

GENETIC AND AGRONOMIC STUDIES OF EFFICIENCY IN  
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## ABSTRACT

Twenty-eight corn inbreds were screened for their growth in pots under two levels of phosphorus, 0.011 ppm and 0.06 ppm in soil solution. Ten inbreds differing in growth under low P were selected to produce a diallel cross. The inbreds showing good growth under low P were Mp68:616, Ph9, CI21E, B14A, and CM104 and those showing poor growth were Ky226, Oh51A, FR9, Va35, and Tx601. The inbreds and their 45 F<sub>1</sub> hybrids were planted in the field in two P treatments, low P (0.011 ppm) and high P (0.1 ppm). Seedling dry weight, grain yield, ear length, 100 kernel weight, and P uptake of these genotypes were generally higher under high P. Significant genotype x P interaction mean squares were observed for seedling dry weight, days to anthesis, grain yield, yield components, P concentration, and P uptake. These results suggest differential response of corn genotypes to levels of P fertilization.

Combining ability analyses for this 10-entry diallel grown in low and high P were performed for P concentration, P uptake, and grain yield. General combining ability (GCA) and specific combining ability (SCA) mean squares were highly significant for these three characters at both levels of P, suggesting that both additive and nonadditive genes are important in controlling the expression of these three characters. In combined analysis, GCA x P and SCA x P interaction mean squares were highly significant for all three characters. The narrow-sense heritabilities estimated from the low P condition were 32.7% for P concentration, 35.4% for P uptake, and 31.7% for grain yield. These estimates were higher than the estimates in the high P condition.

Twelve corn cultivars of diverse genetic background were evaluated for their grain yield in the field under 10 levels of P; 0.003, 0.006,

0.012, 0.025, 0.05, 0.1, 0.2, 0.4, 0.8, and 1.6 ppm in solution. External P requirements of these corn cultivars were estimated by two regression models; a square root model and a linear-response-plateau model. Corn cultivars differed greatly in grain yield production. Although the external P requirements varied and in general ranged from 0.02 to 0.8 ppm when estimated from the square root model, the external P requirement of most corn cultivars ranged from 0.04 to 0.06 ppm when estimated by the same model. The latter range is tentatively recommended for corn production. External P requirements of these corn cultivars estimated from the linear-response-plateau model ranged from 0.02 to 0.1 ppm. In this study, cultivars with extremely low external P requirements (0.02 ppm) and high yield potential were found which suggests that it is possible to select a corn cultivar with low external P requirement and high yield for areas with soils which have low P availability.

Twenty-five corn inbreds were grown under laboratory conditions for 10 days and acid phosphatase (AP) activity of their root extracts was assayed. The AP activity of root extracts of these corn inbreds differed. Six inbreds which differed in the AP activity of their root extracts were selected to produce a diallel cross. General combining ability and specific combining ability mean squares were highly significant, suggesting that additive and nonadditive genes were important in controlling AP activity of root extracts.

Genotypes in a 4-entry diallel were grown in nutrient solution with two levels of aluminum. AP activity of intact roots was assayed. Genotypes differed in AP activity of their intact roots, suggesting that corn genotypes differ in the ability to make organic phosphate available.

Significant genotype x aluminum interaction mean squares were found for AP activity of intact roots and shoot weight. These results suggest genetic variation in corn population in their response to aluminum. GCA and SCA for AP activity of intact roots were highly significant at both levels of aluminum treatment indicating both additive and nonadditive genes were important in controlling AP activity of intact roots.

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## 1. INTRODUCTION

Phosphorus is ubiquitous in living cells and serves many functions in metabolic processes. It is absorbed from the soil in inorganic phosphate ions. Its availability in the soil solution is often the lowest of all major nutrients (Fried and Shapiro, 1961). In addition, some soils have a high phosphate sorption capacity, and thus require high amounts of additional phosphate fertilizers.

Phosphate fertilizers are little used in developing countries, and are a limiting factor in farm productivity. Phosphate amelioration of unproductive soils is economically feasible in developing countries at present, but the energy crisis may place restrictions on this practice in the future. Alternative approaches to massive phosphate fertilization for crop production on low phosphate soils must be sought.

Corn (Zea mays L.) lines are known to differ in nutrient requirements (Robertson et al., 1965; Baker et al., 1967). Breeding offers the possibility of utilizing these differential nutrient requirements to develop cultivars which show an improved growth response under low nutrient levels especially of phosphate. Evidence on the efficiency of phosphate utilization of cultivars and its inheritance is required for a successful breeding program.

This study investigates the efficiency of phosphorus utilization of corn, its inheritance, and its effect on yield. The study also includes acid phosphatase activity and tolerance to aluminum toxicity of corn genotypes.

## 2. LITERATURE REVIEW

Phosphorus has been known to be a limiting element for plants since 1855 (Bould and Hewitt, 1963). Phosphorus is required for the completion of the life cycle, is unreplacable by other elements, is involved directly in plant metabolism, and is a cell constituent (Arnon and Stout, 1939). Although it is a major nutrient, the amount required is smaller than the amounts required of nitrogen and potassium (Gauch, 1972). Plants contain phosphorus in the range of 0.15% to 0.50% of dry matter, depending upon growth conditions, stage of growth, and species.

### 2.1 Phosphorus Deficiency Symptoms

Symptoms of phosphorus deficiency are changes in leaf coloration or necrotic lesions. These symptoms may be affected by factors such as adverse climatic conditions, or disease and insect damage. Symptoms differ in different species and varieties, thus, phosphorus deficiency should be confirmed by other diagnostic criteria (Lyness, 1936; Hoffer, 1941). In corn, the symptoms are expressed in young plants as reddish purple or grayish leaves. These symptoms disappear as plants become older.

Phosphorus deficiency leads to chloroplast abnormalities. Silaeva (1966) reported that phosphorus deficiency caused poor development of lamellae in corn chloroplasts. He also found that severe phosphorus deficiency destroyed the lamellae. Later, Repka et al. (1971) reported that the number of chloroplasts were reduced and this resulted in a decreased photosynthetic rate.

Corn responds greatly to phosphorus fertilization in the early stages of growth (Hanway, 1963). Phosphorus deficient plants develop slower with

delayed silking and maturity (Noll, 1923; Glover, 1953; Peaslee et al., 1971). Phosphorus fertilization produces increased yield due to an increase in number of ears per plant, larger ear size, and larger number of harvestable plants (Colwell, 1946; Miller et al., 1946; Duncan et al., 1958). Olson and Walster (1934) and Glover (1953) reported that at low phosphorus levels there was a larger number of barren stalks.

## 2.2 Phosphorus Requirement for Plants

Phosphorus requirements have been determined from the concentration necessary to produce maximum growth in nutrient solution. Variation reported among species has been large; from 0.16 ppm for corn, sorghum, and soybean (Parker, 1927; Tidmore, 1930) to 1.0 ppm for cotton and pea (Sommer, 1936). Asher and Loneragan (1967) also reported a range from 0.03 ppm for silver grass (Vulpia myuros (L.) Gmel.) to 0.80 ppm for flatweed (Hypochoeris glabra L.) and barrel medic (Medicago tribuloides Desr.).

