypes at all lime rates. The addition of hydrated lime tended to reduce plant weights. The root weight of Cornell 110 was reduced to the greatest extent by the lime treatments. The top/root ratios of the two early genotypes are significantly lower than the two late genotypes at the 0 metric ton/ha lime rate. These data show that under acid soil conditions, the early genotypes possess more root system in relation to the tops while the reverse is true of the later genotypes. The dry weight data of tops and roots clearly show that the increase in top/root ratio of Cornell 110 as influenced by the addition of lime, is not the result of increased top growth, but rather due to decreased root growth. These results may also imply that a toxicity existed at the higher lime rate due to the use of hydrated limestone.

The nutrient content of P, Al, Fe, and Mg within the four genotypes as influenced by lime treatment are presented in Tables 8 and 9 for tops and roots, respectively. High levels of soil Ca are known to suppress the uptake of many plant nutrients. The variability which exists between genotypes for these relationships are not well known.

The addition of lime decreased the accumulation of P by the maize plants. Seneca XX155 absorbed the most P and Cornell 110 accumulated the lowest amount of P.

Table 7. Dry weight of tops, roots, and top/root ratios of four maize genotypes grown in a greenhouse for 35 days in soils receiving lime rates equivalent to 0, 3.3, and 6.7 metric ton/hectare of calcium carbonate. Values represent the mean of five replications.

Genotype	Tops			Roots			Top/root ratio		
	0	3.3	6.7	0	3.3	6.7	0	3.3	6.7
Cornell 110	0.96 c*	0.92 b	0.91 b	0.55 b	0.41 b	0.37 c	1.79 b	2.26 a	2.48 a
Seneca XX155	1.63 a	1.70 a	1.73 a	0.76 a	0.73 a	0.73 a	2.14 ab	2.38 a	2.42 a
Wisconsin 335A	1.20 bc	1.08 b	0.96 b	0.46 b	0.42 b	0.41 bc	2.72 a	2.61 a	2.48 a
Agway 590-X	1.30 bA**	0.86 bB	1.03 bB	0.54 b	0.39 b	0.57 ab	2.54 a	2.15 a	1.92 a

* Figures within a column followed by the same lower case letter are not significantly different at 5%, according to Duncan's New Multiple Range test.

** Upper case letters denote significance within a genotype for any one analysis. Numbers followed by different upper case letters are significantly different at 5%, according to Duncan's New Multiple Range test.

Table 8. Content of phosphorus, aluminum, iron, and magnesium in the tops of four maize genotypes grown in a greenhouse for 35 days in soil which received lime at rates equivalent to 0, 3.3, and 6.7 metric ton/hectare of calcium carbonate. Values represent the mean of five replications.

Genotype	0 metric ton/ha				3.3 metric ton/ha			
	P	Al	Fe	Mg	P	Al	Fe	Mg
Cornell 110	1.10 c*	0.03 b	0.09 b	1.39 c	0.94 a	0.03 a	0.08 b	1.53 c
Seneca XX155	1.86 bAB**	0.06 aA	0.14 a	2.65 a	1.44 aB	0.04 aB	0.16 a	2.81 a
Wisconsin 335A	1.49 bc	0.05 abA	0.12 a	2.26 ab	1.14 a	0.03 aAB	0.11 b	2.10 b
Agway 590-X	2.54 aA	0.05 abA	0.11 ab	2.10 bA	1.35 aB	0.03 aAB	0.08 b	1.48 cB

* Figures within a column followed by the same lower case letter are not significantly different at 5%, according to Duncan's New Multiple Range test.

**Upper case letters denote significance within a genotype for any one analysis. Numbers followed by different upper case letters are significantly different at 5%, according to Duncan's New Multiple Range test.

Table 8. (Continued)

Genotype	6.7 metric ton/ha			
	P	Al	Fe	Mg
	mg			
Cornell 110	1.04 c	0.02 b	0.10 b	1.51 b
Seneca XX155	2.07 aA	0.05 aAB	0.16 a	2.85 a
Wisconsin 335A	1.41 bc	0.02 bB	0.10 b	1.84 b
Agway 590-X	1.77 abB	0.02 bB	0.09 b	1.62 bAB

Table 9. Content of phosphorus, aluminum, iron, and magnesium in the roots of four maize genotypes grown in a greenhouse for 35 days in soil which received lime at rates equivalent to 0, 3.3, and 6.7 metric ton/hectare of calcium carbonate. Values represent the mean of five replications.

Genotype	0 metric ton/ha				3.3 metric ton/ha			
	P	Al	Fe	Mg	P	Al	Fe	Mg
Cornell 110	0.31 b*	3.19 aA**	4.14 aA	0.98 a	0.23 b	0.78 aB	1.06 aB	0.58 b
Seneca XX155	0.45 a	3.27 a	3.54 a	1.09 a	0.44 a	2.35 a	3.60 a	0.99 a
Wisconsin 335A	0.28 b	1.48 b	2.22 a	0.76 a	0.26 b	0.90 a	1.05 a	0.76 ab
Agway 590-X	0.22 b	1.54 b	1.70 a	0.77 a	0.17 b	1.24 a	1.51 a	0.77 ab

* Figures within a column followed by the same lower case letter are not significantly different at 5%, according to Duncan's New Multiple Range test.

**Upper case letters denote significance within a genotype for any one analysis. Numbers followed by different upper case letters are significantly different at 5%, according to Duncan's New Multiple Range test.

Table 9. (Continued)

Genotype	6.7 metric ton/ha			
	P	Al	Fe	Mg
	mg			
Cornell 110	0.21 b	0.77 aB	0.87 aB	0.47 b
Seneca XX155	0.40 a	2.02 a	2.89 a	0.98 a
Wisconsin 335A	0.19 b	0.90 a	1.56 a	0.53 b
Agway 590-X	0.25 b	2.17 a	2.62 a	0.81 ab

Magnesium content of tops was reduced by lime treatments, the two late genotypes showing the greatest decrease. Recent research has provided evidence that soil pH level affects Mg uptake more than does Ca level in soils (Christenson et al. 1973). The basis for this pH effect which was observed in oats grown on a Karlin loamy sand in Michigan was not stated.

Seneca XX155 accumulated much more Fe than the other genotypes at all lime treatments. The content of Fe within the roots of the two early genotypes decreased with the addition of lime. No significant change in Fe content occurred with the late genotypes.

A four-fold reduction in the Al content of roots of Cornell 110 occurred with the addition of 3.3 metric ton/ha of lime. Early genotypes were affected more than the two late genotypes in this regard. The addition of lime caused a sharp reduction in the translocation of Al to the tops of the late genotypes as evidenced by their low Al content. The Al content of roots of the early genotypes was approximately double that of the later genotypes when grown in the absence of lime. A similar relationship was shown with Fe. These data show that under acid soil conditions, the early maturing genotypes accumulate higher amounts of Al in their roots compared to late genotypes. The complexing of P with either Al or Fe to form an insoluble phosphate may explain the retention and increased P content within the roots of the early genotypes as well as the visual Fe deficiency often displayed by these genotypes.

Hydroponics Studies

Study 1. The differential effect of Al on the growth and P uptake and accumulation by the four maize genotypes was investigated under greenhouse-hydroponics conditions. In the first study, low levels of Al (0, 2.5, 5, and 10 ppm) were placed into the nutrient solutions used to grow the genotypes. After 39 days in the nutrient solutions (50 days from seed), dry weight of tops and roots were taken. Figure 8 presents the results of these analyses. It is clear from these data that low levels of Al in the nutrient solution had a stimulating effect on top dry weight. These results agree with those of Lee (1972) who reported stimulated growth of potato by low levels of Al. The top dry weight of Wisconsin 335A and Agway 590-X increased until 10 ppm Al was reached in the nutrient solution. Levels of 10 ppm Al produced a dramatic decrease in top dry weight. Cornell 110 and Seneca XX155 continued to produce higher top dry weight at 10 ppm Al. These results show that later genotypes (Wisconsin 335A and Agway 590-X) are more susceptible to decreases in top growth due to the presence of Al in the root environment when compared to the early genotypes (Cornell 110 and Seneca XX155). Similar results were expressed in terms of root dry weight.

The pH of the nutrient solutions prior to the experiment was 6.2, 5.2, 3.7, and 3.3 for Al concentrations of 0, 2.5, 5, and 10 ppm, respectively. After 12 days growth, the plants changed the pH of the solutions to 6.6, 6.2, 4.8, and 3.5, respectively. Aluminum in the nutrient solution had the effect of lowering the pH. The pH remained low at the high Al levels regardless of the effect of the plant roots.