A better way to determine P requirement is to use the external P requirement. The external P requirement is defined as the concentration of phosphorus required in the soil solution for the plant to produce 95% of the maximum yield when other nutrients are adequate (Fox et al., 1974).

External P requirement reported include 0.05 ppm for grain sorghum (Fox, 1973), 0.20 ppm for newly planted desmodium (Desmodium aparines (Link) DC.), 0.01 ppm for established desmodium, 0.06 ppm for corn grown for grain, and 0.40 ppm for lettuce (Fox et al., 1974). Nishimoto et al. (1977) reported a range of values from 0.04 ppm for head cabbage to 0.30 ppm for lettuce and eggplant.

External P requirement for specific crops are similar on different soil types. The P requirement for lettuce on both Typic Eutrandedpt and Tropeptic Euturstopox soils, for example, was 0.30 ppm (Nishimoto et al., 1977). Similarly, the requirement in Haplustoll, Eustrustox, Gibbshumox, and Hydrandedpt soils was found to be similar (0.06 ppm) for corn (Fox et al., 1974).

External P requirements reported for some species are not always the same. Gardner (1977) reported 0.8 ppm for head lettuce, a value considerably greater than the value of 0.3 ppm reported by Nishimoto et al. (1977). The external P requirement for corn was reported to be 0.06 ppm by Fox et al. (1974), 0.13 ppm by Jones and Benson (1975), and 0.01 ppm by Fox and Kang (1978). These differences in reported external P requirement could be the result of differences in cultivars or environments. Only a few studies have compared the external P requirements between cultivars. Nishimoto et al. (1975) compared two chrysanthemum (Chrysanthemum morifolium Ramat.) cultivars. The two cultivars had the same external P requirement for the first crop of flowers but differences were found for the succeeding crop. Rendle and Kang (1977) reported external P requirements among sweet potato cultivars ranged from a low of 0.05 ppm to a high of 0.18 ppm. The cultivar with the highest P requirement had the greatest absolute yield but the cultivar with the lowest P requirement did not have the lowest yield.

### 2.3 Genetic Variation in Mineral Nutrition

Evaluations of varieties and fertilizer rates are a common practice and often reveal different varietal response to fertilizers (Stringfield and Salter, 1934; Gardener and Rathjen, 1975), but the genetics of these

varietal differences have seldom been studied due to the abundant supply of fertilizers.

These varietal differences have been categorized into differences in yield response and differences in nutrient uptake (Vose, 1963). Differential yield response has been defined as a differential ability to produce dry matter in proportion to the level of nutrient available, whereas differential nutrient uptake has been defined as a differential ability to take up nutrients during the growth period.

The genetics of a differential yield response in corn was first studied by Smith (1934). In his study, 4 inbreds were selected for good and poor responses to phosphate fertilization. The inbreds and their hybrids were evaluated under 4 levels of phosphate. He found that the hybrids responded similarly to the better parent, and concluded that response by corn to phosphorus levels was under genetic control and a good response was dominant to a poor response. Arnold (1969) studied the response of some corn populations to potassium. He evaluated four sets including parents,  $F_1$ ,  $F_2$ , backcrosses, and double crosses over a three-year period at different levels of potassium fertilization. He found a differential response to potassium in only one year and no genetic interpretation was made. Sorawat (1975) studied the response of a 6-entry corn diallel to several levels of nitrogen fertilization. He failed to detect any differences in grain yield in response to nitrogen. The only yield components to show interaction between genotype and nitrogen fertility were ear diameter and kernel weight.

Several studies in other crops have indicated that a differential yield response is controlled by a single gene pair. These studies included responses to potassium in bean (Shea et al., 1967), to boron in

celery (Pope and Munger, 1953a) and in beet (Tehrani et al., 1971), and to magnesium in celery (Pope and Munger, 1953b). Sometimes the inheritance of a differential yield response is quantitative and genetic interpretation is difficult. O'Sullivan et al. (1974) reported that the differential response to nitrogen in tomatoes was determined by a genetic system in which dominant and additive x additive interaction variances were important. Whiteaker et al. (1976) studied the differential response to phosphorus in bean and found different types of segregation from several pairs of parents. They did not quantitatively analyze the segregation data and thus conclusive genetic information was not obtained.

Differences in nutrient uptake have been measured either as the total uptake of the nutrient by the plant or as the concentration of the nutrient in an index tissue. Evidence of a differential nutrient concentration in corn was first reported by De Turk et al. (1933). They reported different phosphorus concentrations in corn seedlings. A genetic study of phosphorus content was attempted by Smith (1934) who described phosphate efficient and inefficient strains as non-responsive and responsive to the supply of phosphate, respectively. Efficient strains were able to utilize phosphate more effectively and had a higher total uptake than inefficient strains. This observation was confirmed by Lyness (1936). According to Smith (1934) and Lyness (1936), better uptake at low phosphate levels was closely related to the number of secondary roots of corn. Smith (1934) indicated that better uptake of phosphate was a dominant character.

Studies on differential nutrient uptake were reported by Robertson et al. (1965, 1968) and Clark (1974). Robertson et al. (1965) reported differential nutrient uptake in corn grown for silage. In 1968, they

also reported differential nutrient uptake in corn grown for grain. Clark (1974) found that corn inbreds differed in nutrient uptake during the early growth stages.

Detailed studies on the inheritance of nutrient concentration in corn were done by Gorsline et al. (1964). They analyzed two sets of diallel crosses for nutrient concentrations in the ear leaf and found highly significant differences between genotypes in phosphorus, potassium, magnesium, copper, zinc, and manganese concentrations. The sources of these differences were partitioned into line and deviation variances which are approximately equal to general and specific combining abilities, respectively. In most cases, the general combining ability was more important than the specific combining ability and the estimates of broad-sense heritabilities varied from 84% (for magnesium) to 5% (for aluminum). The estimated heritability for phosphorus was 84%.

The validity of these heritability estimates was confirmed by Baker et al. (1967). They found good agreement between the predicted and observed concentrations of several nutrients in the hybrids between parents used by Gorsline. Differences in the concentration of nutrients in the ear leaf were reported to be heritable and controlled by a few major genes (Gorsline et al., 1968). Naismith et al. (1974) reported that genes controlling phosphorus concentration in the ear leaf were on the short arm of chromosome 9.

#### 2.4 Aluminum Toxicity and Aluminum Tolerance

Low availability of phosphorus in tropical soils is often related to soil acidity and high solubility of aluminum. High aluminum reduces the growth of plant roots. The reduction in root growth reduces the

efficiency of plants in utilizing phosphorus in soil. Therefore, plants with high tolerance to aluminum toxicity are preferred.

Differences in varietal tolerance to aluminum toxicity have been observed. Vose and Randall (1962) reported that species and varieties varied in aluminum tolerance, and suggested the possibility of selecting for aluminum tolerance. Field evidence for differential tolerance to aluminum toxicity is usually obtained from liming experiments (Reid et al., 1969; Lutz et al., 1971; Foy et al., 1973). Reid et al. (1969) surveyed 138 varieties of winter barley at several levels of lime. They found a differential response to lime with the response due mainly to the yield variation at low lime treatments. In corn, Lutz et al. (1971) reported differential dry matter production of inbreds and hybrids at low pH. Later, Clark (1974) classified corn inbreds according to their sensitivity to aluminum toxicity. However, Clark did not show magnitude of the differences.

Recently, Rhue and Grogan (1977) screened several northern corn inbreds for their tolerance to aluminum toxicity. They utilized nutrient solutions with several levels of calcium and magnesium and found that by varying the calcium concentration in the nutrient solution, differential tolerance to aluminum concentrations was observed among the inbreds. Similar results were observed by varying magnesium concentrations. This method of screening correlated well with the response of corn in acid soils in pot experiments. Utilizing nutrient solution methods, Rhue and Grogan identified inbreds Val7 and R158 as tolerant to aluminum and several inbreds such as B37, C0192, and NY511 were classified as sensitive to aluminum. Rhue and Grogan (1977) also suggested that tolerance to aluminum in this set of inbreds was heritable. Results suggested that

aluminum tolerance was controlled by a single dominant locus. However, the nature of inheritance of aluminum tolerance still needs to be confirmed.

## 2.5 Acid Phosphatase Activity

Several enzymes of animals and plants can hydrolyze the phosphate group from phosphomonoesters and phosphodiesteres. These enzymes are phosphatases which are subdivided into two groups according to their optimum pH. The first subgroup includes alkaline phosphatases that have their optimum activity in the alkaline pH range. The second subgroup comprises the acid phosphatases which have optimum activity in the acid pH range. There are two major sites of acid phosphatase activity, intracellular and extracellular (Schmidt and Laskowski, 1961; Patni and Aaronson, 1974). Intracellular acid phosphatases are localized in lysosomes in animal cells (Wattiaux et al., 1956), and in vacuoles in plant cells (Berjack, 1972). Extracellular acid phosphatases may be bound to the cell walls as reported in Spirodela (Bielecki and Johnson, 1972) and of roots of wheat plants (Hasegawa et al., 1975). These extracellular acid phosphatases of plants are able to change organic phosphate in the growing media into phosphate which is available for uptake.

The activity of acid phosphatase is inhibited by phosphate ions, an end product of the hydrolysis. Enzyme activity which is inhibited by its end product is defined as repressible. Repressible acid phosphatase was first reported in yeast (Schmidt et al., 1956). Repressible acid phosphatase has been studied in plants. Phosphatase activity in S. oligorrhiza (Kurz) Hegelm. increased 25 times in phosphate deficient

media. The increase in enzyme activity was due to the synthesis of a new inducible acid phosphatase as well as an increase in the activity of the repressible acid phosphatase. The rate of increase in activity was greater for the repressible enzyme (Reid and Bielecki, 1970).

Higher plants such as corn and tomato were reported to have the ability to hydrolyze calcium glycerophosphate in nutrient solution (Rogers et al., 1940). This hydrolyzing ability was reported to be greater for phosphorus deficient plants (Rogers et al., 1942). However, Ridge and Rovira (1971) reported trace activity of a phosphatase in intact roots of wheat grown in nutrient solution well supplied with phosphorus. Low phosphatase activity was possibly due to the inhibition or repression of the enzyme by inorganic phosphate (Clark, 1975).

Genetic control of plant enzymes has been extensively studied through electrophoretic separation of isozymes (Scandalios, 1969). Quantitative differences in enzyme activities are controlled genetically and are affected by factors such as substrate, end products, and environment. Genetic studies of quantitative activities of enzymes have been conducted on nitrate reductase (Warner et al., 1969), phosphofructokinase (Luthe and Schrader, 1974), and glucose-6-phosphate dehydrogenase (Schrader, 1974).

Nitrate reductase activity in corn was reported to be controlled by two major genes. One gene controlled the rate of nitrate reductase synthesis and the other gene controlled the turnover rate. This type of gene action resulted in an expression of heterosis in nitrate reductase activity in a hybrid (Schrader et al., 1966; Warner et al., 1969).

Genetic variation of acid phosphatase in corn leaves was reported by Rigo (1966). He found variation in acid phosphatase activity among

inbreds and hybrids. Clark and Brown (1974) reported variation in extracellular acid phosphatase activity in corn roots; they found that phosphatase activity was greater when the plants were grown under phosphorus stress.

### 3. MATERIALS AND METHODS

#### 3.1 Preliminary Greenhouse and Field Experiments

Preliminary screening for differential growth under two levels of P in corn inbreds was done in the greenhouse using soil from Waimanalo Research Station which is classified as a Typic Haplustoll subgroup. It is a silty clay with a pH of 6.5 (1:1, soil: water).

The preliminary screening included 28 inbreds: 74-1721, 74-1610, 74-1629, 38-11, B14A, B37, C123, CM104, CM105, CM109, CM111, F44, H55, H84, H91, H93, H95, K148, Mo17, N28, Oh43, Oh51A, Oh545, PH9, SC301, Tx601, Va35, and W64A. These inbreds were grown without replication in 6-inch pots at two levels of P, no addition (low P) and with P added to provide 0.06 ppm P in soil solution (high P). The required amount of P to be added was determined by the phosphate adsorption curve method (see Appendix B). Phosphorus was applied as  $\text{Ca}(\text{H}_2\text{PO}_4)_2$  and mixed with the soil before potting. Seven seeds of each inbred were planted per pot. After germination nitrogen and potassium were added in solution at a rate equivalent to 90 kg/ha. Plants were watered daily as needed. At the end of 3 weeks, dry weight was measured.

Based on the results of the unreplicated pot test, 15 inbreds (74-1721, 74-1610, 38-11, B37, C123, CM104, F44, H55, H84, H91, H95, K148, Mo17, PH9, and W64A) were selected for further study in a replicated test. This time the pots were arranged in a randomized block design with 2 replications and the plants were harvested at 4 weeks.

Corn grown under low P was also observed in a planting made at the Waimanalo Research Station, located near sea level on the island of Oahu, on November 11, 1975. This planting included all 28 inbreds used in the

first greenhouse screening plus 10 others; A619, A632, Ant. 2, CI21E, FR9, Ga203, Ky226, M14, Mp68:616, and T232. No P fertilizer was added. Nitrogen and potassium were applied at the rate of 90 kg N and K/ha.

On the basis of the results of these three preliminary tests, 10 inbreds were selected to be the parents in a diallel cross for investigating the genetics of phosphorus response in corn (Table 1).