The sensitivity of the later genotypes to Al in the root

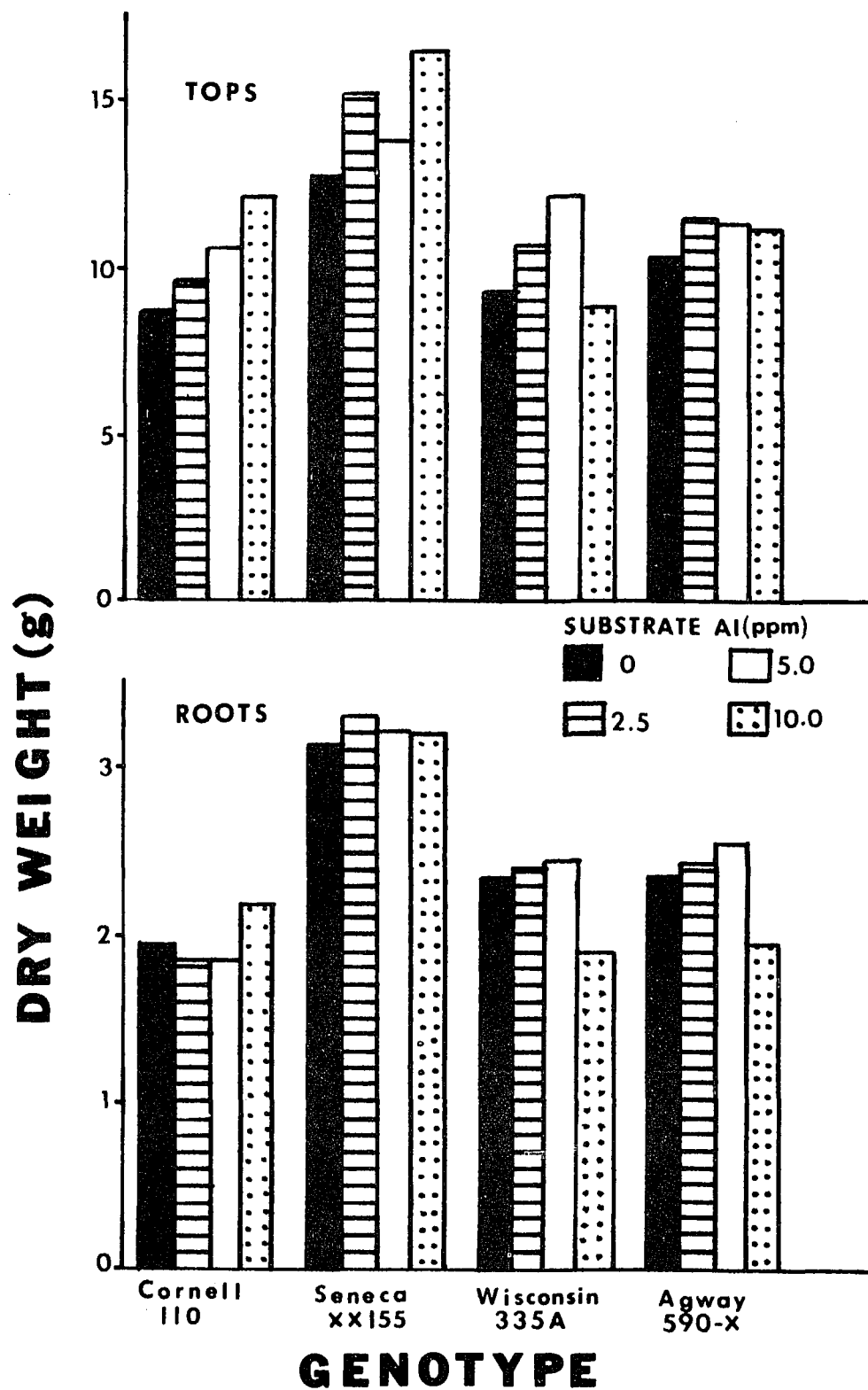


Figure 8. Dry weight of tops and roots of four maize genotypes grown in a nutrient solution at four aluminum levels.

environment may play a major role in the growth of these genotypes in the northeastern U.S. where soils are naturally acid and soluble Al levels are relatively high. It is quite possible that higher P levels observed in the earlier genotypes when compared to the later genotypes may be partially responsible for the ability to resist the harmful effects of Al. This may occur through an aluminum phosphate complex which forms in the tissue, particularly in the roots. Also, under field conditions the root systems of the early genotypes may remain in the upper portions of the soil profile where the pH is higher and P is available to the roots.

Study 2. A second study was initiated to determine the effect of increased levels of soluble Al on the growth and nutritional status of the four genotypes. The Al levels were changed to 0, 10, 25, and 50 ppm Al in the nutrient solutions. The solutions were changed after 19 days and replaced with solutions lacking P. The plants were harvested after 43 days of growth (29 days in hydroponic solution) and the dry weight of tops and roots measured. These data are presented in Table 10. The dry weight of Seneca XX155 was significantly higher than that of the other genotypes when grown at 0, 10, and 25 ppm Al. When grown at the highest Al concentration, a significant reduction in top growth occurred only with Seneca XX155 and Agway 590-X. No sensitivity of the roots was noted to increasing concentration of Al in the nutrient solutions as evidenced by dry weight.

Although the dry weight of all genotypes generally increased with increased Al levels up to 25 ppm Al in the substrate,

Table 10. Dry weight of tops and roots of four maize genotypes grown in a hydroponic solution at four aluminum levels. Values represent the mean of three replications.

Aluminum level (ppm)	Genotype							
	Cornell 110		Seneca XX155		Wisconsin 335A		Agway 590-X	
	Top	Root	Top	Root	Top	Root	Top	Root
0	4.52 a*B**	0.94 bB	6.21 abA	1.54 aA	4.52 aB	0.97 bB	4.75 abB	1.16 aAB
10	4.24 aB	0.80 bB	6.86 aA	1.47 aA	4.96 aB	0.93 bB	4.59 abB	1.01 aB
25	5.12 aB	1.15 abB	7.02 aA	1.88 aA	5.26 aB	1.53 aAB	5.54 aB	1.32 aB
50	4.35 a	1.38 a	4.99 b	1.50 a	4.47 a	1.36 ab	3.59 b	1.41 a

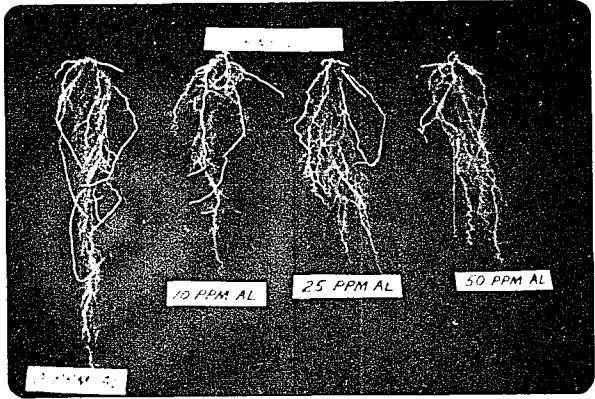
- * Figures within a column followed by the same lower case letter are not significantly different at 5%, according to Duncan's New Multiple Range test.
- **Upper case letters denote significance within an aluminum level for any one analysis. Numbers followed by different upper case letters are significantly different at 5%, according to Duncan's New Multiple Range test.

the visual appearance of the roots of Seneca XX155 and Cornell 110 showed them to be more stunted at the higher Al treatments (Fig. 9). The above two early genotypes showed these symptoms of Al toxicity at treatment levels of 25 and 50 ppm while Wisconsin 335A and Agway 590-X exhibited the effects only at the 50 ppm Al treatment. The stunting and malformation of the root of Al-treated maize appears to be the key to Al toxicity (Rasmussen 1968).

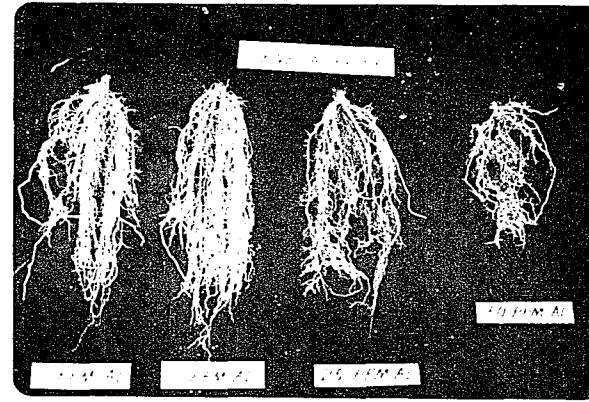
These results do not support the hypothesis that early maize genotypes are less susceptible to high levels of soluble Al except through a tendency to encounter less Al due to a more shallow rooting pattern. However, if the formation of an insoluble Al-phosphate within the root is responsible for a degree of protection from Al it would probably not have occurred in this experiment since P was being withheld from the nutrient solution.