Table 1. List of corn inbreds in the diallel cross

| Inbred      | Growth under<br>P stress | Base population                        |
|-------------|--------------------------|--|
| 1. Mp68:616 | good                     | Ant Group 2, S4                        |
| 2. PH9      | good                     | Philippine Yellow Flint                |
| 3. CI21E    | good                     | CI21 x Hy                              |
| 4. B14A     | good                     | Version of B14 (Iowa Stiff Stalk Syn.) |
| 5. CM104    | good                     | Sib-line from Amarillo Theobromina     |
| 6. Ky226    | poor                     | NCI a double-double cross x Coahuila   |
| 7. Oh51A    | poor                     | (Oh17 x Oh51) x Oh51                   |
| 8. FR9      | poor                     | WF9 Ht                                 |
| 9. Va35     | poor                     | (C103 x T8) x T8                       |
| 10. Tx601   | poor                     | "Yellow Tuxpan" (of Tuxpeño)           |

### 3.2 Evaluation of a 10-entry Diallel at Two Levels of Phosphate Fertilizer

A diallel cross of the 10 inbreds selected on the basis of their growth under low P in the preliminary field experiment was planted at Waimanalo Research Station on November 4, 1976 for a winter test and again on March 24, 1977 for a summer test.

*P was removed (to 0.011 ppm) by 3 consecutive com  
platings & no added P — no data? 14*

The experimental site was plowed and disked. Nitrogen and potassium fertilizer as urea and muriate of potash were incorporated before planting at the rate of 90 kg of N and of K/ha, respectively. Approximately 140 kg N/ha as urea was applied as a side dressing after the plants were thinned (plants were approximately 30 cm tall).

Two levels of phosphate in soil solution were established, 0.011 ppm P (low P) and 0.1 ppm P (high P). The high P in soil solution was created by fertilizing at a rate equivalent to 1500 kg P/ha. The phosphate fertilizer was incorporated before planting.

*What was the soil before?*

Three seeds were planted per hill with spacing of 19 cm between hills and 75 cm between rows. Plants were thinned to one plant per hill at 4 weeks after planting. Irrigation water was supplied by overhead sprinkler as necessary. The experiment was in a split-plot design with 3 replications. Phosphate treatments were assigned to the main-plots and genotypes were randomly assigned to the sub-plots.

Data collected included:

1. Seedling dry weight. Plants were harvested at 4 weeks and dried in oven at 70°C before weighing. Dry weights were based on a composite weight of 4 plants.
2. Days to silking. The mean number of days from planting to silking.
3. Days to anthesis. The mean number of days from planting to the first day of pollen shedding. Days to anthesis was collected for the summer planting only.
4. Ear height. Height in cm from the soil surface to the node of the top ear, mean of 10 plants.
5. Plant height. Height in cm from soil surface to tassel tip, mean of 10 plants.

6. Grain yield. Grain weight in metric tons/ha adjusted to 15.5% moisture.

7. Yield components

- a. Ear weight. Weight in metric tons/ha.
- b. Ear length. The mean of all top ears harvested (cm).
- c. Kernels per row. Mean kernels for a row selected at random from all ears in 7b.
- d. Row number. The mean of number of rows of all ears in 7b.
- e. Kernel depth. Ten randomly selected kernels were measured using a vernier caliper and averaged.
- f. Kernel weight. Weight of 100 kernels (gm).
- g. Number of ears. Number of ears per 10 plants.

8. P concentration in seedlings. Plants collected from the winter planting only were analyzed for P content (see Appendix C for method of P analysis). P concentration was calculated as a percentage of P in the sample used.

9. P uptake by seedlings. P uptake was calculated by multiplying P concentration in seedlings by seedling dry weight. P uptake was expressed as mg P/4 plants.

Analysis of variance based on a split-plot design was performed for all characters studied. The data were analyzed on the basis of plot means.

Three measurements; P concentration, P uptake, and grain yield, were analyzed by Griffing's diallel analysis method 2 (parents and one set of  $F_1$  hybrids), model 1 and 2 (Griffing, 1956). In model 1 (Fixed Model), the parents are chosen as a fixed sample. The general combining ability effects (GCA) and specific combining ability effects (SCA) can be computed. In model 2 (Random Model), the parents are assumed to be a

random sample from the population. The genetic and environmental variances can be computed with this model.

### 3.3 Study of External Phosphate Requirement

An experiment for assessing the external P requirement was conducted at the Poamoho Research Station, located on the northern part of the island of Oahu at 200 m elevation. The soil has been described as a Tropeptic Eustrustox subgroup, with a clayey texture and with a pH of 5 (1:1 soil:water ratio). The experimental site was formerly a slope but has been graded to two bench terraces which resulted in each terrace having a "cut end" and "filled end". These two ends were treated separately in obtaining phosphate sorption curves and in estimating phosphate requirement of the soil.

The desired levels of P in solution included in this experiment were 0.003, 0.006, 0.012, 0.025, 0.05, 0.1, 0.2, 0.4, 0.8, and 1.6 ppm P. However, some of these levels could not be established as indicated by the actual P in solution in Table 2. The levels of phosphate were arranged in an augmented block design (Federer, 1956). The phosphate levels of 0.012, 0.025, 0.05, and 0.1 ppm P were replicated three times. Unreplicated P levels augmented in each replication were 0.003 and 0.4 in Rep. I, 0.006 and 0.2 in Rep. II, and 0.8 and 1.6 in Rep. III.

Twelve cultivars were used in this experiment, 9 hybrids and 3 varieties (Table 3). Hybrid H610, H788, and varieties White Carimagua and Yellow Carimagua were selected on the basis of previous works. The other 8 cultivars were chosen at random.

The required amounts of phosphate (treble superphosphate) were broadcast and incorporated to a depth of 15 cm. Potash was incorporated

Table 2. The desired levels of P in solution and the actual P in solution in experimental plots at Poamoho Research Station, 1977

| Desired P in solution | Actual P in Solution |             |
|-----------------------|----------------------|-------------|
|                       | Cut end*             | Filled end* |
| 0.003                 | 0.003                | 0.006       |
| 0.006                 | 0.007                | 0.03        |
| 0.012                 | I**                  | 0.014       |
|                       | II                   | 0.013       |
|                       | III                  | 0.012       |
| 0.025                 | I                    | 0.025       |
|                       | II                   | 0.025       |
|                       | III                  | 0.025       |
| 0.05                  | I                    | 0.05        |
|                       | II                   | 0.05        |
|                       | III                  | 0.05        |
| 0.1                   | I                    | 0.1         |
|                       | II                   | 0.1         |
|                       | III                  | 0.1         |
| 0.2                   |                      | 0.2         |
| 0.4                   |                      | 0.4         |
| 0.8***                |                      | 0.8         |
| 1.6                   |                      | 1.6         |

\*Cut and filled ends resulting from cutting the slope into two bench terraces.

\*\*Replication number.

\*\*\*Formerly a control plot.

Table 3. Source and description of corn cultivars used in the external P requirement experiment

| Name                  | Description | Pedigree or source                  |
|-----------------------|-------------|-------------------------------------|
| 1. H610               | Hybrid      | B14A x Ant. 2, UH hybrid            |
| 2. H788               | Hybrid      | (CM111 x CI21E) x Ant. 2, UH hybrid |
| 3. H638               | Hybrid      | CM111 x Oh545, UH hybrid            |
| 4. CI21E x Ky226      | Hybrid      | Diallel cross (sec. 3.1)            |
| 5. Ky226 x Oh43       | Hybrid      | UH hybrid                           |
| 6. Mp68:616 x Tx601   | Hybrid      | Diallel cross (sec. 3.1)            |
| 7. CM104 x Va35       | Hybrid      | Diallel cross (sec. 3.1)            |
| 8. CM104 x PH9        | Hybrid      | Diallel cross (sec. 3.1)            |
| 9. X304C              | Hybrid      | Pioneer hybrid for the tropics      |
| 10. Antigua Composite | Variety     | Composite out of Antigua 2D         |
| 11. White Carimagua   | Variety     | CIAT, tolerance to Aluminum         |
| 12. Yellow Carimagua  | Variety     | CIAT, sensitive to Aluminum         |

with the phosphate at the rate of 50 kg/ha. Two corn seeds were planted per hill on March 10, 1977. Spacing was 38 cm between rows and 44 cm between hills. At 5 weeks, plants were thinned to one plant per hill leaving approximately 60,000 plants/ha. Nitrogen fertilizer was applied as urea in the irrigation furrows in 3 applications at the rate of 75, 112, and 112 kg N/ha at 1, 5, and 8 weeks after planting. The experimental plots were irrigated when necessary. Both chemical and mechanical weed control measures were practiced.

Data collected from the experiment included plant height at 4 weeks, dry weight at 5 weeks, days to 50% siling, ear height, plant height, ear length, and grain yield. The data were measured in the same way as that for the 10-entry diallel.

A regression analysis of grain yield on level of P in solution was performed for each cultivar and the external P requirements were estimated from this analysis. External P requirements were also estimated with the linear-response-plateau model (Waugh et al., 1975).

### 3.4 Acid Phosphatase Activity and Aluminum Stress Studies

#### 3.4.1 Acid Phosphatase Activity of Root Extracts

Seeds of 25 inbreds; 38-11, A632, B14A, B37, C123, CI21E, CM104, CM109, CM111, FR9, Ga203, H93, H95, Ky226, Mo17, Mp68:616, N28, Oh43, Oh51A, Oh545, PH9, SC301, Tx601, Va35, and W64A, were surface sterilized in 5% chlorox for 10 minutes prior to germination on moistened papers at room temperature. On the tenth day, the roots were cut from the seedlings, blotted dry, and immediately weighed.

The acid phosphatase enzymes (AP) were extracted by macerating the roots in distilled water, increasing the volume to 15 ml, and filtering with No. 1 Whatman Filter Paper. The filtrates were kept in the freezer until all extractions were completed. These filtrates were assayed for AP activity and protein content.

Acid phosphatase activity was determined by a modified Sommer's method (Haskins, 1955) as follows: First, 1 ml of 0.01 M disodium p-nitrophenyl phosphate (pNPP) is added to 4 ml of buffer (0.05 M citric acid, 0.075 M ethylene diamine, pH 4); next, 0.5 ml of extracted enzyme filtrate is added; it is incubated for 10 minutes at 37° - 39°C, and last, 1 ml of 1 N NaOH is added to stop the reaction. The incubation

tubes are allowed to cool to room temperature and the optical density is read at 410 nm on a spectrophotometer. The reading is converted to  $\mu$ moles p-nitrophenol (pNP) by comparison with standardized pNP values. The activity can be expressed as  $\mu$ moles pNP/gm fresh weight/hr (fresh weight basis) or as  $\mu$ moles pNP/mg protein/hr (specific activity).

For the latter, protein content must also be determined. This was determined by the method of Lowry et al. (1951). One ml of solution A (0.5%  $\text{CuSO}_4$  in 1% sodium tartrate) is added to 50 ml of solution B (2%  $\text{NaCO}_3$  in 0.1 N NaOH) to make solution C and allowed to hydrolyze for 15 minutes after which 0.15 ml of Folin-Ciocalteu reagent is added. After 30 minutes the optical density of the mixture is read on a spectrophotometer at 500  $\mu\text{m}$ . Crystalline albumin bovine is used as the standard.

On the basis of their AP activities, 6 inbreds (B14A, GM104, Ky226, Mp68:616, Tx601, and Va35) were selected to be the parents in a diallel cross to be analyzed for the inheritance of AP activity.

Both experiments were arranged in randomized complete block designs with 4 replications for the original inbreds and 3 replications for the entry in the diallel cross.

#### 3.4.2 Acid Phosphatase Activity of Intact Roots

A 4-entry diallel involving Ky226, Mp68:616, Tx601, and Va35 (parents chosen randomly from a 10-entry diallel in 3.1) were germinated for one week in room condition after which eight seedlings selected for uniformity, were transferred without the attached seed to individual 9-liter plastic pots containing nutrient solution. The nutrient solution consisted of 39 mg  $\text{NO}_3\text{-N}$ , 10 mg  $\text{NH}_4\text{-N}$ , 3 mg P, 55 mg K, 102 mg Ca, 15 mg Mg, 14 mg S, 15 mg Cl, 3 mg Fe (FeHEDTA), 0.36 mg Mn,

0.02 mg B, 0.11 mg Zn, 0.03 mg Cu, and 0.06 mg Mo per liter, pH adjusted to 5. Two levels of Al (0 and 6 mg/liter) were used to examine the effect of Al on AP activity. Plants were grown in growth chambers at  $25^{\circ} \pm 2^{\circ}\text{C}$  under 16 hr of light. Pots were arranged in a randomized block design with two replications. One growth chamber constituted one replicate.

At the end of one week in nutrient solution, AP activity of intact roots was determined on 4 plants, individually. The method of determination of AP activity of intact roots is as follow: First, the assay solution consisting of the nutrient solution used in the growth chamber at  $\frac{1}{2}$  strength with the omission of P and Al is prepared, then, the substrate of AP enzyme (pNPP) is added to the assay solution to the concentration of 0.2 mM pNPP and pH is adjusted to 4. Second, 4 seedlings are removed from the 9-liter plastic pots and rinsed with distilled water. Each seedling is introduced into a beaker containing 250 ml of assay solution. At 15, 30, and 45 minutes, 3 ml samples are drawn from each beaker and put into tubes containing 2 ml of 2 N NaOH. The optical density is read at 410 nm. Concentrations of pNP were calculated with reference to a standard curve for pNP. After determination of AP activity, seedlings were removed from the assay solution and cut into two parts, shoot and roots, and dried in the oven at  $70^{\circ}\text{C}$  for one week. The dried weights were obtained. The AP activity is expressed as  $\mu$  moles pNP/gm of root dry weight/hr.

At the end of two weeks in nutrient solution, AP activity of intact roots was determined on the other 4 plants in a similar manner.

Data on AP activity of intact roots was subjected to an analysis of variance based on the fixed model. Combining ability analysis based on Griffing's method 2 (parents and  $F_1$  included) model 1 (fixed model) was also applied to this set of data.