The tendency of a genotype to accumulate P may influence its depth of rooting into an acid soil. Reeve and Sumner (1970) attributed the beneficial effects of P fertilization of acid soils to the elimination of Al toxicity and the resulting increased ability of plants to absorb P, rather than to increased P availability in soils. Improved root development with starter fertilizers high in P may be associated with an improved tolerance to Al. In this regard, the exposure of cotton roots to 1 ppm of Al for 12 hours will cause severe cytological abnormalities in the dividing cells (Huck 1972).

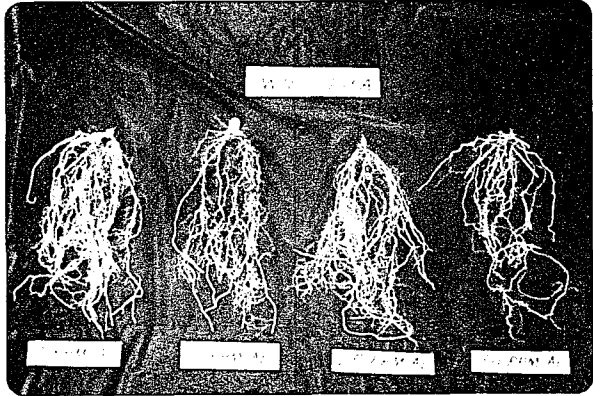
Results of the chemical analysis of tops and roots of the four genotypes are presented in Tables 11, 12, 13, and 14. In all



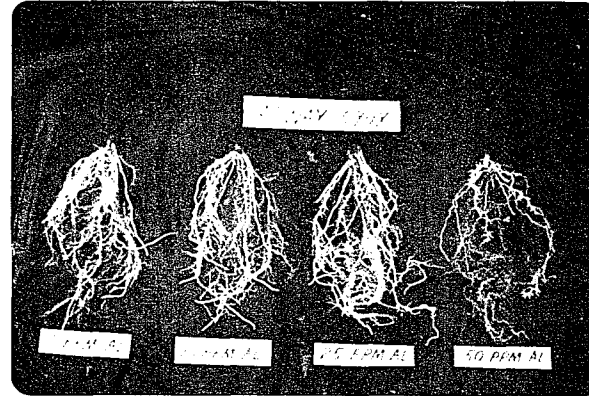
A



B



C



D

Figure 9. Root systems of Cornell 110 (A), Seneca XX155 (B), Wisconsin 335A (C), and Agway 590-X (D) grown in nutrient solutions containing 0, 10, 25, and 50 ppm aluminum.

Table 11. Content of phosphorus and aluminum in the tops of four maize genotypes grown in a hydroponic solution at four aluminum levels. Values represent the mean of three replications.

Aluminum level (ppm)	Genotype							
	Cornell 110		Seneca XX155		Wisconsin 335A		Agway 590-X	
	P	Al	P	Al	P	Al	P	Al
	mg							
0	18.8 a*	0.17 a	25.8 a	0.23 a	17.7 a	0.15 a	17.5 a	0.17 a
10	18.4 a	0.25 a	19.1 a	0.30 a	13.4 a	0.23 a	10.6 a	0.22 a
25	14.5 aAB	0.19 a	22.0 aA	0.29 a	13.9 aAB	0.15 a	9.3 aB	0.24 a
50	6.2 b	0.28 a	16.1 a	0.30 a	7.3 a	0.21 a	7.6 a	0.21 a

* Figures within a column followed by the same lower case letter are not significantly different at 5%, according to Duncan's New Multiple Range test.

**Upper case letters denote significance within an aluminum level for any one analysis. Numbers followed by different upper case letters are significantly different at 5%, according to Duncan's New Multiple Range test.

Table 12. Content of magnesium and iron in the tops of four maize genotypes grown in a hydroponic solution at four aluminum levels. Values represent the mean of three replications.

Aluminum level (ppm)	Genotype							
	Cornell 110		Seneca XX155		Wisconsin 335A		Agway 590-X	
	Mg	Fe	Mg	Fe	Mg	Fe	Mg	Fe
mg								
0	7.4 a*B**	0.45 aAB	13.1 aA	0.54 abA	8.8 aB	0.41 abAB	10.0 aB	0.35 bB
10	6.9 aC	0.32 aB	12.3 abA	0.63 aA	10.2 aAB	0.44 abB	8.9 aBC	0.37 abB
25	7.7 abB	0.45 aB	10.1 bA	0.62 aA	7.7 aAB	0.53 aA	7.7 aAB	0.50 aA
50	3.7 b	0.35 a	5.5 c	0.42 b	4.8 b	0.32 b	3.5 b	0.33 b

* Figures within a column followed by the same lower case letter are not significantly different at 5%, according to Duncan's New Multiple Range test.

**Upper case letters denote significance within an aluminum level for any one analysis. Numbers followed by different upper case letters are significantly different at 5%, according to Duncan's New Multiple Range test.

Table 13. Content of phosphorus and aluminum in the roots of four maize genotypes grown in a hydroponic solution at four aluminum levels. Values represent the mean of three replications.

Aluminum levels (ppm)	Genotype															
	Cornell 110		Seneca XX155		Wisconsin 335A		Agway 590-X									
	P	Al	P	Al	P	Al	P	Al								
	mg															
0	3.5	ab*B**0.3	c	13.7	aA	0.5	c	7.2	aB	0.4	c	13.9	aA	0.7	c	
10	1.3	bB	0.5	c	9.8	abA	1.3	c	5.6	aAB	0.6	c	4.9	bAB	0.8	c
25	3.4	ab	4.8	b	6.6	b	5.9	b	4.2	a	5.1	b	3.4	b	4.6	b
50	7.4	a	9.7	a	7.8	b	10.7	a	7.9	a	7.9	a	7.3	b	8.1	a

* Figures within a column followed by the same lower case letters are not significantly different at 5%, according to Duncan's New Multiple Range test.

**Upper case letters denote significance within an aluminum level for any one analysis. Numbers followed by different upper case letters are significantly different at 5%, according to Duncan's New Multiple Range test.

Table 14. Content of magnesium and iron in the roots of four maize genotypes grown in a hydroponic solution at four aluminum levels. Values represent the mean of three replications.

Aluminum level (ppm)	Genotype							
	Cornell 110		Seneca XX155		Wisconsin 335A		Agway 590-X	
	Mg	Fe	Mg	Fe	Mg	Fe	Mg	Fe
	mg							
0	2.49 a*B**	0.50 b	3.52 aA	0.75 b	2.25 bB	0.48 b	2.50 aB	0.87 ab
10	2.29 aB	0.39 b	3.96 aA	0.72 b	2.26 bB	0.48 b	2.18 aB	0.59 b
25	2.57 aBC	0.89 a	3.67 aA	1.14 a	3.43 aAB	1.08 a	2.40 aC	1.03 a
50	2.04 a	1.00 a	1.78 b	1.09 a	1.49 b	0.74 ab	1.30 b	0.96 a

* Figures within a column followed by the same lower case letter are not significantly different at 5%, according to Duncan's New Multiple Range test.

**Upper case letters denote significance within an aluminum level for any one analysis. Numbers followed by different upper case letters are significantly different at 5%, according to Duncan's New Multiple Range test.

genotypes, P concentration and content of the plant tops decrease with increasing Al concentration in the nutrient solution. The correlation coefficient for mg P in the plant tops versus Al level in the nutrient solution was -0.80, -0.38, -0.65, and -0.58 with 10 degrees of freedom for Cornell 110, Seneca XX155, Wisconsin 335A, and Agway 590-X respectively.

Aluminum has been found to precipitate on the surface of the epidermal cells of the roots with no penetration into the cortex as long as the root surface remained intact. The localization of P was exactly the same as that of Al suggesting a precipitation of P by Al in roots of Zea mays (Rasmussen 1968).

Table 11 shows that the foliage of early genotypes (Cornell 110 and Seneca XX155) generally exhibits a higher P content than the later maturing genotypes (Wisconsin 335A and Agway 590-X). These results agree with related work presented previously (Bruetsch and Estes 1976) and in this manuscript (root temperature studies) which show that early maize genotypes tend to accumulate higher amounts of P than the later maturing plants.

A review of data in Tables 11 and 13 shows that the movement of Al from the roots to tops is slight. The association between the Al concentration in the nutrient solution and in the plant tissue is very weak for tops but strong for roots. The precipitation of Al as an insoluble phosphate which subsequently becomes unavailable for transport within the vascular system has been suggested (Rasmussen 1968). The influence of Al treatments on the translocation of P differs greatly between genotypes

(Tables 11 and 13). Far more P moves to the tops in Cornell 110 than in Agway 590-X at any Al treatment except the 50 ppm level.

The presence of appreciable levels of Al in the tissue of the control plants appears related to the presence of insoluble phosphates in the sand in which the plants were growing which were not completely removed by the acid washing procedure prior to initiation of Study 2. No significant differences occurred in the content of Al in the tops of the plants as influenced by the four Al treatments. Growth at 50 ppm Al produced an increase of 19.2X the Al content of roots of control plants. Thus, the impact of substrate Al is on the root system rather than the tops of maize plants. These data support the hypothesis that early genotypes are using P to inactivate Al in the roots under conditions of high soluble Al in the root zone. Improved translocation of P is implied under conditions of low soluble Al in the root zone.