#### 4. GENOTYPIC RESPONSE TO PHOSPHATE

Responses of corn to P stress were studied under greenhouse and field conditions in the same soil. Two levels of P were used, low P (0.011 ppm P in solution) and high P (0.1 ppm P in solution). Greenhouse experiments were carried out in pots using 28 inbreds, of which 15 were advanced to replicated trials. The field experiments involving a 10-entry diallel were carried out at the Waimanalo Research Station in a split-plot design with P treatments as main plots.

##### 4.1 Results and Discussion

###### 4.1.1 Preliminary Screening

Results from the preliminary experiment are summarized in Appendix A1. In this experiment, phosphate (P) fertilization increased dry matter production of inbreds significantly ( $t = 9.36^{**}$ ) in 3-week old plants. The greatest increase of 131% was observed in inbred 38-11. Large increases were also observed in inbreds 74-1629, H95, and H91. Several inbreds appeared to be tolerant to low P and showed small response to P fertilization. These inbreds included H55, K148, 74-1610, and Oh51A. However, these data must be considered as preliminary in the absence of replication.

A replicated pot experiment was conducted and the result showed an average increase of 48% in dry weight at 4 weeks (Table 4). The analysis of variance indicated that inbreds differed significantly (Table 5). Due to the absence of a G x P interaction, however, the inbreds could be said to respond similarly to P. Although inbred H55 showed a large response to P in this experiment, it did not respond in the preliminary test (Appendix A1).

Table 4. Dry weight of corn grown in pots for four weeks

| Inbreds | Low P                 | High P | % increase |
|---------|-----------------------|--------|------------|
|         | ———— gm/4 plants ———— |        |            |
| 74-1721 | 3.8 <sup>a</sup>      | 4.7 -  | 24         |
| 74-1610 | 3.2                   | 4.4    | 38         |
| 38-11   | 2.9                   | 4.3    | 48         |
| B37     | 3.4                   | 5.8    | 71         |
| C123    | 3.9                   | 5.2    | 33         |
| CM104   | 3.8                   | 5.9    | 55         |
| F44     | 2.8                   | 3.6    | 29         |
| H55     | 2.9                   | 4.8 -  | 66         |
| H84     | 4.3                   | 7.0    | 63         |
| H91     | 2.4                   | 4.0    | 67         |
| H95     | 3.3                   | 4.9 -  | 48         |
| K148    | 2.9                   | 4.0    | 38         |
| Mo17    | 4.9                   | 6.4    | 31         |
| PH9     | 3.1                   | 4.0    | 29         |
| W64A    | 2.9                   | 4.6 -  | 59         |
| Average | 3.3                   | 4.9    | 48         |

<sup>a</sup>Data are the average of 2 pots ("rep")

Table 5. Analysis of variance of dry weight of corn grown in pots for four weeks

| Source         | df | Mean squares        |
|----------------|----|---------------------|
| Rep            | 1  | 5.57 <sup>**a</sup> |
| pb             | 1  | 5.52 <sup>**</sup>  |
| G <sup>b</sup> | 14 | 84.61 <sup>**</sup> |
| G x P          | 14 | .74                 |
| Error          | 29 | 1.16                |

<sup>a</sup>\* and <sup>\*\*</sup> in this and subsequent tables indicate significance at 5% and 1% levels, respectively.

<sup>b</sup>P and G in this and subsequent tables refer to Phosphorus and Genotype, respectively.

#### 4.1.2 Response of a 10-entry Diallel in the Field

Seedling dry weights of the 10-entry diallel grown under low P (0.011 ppm P) and high P (0.1 ppm P) are summarized in Appendix A2. The analysis of the data (Table 6) indicated that the effect of P was highly significant in the winter planting with a 106% mean increase in seedling dry weight. The P mean square in the summer planting was not significant although the mean increase in seedling dry weight was 88% and in no instance did dry weights at low P exceed those at high P. Differences among the 55 genotypes were highly significant for both plantings. The G x P interaction was significant at the 1% level for the winter planting and significant at the 5% level for the summer planting indicating differences in genotypic response to high P in both plantings.

Based on the BLSD (Bayes Least Significant Difference) test, the seedling dry weight of inbreds PH9, CM104, CI21E, FR9, and 30 of the 45 hybrids showed significant response to P in the winter planting. No specific genetic patterns were apparent in the data. However, most crosses involving Mp68:616, K6226, CM104, FR9, PH9, and Va35 responded significantly to P. In the summer planting, CM104 and 10 of the 45 hybrids responded significantly to P. The magnitude of response to P by all inbreds except CM104 was similar for both plantings. The similarity of the magnitude of response of inbreds to P and the differential increase in seedling dry weight of 10 parental inbreds in both summer and winter planting are presented in Figure 1.

Days to silking for both winter and summer plantings are summarized in Appendix A3. The analyses of variance are presented in Table 7. In both plantings, the P and G mean squares were highly significant. The absence of G x P interaction indicated that all

Table 6. Analysis of variance for corn dry weight grown at two seasons at two levels of P for four weeks (mean data in Appendix A2)

| Source    | Winter |              | Summer |              |
|-----------|--------|--------------|--------|--------------|
|           | df     | Mean squares | df     | Mean squares |
| Rep       | 2      | 36.1         | 1      | 13.2         |
| P         | 1      | 931.2**      | 1      | 1122.9       |
| Error (a) | 2      | 13.5         | 1      | 97.3         |
| G         | 54     | 12.2**       | 54     | 28.6**       |
| G x P     | 54     | 6.2**        | 54     | 7.9*         |
| Error (b) | 216    | 2.2          | 108    | 5.5          |

*Handwritten notes: "only 2 reps" next to Summer df=1; "1:1 load sum" next to Summer Mean squares=97.3.*

Table 7. Analysis of variance for days to silking of corn grown at two seasons at two levels of P (mean data in Appendix A3)

| Source    | df  | Mean squares |         |
|-----------|-----|--------------|---------|
|           |     | Winter       | Summer  |
| Rep       | 2   | 64.5         | 52.8    |
| P         | 1   | 1265.4**     | 925.4** |
| Error (a) | 2   | 41.0         | 4.8     |
| G         | 54  | 94.0**       | 83.0**  |
| G x P     | 54  | 3.9          | 3.1     |
| Error (b) | 216 | 4.4          | 2.2     |

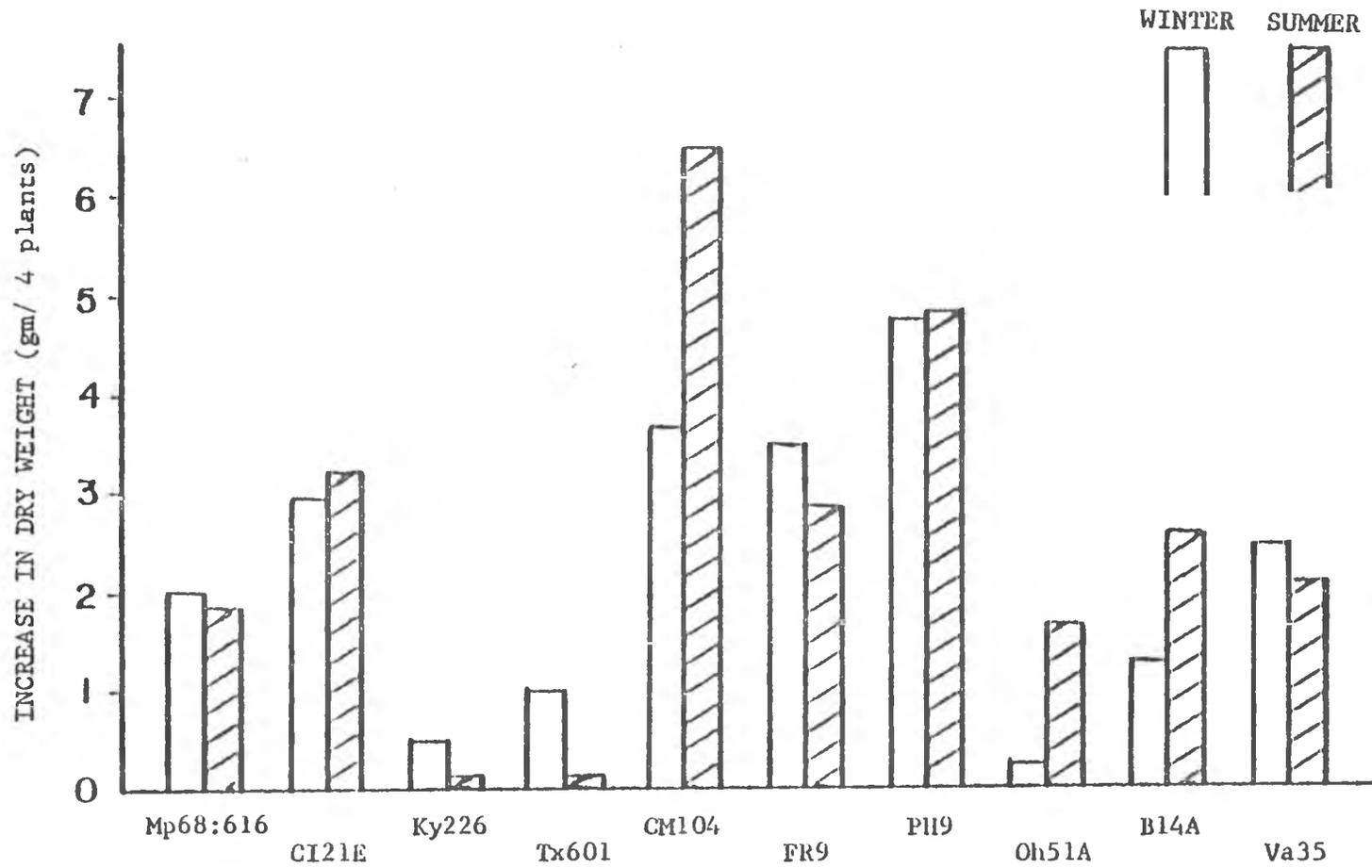


Figure 1. Differential increase in dry weight of inbreds.

genotypes behaved similarly in their responds to P. Mean silking date of the low P treatment was delayed by 3.9 days in the winter and 3.3 days in the summer.

Days to anthesis from the summer planting are presented in Appendix A3. The analysis of variance on a split-plot design of days to anthesis (Table 8) indicated highly significant P and G mean squares. The G x P interaction was small but still highly significant, indicating a differential response of genotypes in days to anthesis to low P. Days to anthesis of all inbreds, except Va35, were significantly delayed by low P. The longest delay of 6 days was observed in inbred FR9. The average delay in anthesis over all genotypes was 3 days. Days to anthesis of all the crosses involving Va35 were also delayed significantly by P stress.

Ear and plant height data of winter and summer plantings are summarized in Appendix A4. The analysis of variance on a split-plot design are presented separately for each season (Table 9). The effect of P was not significant for ear and plant height in the winter planting, although heights were consistently greater on high P plots. Both ear and plant height increased significantly in the summer planting. Genotypic differences in ear and plant heights were highly significant in both plantings. The G x P interaction mean squares were small and not significant.

The winter planting was severely attacked by mosaic and later by birds so no winter yield data were obtained. Mean grain yield and yield components data from the summer planting are summarized in Appendix A5 to A7. These summaries included grain yield, ear weight, ear length, number of rows of kernels, kernels per row, kernel depth,

Table 8. Analysis of variance for days to anthesis of corn grown in the summer under two levels of P (mean data in Appendix A3)

| Source    | df  | Mean squares |
|-----------|-----|--------------|
| Rep       | 2   | 52.2         |
| P         | 1   | 714.3**      |
| Error (a) | 2   | 11.2         |
| G         | 54  | 60.2**       |
| G x P     | 54  | 2.1**        |
| Error (b) | 216 | 1.2          |

Table 9. Analysis of variance for corn ear height and plant height grown under two levels of P in two seasons (mean data in Appendix A4)

| Source    | df  | Mean squares |        |              |        |
|-----------|-----|--------------|--------|--------------|--------|
|           |     | Ear height   |        | Plant height |        |
|           |     | Winter       | Summer | Winter       | Summer |
| Rep       | 2   | 3069         | 1384   | 3343         | 5038   |
| P         | 1   | 15614        | 13047* | 11916        | 32920* |
| Error (a) | 2   | 1002         | 430    | 1020         | 836    |
| G         | 54  | 1365**       | 2135** | 3225**       | 3343** |
| G x P     | 54  | 158          | 88     | 321          | 232    |
| Error (b) | 216 | 126          | 97     | 320          | 198    |

100-kernel weight and ears per 10 plants. Analyses of variance in the split-plot design for these grain yields and yield components are presented in Table 10.

The analyses of variance for yield and yield components showed that genotypes differed significantly at the 1% level for all characters (Table 10). Only the P mean square for ear length and 100 kernel weight were significantly different at the 5% level. However, the increases in yield and yield components were observed in nearly all genotypes. The more important result was the significant G x P interaction which was found for all characters except number of rows of kernels and number of ears per 10 plants. It should be noted that the genotypes interacted with P for the characters with large variation such as grain yield and ear length. The genotypes did not interact with P for characters with low variability such as number of rows of kernels and number of ears per 10 plants. The average increase for ear length and 100 kernel weight over all genotypes (Appendix A6 and A7) was 1.0 cm and 3.1 gm, respectively, and these increases were significant at the 5% level. Although the effect of P was not significant for grain yield, all genotypes except CM104, CM104 x PH9, and Oh51A x Tx601, had a higher grain yield under high P. Based on the BLSD of the G x P interaction, a significant increase in yield due to high P was observed for the inbreds FR9 and PH9 and for 13 hybrids. Only three crosses out of nine involving FR9 and PH9 had a significant response to P. The greatest response was found in hybrid B14A x FR9 which showed an increase of 4.84 metric tons/ha. A slight decrease in yield with increasing P was observed for the hybrid CM104 x PH9. The greatest yield under high P, 14.06 metric tons/ha, was obtained from hybrid CM104 x Tx601. The