The efficiency of Mg entry into the plant roots is also greatly affected by the Al treatments. The indirect effect of Al on chlorophyll synthesis and photosynthetic activity is therefore implicated. The Mg content of the tops of the plants is more affected by the substrate Al treatments than is the Mg status of the roots. Only the 50 ppm Al treatment significantly decreased the Mg content of root tissue (Table 14). The entry of Mg into the roots at the highest Al treatment is strongly associated with maturity rating, the earliest plants containing the most Mg. These data indicate an interference with Mg uptake and/or translocation by Al and support the findings of Lee (1972) and Rees and Sidrak (1961) who indicated that high levels of Al may reduce Mg uptake in plants. Aluminum toxicity in rice has

also been characterized by lower concentrations of Mg in plant tops (Ota 1968). The mechanism to explain the Mg stress imposed by high Al treatments is unknown. However, Al may simply be more effective than Mg in competing for exchange sites on the root. A saturation of a common carrier by Al may also be occurring.

The uptake pattern of Fe was very similar to that of Al. In this regard, the content of Fe in the roots of all the maize genotypes tended to increase with increasing Al concentration of the root zone (Table 14). This supports an observation at harvest that the roots of all the genotypes showed increasing intensity of red color with increasing concentration of Al in the nutrient solution. Since the sequestrene Fe used for the nutrient solution was red, it is assumed that Fe was being increasingly adsorbed on or in the roots as the Al level of the nutrient solution increased. Since the pH of the nutrient solution decreased with increasing Al treatment, the above may be related to the improved Fe solubility in the high Al treatments. Therefore, since Fe behaved similarly to Al, it is probable that both Fe and Al can significantly affect P nutrition.

At harvest, the plant tops visibly showed Fe-deficiency symptoms in all of the genotypes. These deficiency symptoms decreased with increasing Al concentration in the root zone. Also, the earlier genotypes (Cornell 110 and Seneca XX155) had much more pronounced Fe-deficiency symptoms than Wisconsin 335A or Agway 590-X.

Laboratory Investigations

Seed Analysis

To determine if the nutrient content between plants and seeds showed similarities, seeds of the four genotypes were weighed and analyzed for P and Fe (Table 15). It can be seen that the average weight of a seed of Seneca XX155 or Wisconsin 335A is significantly higher than that of Cornell 110 or Agway 590-X. The genotypes with the more massive seeds would obviously be able to supply more nutritional support to the young seedling in its early development.

No statistical significance was attained with respect to concentration or content of P and Fe, although Fe level in the seed declined with maturity of the genotype. This is in agreement with other research where a strong correlation ($r = -0.54$, 10df) existed between Fe concentration and growing degree days of the genotypes and early maturing genotypes accumulated more Fe in the tops when compared to later genotypes (Bruetsch and Estes 1976). The high amount of stored Fe in the seeds does not appear related to the tendency of a genotype to show a deficiency symptom to Fe.

Field Investigations

To determine if results of greenhouse studies assume significance under field conditions, two studies were conducted. Study 1 utilized various P treatments and Study 2 utilized two different cultural methods (no-till and conventional tillage) to determine their importance on the nutrition of the genotypes previously used.

Study 1. Table 16 gives the results of the soil analysis of the

Table 15. Seed weight and concentration and content of phosphorus and iron of seeds of four maize genotypes. Values represent the mean of three replications.

Genotype	Seed weight g	Concentration		Content	
		P %	Fe ppm	P mg	Fe
Cornell 110	0.21 b*	0.22 a	220 a	0.47 a	0.05 a
Seneca XX155	0.28 a	0.22 a	136 a	0.61 a	0.04 a
Wisconsin 335A	0.27 a	0.15 a	119 a	0.42 a	0.03 a
Agway 590-X	0.20 b	0.24 a	107 a	0.50 a	0.02 a

* Figures within a column followed by the same letter are not significantly different at 5%, according to Duncan's New Multiple Range test.

Table 16. Analysis of soil used in the first field study. Values represent the mean of three replications.

Analysis	Result	% Base saturation
pH	5.30	
Phosphorus	4.19 ppm	
Aluminum	15.19 ppm	
Iron	42.80 ppm	
Zinc	3.38 ppm	
Exchangeable bases		
Magnesium	0.43 meq/100g	6.05
Calcium	5.81 meq/100g	81.83
Potassium	0.57 meq/100g	8.02
Sodium	0.24 meq/100g	3.38
Cation exchange capacity	7.10 meq/100g	

field used in this study. Plants were grown in plots receiving either 0, 112, or 224 kg/ha P_2O_5 as a treatment. Plant samples were taken after 53 days of growth and analyzed for dry weight, P, and Fe (Table 17). A significant positive correlation existed ($r= 0.35$, 46df) between yield and P_2O_5 treatment indicating an increase in top growth with increasing P application. Greatest increases in dry weight occurred with Seneca XX155 and Wisconsin 335A after 53 days of growth. There was no significant difference observed in P concentration of the tops in any genotype but total content of P did generally increase with applied P. The content of Fe generally increased with increased P_2O_5 application in all the genotypes except Agway 590-X. Thus, the application of P to field soils does not appear to reduce translocation of Fe in the plant as observed in hydroponic studies. Unrestricted root expansion, high levels of soil Fe, and P fixation by soil may be reasons for these results.

Plants in this study were harvested again after 127 days and analyzed for yield, P, Al, Fe, and Mg (Tables 18 and 19). Higher yields were observed in the later genotypes (Wisconsin 335A and Agway 590-X) when compared with the early genotypes (Cornell 110 and Seneca XX155). These data show that early genotypes are more responsive to applied P_2O_5 than late genotypes as reflected by a closer association between amount applied and amount absorbed (Table 19). These results support the findings of Study 2 of the hydroponics research where early lines accumulate higher levels of P if it is available to the root. Since P was applied uniformly to the plots and not banded, the early genotypes may also be taking up more P simply because of a more

Table 17. Dry weight, and concentration and content of phosphorus and iron in the tops of four maize genotypes grown for 53 days in a field which received 0, 112, and 224 kilograms per hectare P_2O_5 . Values represent the mean of four replications.

Genotype	P_2O_5 applied (kg/ha)	Dry weight		Phosphorus		Iron	
		g	%	mg/plant	ppm	mg/plant	
Cornell 110	0	58.65 abc*	0.09 a	57.0 b	78.5 abc	4.5 bcd	
	112	60.73 abc	0.09 a	58.4 b	72.0 bc	4.4 bcd	
	224	57.90 abc	0.11 a	67.5 b	88.0 ab	5.1 abc	
Seneca XX155	0	43.14 c	0.11 a	48.1 b	86.5 ab	3.7 cd	
	112	56.04 bc	0.12 a	61.2 b	75.7 bc	4.1 bcd	
	224	63.05 ab	0.09 a	60.4 b	89.7 ab	5.7 ab	
Wisconsin 335A	0	48.21 bc	0.15 a	74.7 ab	83.7 abc	3.9 cd	
	112	57.22 abc	0.12 a	71.7 ab	94.2 a	5.3 abc	
	224	73.13 a	0.12 a	95.6 a	86.7 ab	6.3 a	
Agway 590-X	0	53.56 bc	0.12 a	65.2 b	78.7 abc	4.2 bcd	
	112	47.95 bc	0.10 a	49.3 b	80.2 abc	3.7 cd	
	224	53.09 bc	0.12 a	64.4 b	66.2 c	3.4 d	

* Figures within a column followed by the same letter are not significantly different at 5%, according to Duncan's New Multiple Range test.

Table 18. Yield, and concentration of phosphorus, aluminum, iron, and magnesium in the tops of four maize genotypes grown for 127 days in a field which received 0, 112, and 224 kilograms per hectare P₂O₅. Values represent the mean of four replications.

Genotype	P ₂ O ₅ applied (kg/ha)	Yield (metric tons/ha)	%P	ppm Al	ppm Fe	%Mg
Cornell 110	0	30.96 abc*	0.26 d	82 abc	83 ab	0.25 b
	112	34.74 abc	0.29 cd	97 ab	94 ab	0.26 b
	224	27.46 c	0.41 ab	47 bc	73 b	0.28 b
Seneca XX155	0	31.80 abc	0.30 bcd	74 abc	79 ab	0.32 ab
	112	34.32 abc	0.46 a	83 abc	85 ab	0.34 ab
	224	32.22 abc	0.38 abc	65 abc	77 ab	0.34 ab
Wisconsin 335A	0	27.74 bc	0.32 bcd	59 abc	80 ab	0.34 ab
	112	36.56 ab	0.36 abcd	73 abc	93 ab	0.40 a
	224	36.00 abc	0.31 bcd	105 a	104 a	0.33 ab
Agway 590-X	0	39.08 a	0.33 bcd	66 abc	80 ab	0.31 ab
	112	35.44 abc	0.29 cd	64 abc	77 ab	0.27 b
	224	39.65 a	0.32 bcd	42 c	69 b	0.27 b

* Figures within a column followed by the same letter are not significantly different at 5%, according to Duncan's New Multiple Range test.

Table 19. Content of phosphorus, aluminum, iron, and magnesium in the tops of four maize genotypes grown for 127 days in a field which received 0, 112, and 224 kilograms per hectare P_{25} . Values represent the mean of four replications.

Genotype	P_{25} applied (kg/ha)	Phosphorus	Aluminum	Iron	Magnesium
		mg/plant top			
Cornell 110	0	529 abc*	15.6 ab	16.2 ab	417 a
	112	545 abc	18.2 a	17.7 a	487 a
	224	705 a	8.0 b	12.7 abc	492 a
Seneca XX155	0	416 bc	8.7 b	10.1 bc	463 a
	112	633 ab	12.1 ab	12.0 abc	483 a
	224	580 abc	8.7 b	11.3 bc	510 a
Wisconsin 335A	0	350 c	7.2 b	9.6 c	405 a
	112	530 abc	10.9 ab	13.7 abc	551 a
	224	481 abc	18.9 a	17.6 a	549 a
Agway 590-X	0	597 abc	12.0 ab	14.3 abc	570 a
	112	539 abc	12.3 ab	14.5 abc	513 a
	224	514 abc	6.5 b	11.0 bc	423 a

* Figures within a column followed by the same letter are not significantly different at 5%, according to Duncan's New Multiple Range test.

shallow root system.

The total content of Mg was higher in all genotypes except Agway 590-X with increased P_2O_5 application. The results of this field study support findings in the second hydroponics study which showed decreases in tissue Mg with increasing Al levels in the root environment. High levels of P applied to a soil may render Al inactive and permit greater entry of Mg into the root. No consistent relationships existed between maturity rating, applied P_2O_5 , and Al and Fe levels of the plant tops. These results are not surprising since significant differences in the hydroponics studies were primarily confined to the root systems of the plants.

Study 2. Because no-till systems of maize and forage crops production represent an avenue to reduce production costs, this technique was incorporated into Study 2. With no-till, plowing may not occur, and soil pH and soluble Al at lower soil depths may cause an unusual and inefficient pattern of nutrient use. Root morphology and root depth of a genotype may play an important role in plant growth and nutrient uptake under no-till culture where the soil is left largely undisturbed.

This study was undertaken to determine the response of the four maize genotypes to no-till conditions when compared to conventional tillage culture. Figure 10 illustrates the two tillage systems used in this investigation. Special emphasis was placed on the root systems of the genotypes and the possible relationships to maturity rating and nutrient uptake.

Soil samples were taken from the plowed and no-till plots



A



B

Figure 10. No-till (A) and conventional tillage (B) systems used in the second field investigation.

prior to planting. The soil samples were taken at 10 cm increments to a depth of 40 cm and analyzed for cation exchange capacity (CEC), pH, P, Al, Fe, and Zn. The results of these soil analyses are presented in Table 20.

Cation exchange capacity decreased with depth in the no-till (undisturbed) soil as did the exchangeable bases with the exception of Na (Table 20). Phosphorus concentration of the no-till soil was substantially higher in the top 10 cm indicating a lack of movement of fertilizer P applied to the surface in a no-till study the previous year. Soil pH decreased with depth showing the presence of highly acid subsoils, a condition favoring increased solubility of Al and Fe.

Results of the analysis of the plant tops grown under no-till and conventional tillage systems for 37, 62, 95, and 110 days are given in Tables 21, 22, 23, 24, 25, and 26. After 37 days under no-till conditions, dry weight of the plant tops showed a decrease with increasing maturity of the genotypes. This decrease indicated better growth of the early genotypes early in the season under no-till conditions when compared to the later genotypes. After 37 days, P content of the tops decreased with maturity rating of the genotypes under no-till conditions, a result not occurring under conventional tillage (Table 21). This decrease indicates that the early genotypes at this stage of development are more efficient in P absorption when compared to the late genotypes. This may be especially true when the soil temperatures are relatively cool, on mulched plots which are not disturbed by plowing, and when the fertilizer P is applied on the

Table 20. Analysis of the soil used in the no-tillage field investigation. Values represent the mean of three replications.

Culture system	Analysis	Depth of soil sample (cm)				
		0-10	10-20	20-30	30-40	
No-tillage system	Exchangeable bases (meq/100g)					
	Mg	0.89	0.80	0.68	0.38	
	Ca	3.87	2.30	1.95	0.75	
	K	0.58	0.15	0.13	0.03	
	Na	0.22	0.21	0.21	0.19	
	Cation exchange capacity	6.51	6.12	5.93	4.22	
	P (ppm)	3.9	1.9	2.0	1.7	
	Al (ppm)	12.9	21.9	25.7	33.3	
	Fe (ppm)	46.4	53.9	71.7	32.4	
	Zn (ppm)	4.0	3.1	4.2	1.7	
	pH	5.63	4.92	4.74	4.73	
	Conventional tillage system	F (ppm)	1.8	1.7	1.8	1.6
		Al (ppm)	24.1	23.7	23.8	37.6
Fe (ppm)		37.8	41.8	41.9	28.4	
Zn (ppm)		4.3	3.2	4.5	1.7	
pH		4.78	4.99	4.75	4.68	

Table 21. Top dry weight, and concentration and content of phosphorus, iron, aluminum, and magnesium in the tops of four maize genotypes grown for 37 days under no-till or conventional tillage systems. Values represent the mean of four replications.

Genotype	Tillage system	Concentration				Dry weight (g)
		% P	ppm Fe	ppm Al	% Mg	
Cornell 110	No-till	0.34 a*	107 a	8.7 a	0.27 a	6.52 a
	Conventional	0.28 A**	192 AB [#]	20.7 A	0.34 A	4.76 A
Seneca XX155	No-till	0.28 a	146 a	17.4 a	0.28 a	5.82 ab
	Conventional	0.34 A	199 AB	24.8 A	0.35 A	4.93 A
Wisconsin 335A	No-till	0.30 a	94 a	7.6 a	0.31 a	4.61 ab
	Conventional	0.28 A	245 A [#]	30.8 A [#]	0.35 A	4.96 A
Agway 590-X	No-till	0.29 a	102 a	9.8 a	0.29 a	4.03 b
	Conventional	0.32 A	179 B [#]	29.3 A [#]	0.38 A	4.59 A

* Lower case letters within a column that are different indicate significant differences between genotypes under the no-till culture system. These differences are significant at 5%, according to Duncan's New Multiple Range test.

**Upper case letters within a column that are different indicate significant differences between genotypes under the conventional tillage system. These differences are significant at 5%, according to Duncan's New Multiple Range test.

Indicates significant differences within a genotype between the no-till and conventional tillage systems. These differences are significant at 5%, according to Duncan's New Multiple Range test.

Table 21. (Continued)

Genotype	Tillage system	Content (mg)			
		P	Fe	Al	Mg
Cornell 110	No-till	22.4 a	0.70 ab	0.05 ab	18.2 a
	Conventional	13.8 A	0.92 AB	0.10 A	16.5 A
Seneca XX155	No-till	18.0 ab	0.78 a	0.10 a	16.3 a
	Conventional	16.7 A	0.98 AB	0.12 A	17.4 A
Wisconsin 335A	No-till	15.1 ab	0.42 bc [#]	0.03 b [#]	14.8 a
	Conventional	14.0 A	1.20 A	0.15 A [#]	17.9 A
Agway 590-X	No-till	12.2 b	0.34 c	0.03 b [#]	11.6 a
	Conventional	14.3 A	0.75 B	0.11 A [#]	17.9 A

Table 22. Top dry weight, and concentration and content of phosphorus, iron, aluminum, and magnesium in the tops of four maize genotypes grown for 62 days under no-till or conventional tillage systems. Values represent the mean of four replications.

Genotype	Tillage system	Concentration				Dry weight (g)
		% P	ppm Fe	ppm Al	% Mg	
Cornell 110	No-till	0.20 a*	42.5 a	37.2 a	0.25 b	63.4 a
	Conventional	0.15 A**	42.9 A	37.0 A	0.29 B	59.8 A
Seneca XX155	No-till	0.20 a	39.2 a [#]	54.0 a	0.29 a	67.0 a
	Conventional	0.16 A	49.3 A [#]	49.9 A	0.28 B	80.9 A
Wisconsin 335A	No-till	0.23 a [#]	40.3 a	36.1 a	0.28 ab	68.4 a
	Conventional	0.15 A [#]	43.8 A	47.7 A	0.31 AB	68.0 A
Agway 590-X	No-till	0.20 a	39.9 a	41.6 a	0.28 ab [#]	44.4 a
	Conventional	0.19 A	44.5 A	72.2 A	0.34 A [#]	67.5 A

* Lower case letters within a column that are different indicate significant differences between genotypes under the no-till culture system. These differences are significant at 5%, according to Duncan's New Multiple Range test.

** Upper case letters within a column that are different indicate significant differences between genotypes under the conventional tillage system. These differences are significant at 5%, according to Duncan's New Multiple Range test.

Indicates significant differences within a genotype between the no-till and conventional tillage systems. These differences are significant at 5%, according to Duncan's New Multiple Range test.

Table 22. (Continued)

Genotype	Tillage system	Content (mg)			
		P	Fe	Al	Mg
Cornell 110	No-till	116.5 ab	2.7 a	2.2 a	155 ab
	Conventional	90.0 A	2.6 B	2.2 A	179 A
Seneca XX155	No-till	139.8 ab	2.7 a	3.6 a	199 a
	Conventional	131.9 A	3.9 A	3.8 A	233 A
Wisconsin 335A	No-till	164.5 a	2.6 a	2.2 a	193 a
	Conventional	108.0 A	3.0 AB	3.2 A	213 A
Agway 590-X	No-till	91.1 b	1.7 a	1.8 a	128 b [#]
	Conventional	132.4 A	3.0 AB	4.6 A	229 A

Table 23. Top dry weight, and concentration and content of phosphorus, iron, aluminum, and magnesium in the tops of four maize genotypes grown for 93 days under no-till or conventional tillage systems. Values represent the mean of four replications.

Genotype	Tillage system	Concentration				Dry weight (g)
		% P	ppm Fe	ppm Al	% Mg	
Cornell 110	No-till	0.19 a*	406 a	47.8 a	0.22 a	348.9 a
	Conventional	0.17 AB**	450 A	51.9 A	0.25 A	291.4 A
Seneca XX155	No-till	0.15 a	313 b _#	41.5 a	0.22 a	179.5 b
	Conventional	0.12 B	401 A _#	43.6 A	0.25 A	255.0 A
Wisconsin 335A	No-till	0.18 a	293 b _#	58.1 a	0.22 a	235.8 b
	Conventional	0.18 AB	455 A _#	47.8 A	0.26 A	245.4 A
Agway 590-X	No-till	0.14 a	274 b	31.2 a	0.23 a	261.6 ab
	Conventional	0.21 A	316 B	45.5 A	0.25 A	269.5 A

* Lower case letters within a column that are different indicate significant differences between genotypes under the no-till culture system. These differences are significant at 5%, according to Duncan's New Multiple Range test.

**Upper case letters within a column that are different indicate significant differences between genotypes under the conventional tillage system. These differences are significant at 5%, according to Duncan's New Multiple Range test.

Indicates significant differences within a genotype between the no-till and conventional tillage systems. These differences are significant at 5%, according to Duncan's New Multiple Range test.

Table 23. (Continued)

Genotype	Tillage system	Content (mg)			
		P	Fe	Al	Mg
Cornell 110	No-till	699 a	139.3 a	16.5 a	793 a
	Conventional	524 A	134.9 A	15.6 A	738 A
Seneca XX155	No-till	317 b	64.0 b [#]	8.5 a	452 b
	Conventional	314 A	101.3 AB [#]	11.0 A	644 A
Wisconsin 335A	No-till	423 ab	69.2 b [#]	13.2 a	525 b
	Conventional	439 A	112.7 AB [#]	11.9 A	651 A
Agway 590-X	No-till	357 ab	71.7 b	8.2 a	604 ab
	Conventional	567 A	86.3 B	12.4 A	671 A

Table 24. Population, percent dry matter, ear dry weight, silage produced, and dry matter production of four maize genotypes grown for 110 days under no-till or conventional tillage systems. Values represent the mean of four replications.

Genotype	Tillage system	Population (plants/ha)	Percent dry matter	Ear dry weight (g)	Silage (metric ton/ha)	Dry matter (metric ton/ha)
Cornell 110	No-till	10125 ab*	26.8 a [#]	353 a	35.2 ab	9.4 a
	Conventional	8808 B**	31.4 A [#]	449 A	26.2 B	8.2 B
Seneca XX155	No-till	8808 b	19.6 b [#]	288 ab	31.6 b	6.2 b
	Conventional	8910 B	26.1 B [#]	412 A	27.2 B	6.9 B
Wisconsin 335A	No-till	9112 ab	21.1 b	275 ab	37.1 ab	7.8 ab
	Conventional	10428 AB	21.7 C	384 AB	31.6 B	6.7 B
Agway 590-X	No-till	11643 a	19.1 b	201 b	40.6 a	7.7 ab [#]
	Conventional	12352 A	21.9 C	270 B	48.7 A	10.7 A [#]

* Lower case letters within a column that are different indicate significant differences between genotypes under the no-till culture system. These differences are significant at 5%, according to Duncan's New Multiple Range test.

**Upper case letters within a column that are different indicate significant differences between genotypes under the conventional tillage system. These differences are significant at 5%, according to Duncan's New Multiple Range test.

Indicates significant differences within a genotype between the no-till and conventional tillage systems. These differences are significant at 5%, according to Duncan's New Multiple Range test.

Table 25. Concentration and content of phosphorus, iron, aluminum, and magnesium in the tops of four maize genotypes grown to 110 days under no-till or conventional tillage systems. Values represent the mean of four replications.

Genotype	Tillage system	Concentration			
		% P	ppm Fe	ppm Al	% Mg
Cornell 110	No-till	0.17 ab*	359 a	35.3 a	0.26 a
	Conventional	0.22 A **	257 B	29.1 A	0.25 A
Seneca XX155	No-till	0.23 a	321 a	35.3 a	0.26 a
	Conventional	0.21 A	209 B	31.1 A	0.23 A
Wisconsin 335A	No-till	0.18 ab	331 a	29.0 a	0.25 a
	Conventional	0.20 A	286 AB	39.4 A	0.23 A
Agway 590-X	No-till	0.15 b	230 a [#]	37.4 a	0.21 a
	Conventional	0.13 B	407 A [#]	43.5 A	0.26 A

* Lower case letters within a column that are different indicate significant differences between genotypes under the no-till culture system. These differences are significant at 5%, according to Duncan's New Multiple Range test.

**Upper case letters within a column that are different indicate significant differences between genotypes under the conventional tillage system. These differences are significant at 5%, according to Duncan's New Multiple Range test.

Indicates significant differences within a genotype between the no-till and conventional tillage systems. These differences are significant at 5%, according to Duncan's New Multiple Range test.

Table 25. (Continued)

Genotype	Tillage	Content (mg)			
		P	Fe	Al	Mg
Cornell 110	No-till	418.0 ab	85.9 a	8.4 a	613 a
	Conventional	555.1 A	62.8 B	7.2 A	614 A
Seneca XX155	No-till	521.7 a	68.7 ab	7.6 a	573 ab
	Conventional	537.8 A	53.0 B	8.4 A	592 A
Wisconsin 335A	No-till	484.7 ab	83.9 a	7.6 a	672 a
	Conventional	514.1 A	73.0 AB	9.9 A	600 A
Agway 590-X	No-till	306.6 b	46.2 b [#]	7.7 a	438 b [#]
	Conventional	352.0 A	105.5 A [#]	10.8 A	720 A [#]

Table 26. Removal of phosphorus, iron, aluminum, and magnesium from soil by four maize genotypes grown to 110 days under no-till or conventional tillage systems. Values represent the mean of four replications.

Genotype	Tillage system	kg/ha removed			
		P	Fe	Al	Mg
Cornell 110	No-till	22.96 a*	4.93 a	0.50 a	36.93 a
	Conventional	29.78 A**	3.36 B	0.38 B	32.44 B
Seneca XX155	No-till	28.84 a	3.68 a	0.41 a	30.73 a
	Conventional	28.09 A	2.80 B	0.38 B	31.95 B
Wisconsin 335A	No-till	26.72 a	4.68 a	0.42 a	36.93 a
	Conventional	32.47 A	4.64 B	0.62 AB	38.25 AB
Agway 590-X	No-till	21.72 a	3.24 a#	0.54 a	31.21 a#
	Conventional	26.08 A	8.15 A#	0.83 A	53.92 A#

* Lower case letters within a column that are different indicate significant differences between genotypes under the no-till culture system. These differences are significant at 5%, according to Duncan's New Multiple Range test.

**Upper case letters within a column that are different indicate significant differences between genotypes under the conventional tillage system. These differences are significant at 5%, according to Duncan's New Multiple Range test.

Indicates significant differences within a genotype between the no-till and conventional tillage systems. These differences are significant at 5%, according to Duncan's New Multiple Range test.

surface. The genetic endowment of a shallower root system in the early genotypes compared to the later genotypes may also be a factor in the above response.

The early genotypes may utilize P to confer some degree of protection from toxic levels of Al (≈ 25 ppm) which exists at the 20-30 cm soil depth. Visual effects of 25 and 50 ppm soluble Al on root development were seen in Figure 9. Since P is not mobile in the soil and tends to stay in the upper regions of the soil profile, roots of the early genotypes may remain shallow rather than extend to a greater depth. The relatively shallow root system of an early genotype (Seneca XX155) and the deeper, more vertical root system of a later genotype (Wisconsin 335A) after 62 days growth are shown in Figure 11. The differences in root extensiveness and morphology may explain the increased growth and P uptake of the early maturing genotypes after 37 days in the field.

Iron content of the later genotypes after 37 days growth was significantly lower than that of the earlier maturing genotypes. The concentration of Fe decreased as the plants matured, indicating that most Fe is taken up very early in the season and is diluted when the plant mass increases. Throughout the growing season Fe, Al, and Mg content of the tops was higher under conventional tillage than under no-till conditions. These differences between cultural methods were especially large early in the season. Plowing the soil will tend to make root penetration easier as well as permit a greater production of fine roots which may explain the greater growth and increased nutrient uptake of the plants under conventional tillage.

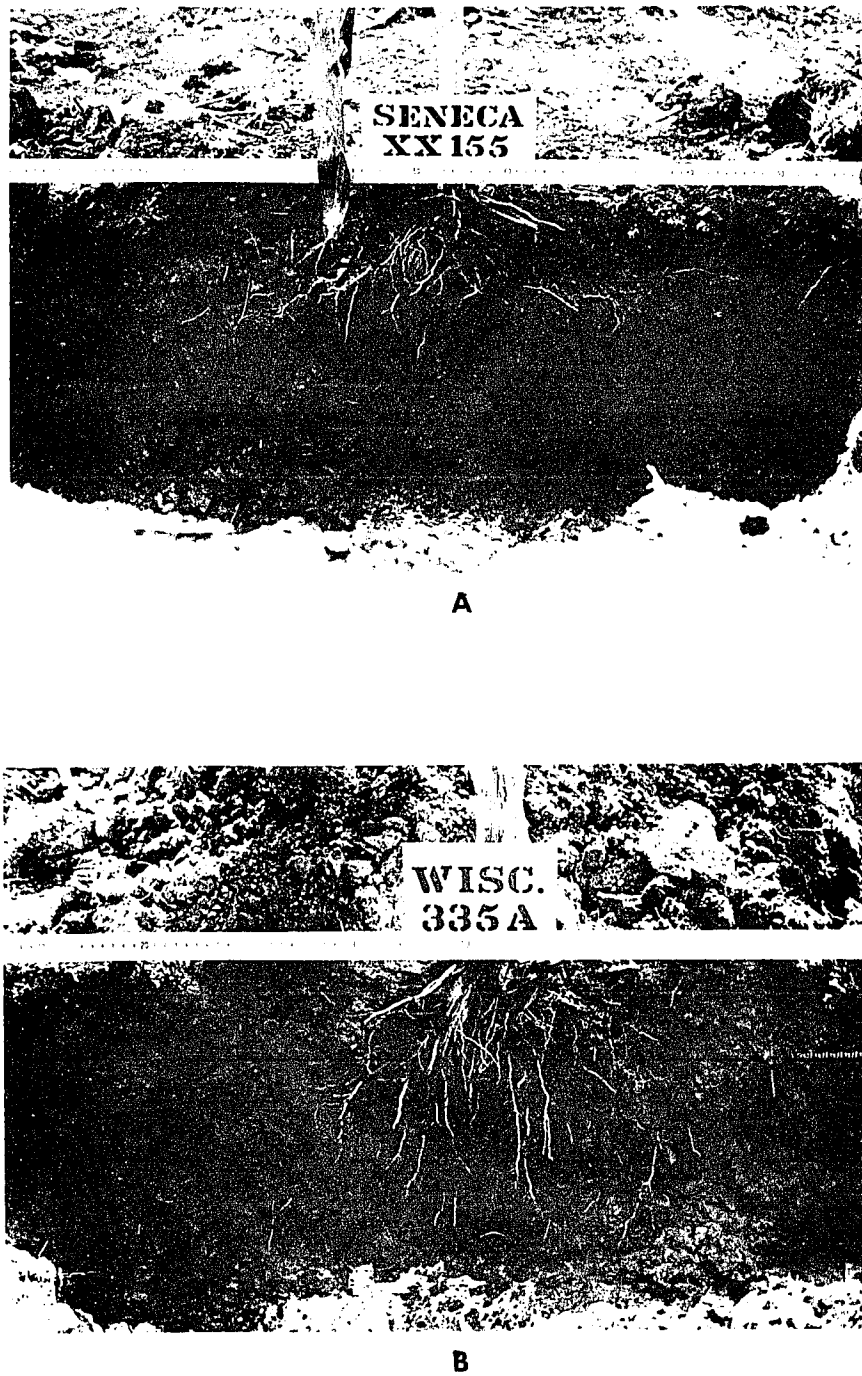


Figure 11. Shallow rooting pattern (A) of Seneca XX155, an early maturing genotype as opposed to the deep rooting pattern (B) produced by Wisconsin 335A, a later maturing line.

Aluminum content was higher in the early maturing genotypes, a reflection of their higher dry weight relative to the late genotypes after 37 days of growth. Magnesium content at this stage of development tended to be lower in the later maturing genotypes. This effect was observed throughout the growing season (Tables 22, 23, 24, 25, and 26).

After 62 and 93 days of growth (Tables 22 and 23), no significant differences in weight existed in plants grown under either cultural method. However, P concentration and content were higher in the early genotypes under no-till conditions and higher in the later genotypes under conventional tillage. These data probably reflect the shallow rooting pattern of the early genotypes and consequently more roots in the high soil P zones under no-till culture.

After 110 days of growth the plant tops were harvested and yield data were taken (Table 24). The later genotypes (Wisconsin 335A and Agway 590-X) had higher populations under the conventional culture. Under no-till conditions, Seneca XX155 produced populations which were significantly lower than the other genotypes. All the genotypes exhibited a higher percent dry matter under conventional tillage when compared to the no-till system. These results are probably due to less soil moisture during the growing season under conventional tillage in comparison to the no-till plots. The shallower root systems of the early genotypes tend to magnify the consequences of low soil moisture with the conventional tillage system.

Ear dry weight (Table 24) of the early maturing genotypes was greater than those of the later genotypes. This was probably

due to the fact that the later genotypes were not fully mature after 110 days of growth. The dry weight of ears was always greater under conventional tillage when compared to no-till culture.

Silage yield after 110 days (Table 24) was higher under no-till conditions when compared to conventional tillage in all the genotypes except Agway 590-X. This likely resulted from a higher soil moisture under no-till conditions, a higher percent moisture in the plant tissue, and a delayed maturity. Agway 590-X, which is the latest maturing genotype, was not fully mature and therefore contained more water than was present in the other genotypes. Due to the higher water content of both Wisconsin 335A and Agway 590-X, silage yield for these genotypes was higher under both culture systems. The earliest maturing genotype (Cornell 110) produced the most dry matter under no-till conditions while the latest genotype (Agway 590-X) produced the most dry matter under conventional tillage conditions (Table 24). Such results indicate that the choice of hybrid may be dictated by the culture method to be used.

Plant tissue levels of P, Fe, Al, and Mg at harvest are presented in Table 25. The utilization of P was better by all genotypes when under conventional tillage. The absorption of P under conventional tillage decreased with increasing maturing of the genotypes. This decrease indicates a greater and more rapid P uptake by the early genotypes compared to the late genotypes in a 110 day growing season. Similar results were seen in Figure 4 where ^{32}P was utilized to determine the rate of P absorption by the genotypes. An elevated Al level in the tops

of plants grown under conventional tillage did not seem to interfere with the absorption of P or Mg.

Under conventional tillage, Al and Fe levels in the plant tissue generally increased with increasing maturity of the genotype. These data would imply a higher mobility of Al and Fe in the late genotypes and less tendency for immobilization of these elements via a P-Al or P-Fe interaction within the root. The association between Al and Fe in terms of similarity of uptake pattern was seen in the field study with P_2O_5 rates and in the hydroponic studies. Their role in affecting phosphate utilization by plants growing in acid soils appears significant.

Magnesium concentration and content did not show any apparent relationship to maturity rating of the genotypes or to the type of tillage practice employed. However, it is apparent that Agway 590-X showed superior uptake of both Fe and Mg when compared to the other genotypes, especially under conventional tillage practices. The reverse was true with respect to the concentration and content of P by Agway 590-X. Under both tillage practices, Agway 590-X showed less uptake and accumulation of P. Under conventional tillage it also absorbed the highest amount of Al and Fe of any of the genotypes. However, the highest dry matter yield was produced from this genotype under conventional conditions. Thus, no harmful effect was apparent from the relatively high Al and Fe or low P levels under those field conditions.

Table 26 presents the total removal of P, Fe, Al, and Mg per hectare by the maize genotypes. Agway 590-X removed significantly higher amounts of Fe, Al, and Mg under conventional

tillage practices. However, under both no-till and conventional tillage Agway 590-X showed less P removal when compared to the other genotypes. There was no correlation between maturity rating of the genotypes and total P removal probably due to the increased population of the later genotypes at harvest.

When comparing the elemental removal of Fe, Al, and Mg by the genotypes, it can be seen that the early lines (Cornell 110 and Seneca XX155) remove more of these elements under no-till conditions while the later genotypes (Wisconsin 335A and Agway 590-X) remove more under conventional tillage. These data show increased efficiency of absorption of these elements by the early lines under no-till culture; the efficiency of the later genotypes is enhanced by conventional tillage practices. Such results indicate that consideration should be given to matching the proper maize genotype to the proper culture practice in order to achieve the highest possible performance from applied fertilizers.

SUMMARY AND CONCLUSIONS

Four maize genotypes (Cornell 110, Seneca XX155, Wisconsin 335A, and Agway 590-X) were selected for these investigations. Cornell 110 is the earliest and Agway 590-X the latest. These genotypes were chosen to determine bases for the differential uptake and accumulation of nutrients, especially P, by long and short season lines. Experiments were conducted to investigate the effects of root temperature, volume, and morphology, root zone pH and Al concentration, and no-till culture on the nutritional behavior of early and late season genotypes.

Under hydroponic conditions in the root temperature study, it was shown that dry weight of tops and roots were generally higher at a root temperature of 25C than at 15.5C. Early genotypes grew faster than later genotypes, regardless of root temperature. Also, an association between the maturity rating of the genotypes and their accumulation of P and Fe was observed; early genotypes contained more P in both tops and roots while Fe translocation from roots to tops seemed to be retarded. A P-Fe precipitate in or on the root is a strong possibility.

The differential rate of P uptake by the four genotypes was investigated under greenhouse conditions using radioactive ^{32}P . At seven weeks of age, the early genotypes (Cornell 110 and Seneca XX155) contained substantially more radioactivity than did Wisconsin 335A or Agway 590-X. These results indicate that differences did exist in P-absorption rates among genotypes and that the early genotypes showed a greater ability to absorb P from a hydroponic solution when compared to later genotypes.

Also, visible Fe-deficiency symptoms were observed in all the genotypes, particularly the early ones. These symptoms suggest that a P-Fe complex was formed in or on the root which prevented Fe from being translocated to the tops. Also, as was shown in the root temperature studies, the early lines accumulated significantly more dry matter than the later genotypes when grown for the same length of time.

Variation in root volume among the genotypes was investigated as a possible explanation for their differential growth and nutrient uptake. Differences in root volume did exist between the genotypes but no trends were apparent to associate these differences with previously observed nutrient absorption characteristics.

Differences in sensitivity of the four genotypes to various degrees of soil acidity was investigated under greenhouse conditions. Under highly acid soil conditions, early genotypes possess more root system in relation to the tops while the reverse was true of the later genotypes. Dry weight data show that the increase in top/root ratio was the result of decreased root growth with increased soil pH rather than increased top growth. A substantial reduction in Fe and Al content of the roots of the early lines was observed with the addition of lime to the soil. However, in the absence of applied lime where the soil was highly acidic, Fe and Al content of the roots of the early genotypes was substantially higher than that of the later lines. These data suggest that under acid soil conditions, P may be complexing with Fe or Al to form an insoluble phosphate in the roots of the early

genotypes. An Fe-phosphate may also explain the visual Fe-deficiency symptoms expressed by the early maturing lines.

The effect of Al on growth and differential uptake of P by the genotypes was further investigated by growing the plants in nutrient solutions containing low concentrations (0, 2.5, 5, and 10 ppm) of Al. It was shown that low levels of Al in the nutrient solution had a stimulatory effect on top dry weight. Increased Al levels produced higher top dry weight of the early lines (Cornell 110 and Seneca XX155) while the later genotypes (Wisconsin 335A and Agway 590-X) increased top dry weight until 10 ppm Al was reached, at which point it decreased. These results suggest that later genotypes are more susceptible to decreases in top growth due to the presence of soluble Al in the root environment than are early maturing lines. This sensitivity to Al by later genotypes may play a significant role in their growth in the northeastern U.S. where acid soils are common and soluble Al levels are relatively high.

The high content of P observed in the early genotypes may be partially responsible for the ability of these genotypes to withstand high amounts of soluble Al in the root zone. A P-Al complex may form in the tissue rendering the Al harmless. Under field conditions, the roots of the early genotypes may also remain near the surface where the pH is higher and P is more available to the roots.

A second greenhouse-hydroponics study was initiated to determine the effect of increased levels of Al on the four genotypes. The plant roots were exposed to Al levels of 0, 10, 25, and 50 ppm. When the nutrient solutions were changed after 19

days of growth, P was withheld to reduce the P-Al interaction and therefore increase the sensitivity of the Al response.

The impact of substrate Al was on the root system only, the tops showed no response to added Al in the root zone. However, the effect of Al on the plant tops may be through a reduction of P translocation. Dry weight of all the genotypes increased with increasing Al levels up to 25 ppm. At 25 and 50 ppm Al in the nutrient solution, the roots of Cornell 110 and Seneca XX155 showed stunting and malformation. These symptoms of Al toxicity did not occur in the later genotypes (Wisconsin 335A and Agway 590-X) until 50 ppm Al was reached in the nutrient solution. These results support the theory that P in the roots of early lines affords a degree of protection from Al in the root zone. Since no P was present in the solution, the roots of the early lines were not protected and an Al toxicity resulted. At low Al concentrations in the root zone, the translocation of P was increased in the early lines. These lines accumulated more P compared to the later maturing genotypes. Soluble Al in the root zone also appeared to affect the entry of Mg into the roots and was strongly associated with the maturity rating of the genotypes. The earliest plants contained the most Mg. The Al-Mg interaction could occur because Al is more effective in competing for exchange sites on the root or a common carrier of Al and Mg may be saturated by Al.

Two field studies were initiated to determine if the results of the greenhouse experiments assumed significance under field conditions. In Study 1, the four genotypes were planted in plots receiving 0, 112, and 224 kg/ha P_{205} . After 53 days of

growth, a significant increase in yield occurred with increasing P applications. After 127 days of growth the data show that early genotypes were more responsive to added P as reflected by a close association between applied P and absorbed P. These results support the findings of the hydroponics study and show that early lines accumulated more P when it was available to the root. The P_2O_5 was applied uniformly to the plots and not banded; the early genotypes may be taking up more P simply due to a more shallow rooting pattern.

The total content of Mg in all the genotypes in the first field study increased with increasing P_2O_5 application. These results lend support to the findings of the greenhouse-hydroponics study where tissue Mg levels decreased with increasing Al levels in the root environment. High levels of P in a soil can render Al inactive and permit a greater uptake of Mg by the root.

In the second field study, the four genotypes were tested under no-till and conventional tillage practices. After 37 days growth under no-till conditions, P content and dry weight of the tops decreased with maturity rating of the genotypes indicating higher P uptake and better growth of the early lines early in the season under no-till conditions. This may be especially important when soil temperature is relatively cool, as is the case in the Northeast in the spring, especially under no-till conditions.

The roots of the early genotypes tend to remain shallow and do not extend very deep into the acid subsoil where soluble Al may create toxic conditions. The liming of soils and the associated benefits to crops is likely related to reduced soluble

Al rather than to the added Ca or increased pH. Early genotypes may utilize P more efficiently under no-till conditions since it is not mobile in the soil and tends to stay in the upper regions of the soil profile. The shallower rooting pattern of the early lines may also be responsible for the higher P content exhibited by these genotypes when compared to the later lines.

Throughout the growing period, Fe, Al, and Mg content was higher under conventional tillage when compared to no-till conditions, undoubtedly due to increased root penetration when the soil is loosened by plowing. However, P concentration and content was higher in the early genotypes under no-till conditions and higher in the later genotypes under conventional tillage. These results reflect the fact that the early lines have shallower root systems and consequently more roots in the high P zones of the soil.

The earliest genotype (Cornell 110) produced the most dry matter under no-till conditions while the latest genotype (Agway 590-X) produced the most under conventional tillage. Also, it was shown that the early lines removed more Fe, Al, and Mg from the soil under no-till conditions while the later genotypes removed more under conventional tillage. These results indicate that the choice of which hybrid to plant may be dictated by the culture method to be used in order to achieve the highest possible performance from applied fertilizers.

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