Table 10. Analyses of variance for grain yield and yield components of corn grown at two levels of P, summer planting (mean data in Appendix A5, A6, and A7)

| Source    | df  | Mean squares |            |
|-----------|-----|--------------|------------|
|           |     | Grain yield  | Ear weight |
| Rep       | 2   | 14.73        | 24.09      |
| P         | 1   | 238.49       | 312.55     |
| Error (a) | 2   | 17.49        | 18.18      |
| G         | 54  | 47.90**      | 67.83**    |
| G x P     | 54  | 2.49**       | 3.03**     |
| Error (b) | 216 | 1.30         | 1.62       |

| Source    | df  | Mean squares |                 |            |              |               |               |
|-----------|-----|--------------|-----------------|------------|--------------|---------------|---------------|
|           |     | Ear length   | Kernels per row | Row number | Kernel depth | Kernel weight | Ears/10 plant |
| Rep       | 2   | 13.918       | 135.84          | 2.752      | 5.282        | 131.81        | 1.395         |
| P         | 1   | 89.128*      | 292.72          | 23.949     | 20.926       | 769.74*       | 9.200         |
| Error (a) | 2   | 5.801        | 114.33          | 11.079     | 4.364        | 24.03         | 5.306         |
| G         | 54  | 29.426**     | 217.34**        | 8.806**    | 3.994**      | 122.08**      | 9.168**       |
| G x P     | 54  | 2.035**      | 10.83*          | .742       | .363**       | 11.03**       | 1.567         |
| Error (b) | 216 | .975         | 7.20            | .745       | .163         | 6.09          | 1.461         |

highest yield under low P, 12.83 metric tons/ha, was obtained from hybrid Ky226 x Tx601.

The means of P concentration and P uptake of a 10-entry diallel grown under low and high P in the winter planting are summarized in Tables 11 and 12, respectively. The P concentrations are presented as percent of dry matter in the seedlings and P uptake, the product of P concentration and dry matter production, expressed as mg P/4 plants. The data for P uptake were calculated from the data on P concentration (Table 11) and dry matter yield (Appendix A2). The analyses of variance of P concentration and P uptake (Table 13) showed that high soil P did not have a significant effect on P concentration in the plant but the total uptake in the plant increased significantly under high P treatment.

Although, there was no significant effect of soil P on P concentration in the plant, P concentrations in all genotypes were consistently higher under high P. It should be noted that the test of the P effect was very poor with only 2 degree of freedom. More important was the highly significant G x P interaction mean square. The grand means for P concentration of seedlings grown under low and high P were 0.239% and 0.360%, respectively. Parent and  $F_1$  means under low P were 0.213% and 0.245% of dry matter, respectively, while they were 0.318% and 0.369% under the high P. The range of P concentration in the inbred was from 0.174% to 0.287% for the low P and from 0.247% to 0.389% for the high P. Three parental lines, Ky226, PH9, and B14A, had a high P concentration when grown under low P. The highest P concentration under low P was obtained in PH9 which was developed from Philippine Yellow Flint. This line also had a high P concentration under high P. The inbred with lowest P concentration under low P also had the lowest array

Table 11. Phosphorus concentrations in corn seedlings (in percent of plant dry matter) grown under low P (upper value) and high P (lower value) for four weeks

| Parents  | Mp<br>68:616 | CI21E        | Ky226        | Tx601        | CM104        | FR9          | PH9          | Oh51A        | B14A         | Va35         | Array<br>means |
|----------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|----------------|
| Mp68:616 | .204<br>.305 | .236<br>.351 | .262<br>.340 | .228<br>.352 | .275<br>.381 | .210<br>.445 | .244<br>.404 | .264<br>.327 | .232<br>.354 | .211<br>.417 | .237<br>.368   |
| CI21E    |              | .203<br>.398 | .222<br>.476 | .243<br>.357 | .300<br>.393 | .239<br>.316 | .269<br>.415 | .245<br>.401 | .232<br>.386 | .210<br>.363 | .240<br>.376   |
| Ky226    |              |              | .235<br>.280 | .287<br>.376 | .267<br>.432 | .262<br>.330 | .314<br>.389 | .247<br>.305 | .214<br>.364 | .224<br>.427 | .253<br>.372   |
| Tx601    |              |              |              | .205<br>.298 | .202<br>.382 | .267<br>.369 | .271<br>.366 | .192<br>.406 | .204<br>.290 | .221<br>.330 | .232<br>.343   |
| CM104    |              |              |              |              | .217<br>.362 | .238<br>.410 | .269<br>.346 | .220<br>.358 | .275<br>.308 | .232<br>.328 | .249<br>.370   |
| FR9      |              |              |              |              |              | .176<br>.325 | .317<br>.312 | .218<br>.405 | .290<br>.371 | .216<br>.409 | .243<br>.369   |
| PH9      |              |              |              |              |              |              | .287<br>.375 | .297<br>.408 | .287<br>.344 | .226<br>.374 | .278<br>.363   |
| Oh51A    |              |              |              |              |              |              |              | .196<br>.282 | .197<br>.318 | .200<br>.283 | .228<br>.349   |
| B14A     |              |              |              |              |              |              |              |              | .241<br>.247 | .218<br>.279 | .239<br>.326   |
| Va35     |              |              |              |              |              |              |              |              |              | .174<br>.312 | .213<br>.352   |

Low P; Grand mean = .239, Parent = .213,  $F_1$  = .245  
 High P; Grand mean = .360, Parent = .318,  $F_1$  = .369

Table 12. Phosphorus uptake in corn seedlings grown under low P (upper value) and high P (lower value) for four weeks (mg P/4 plants)

| Parents  | Mp     |       |       |       |       |       |       |       |       |       | Array means |
|----------|--------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------------|
|          | 68:616 | CI21E | Ky226 | Tx601 | CM104 | FR9   | PH9   | Oh51A | V14A  | Va35  |             |
| Mp68:616 | 5.11   | 9.21  | 12.41 | 7.52  | 14.83 | 6.03  | 10.54 | 10.41 | 9.69  | 7.46  | 9.32        |
|          | 13.66  | 13.88 | 21.44 | 26.38 | 32.74 | 37.08 | 41.85 | 16.36 | 27.08 | 47.43 | 27.79       |
| CI21E    |        | 3.92  | 7.30  | 8.18  | 10.88 | 5.68  | 11.99 | 9.07  | 7.61  | 7.12  | 8.10        |
|          |        | 20.09 | 39.44 | 22.79 | 22.28 | 18.40 | 35.33 | 22.99 | 21.94 | 17.70 | 23.48       |
| Ky226    |        |       | 2.84  | 9.71  | 8.20  | 5.85  | 10.59 | 5.73  | 6.04  | 6.68  | 7.54        |
|          |        |       | 4.41  | 26.95 | 34.71 | 12.30 | 40.89 | 7.15  | 20.75 | 34.33 | 24.24       |
| Tx601    |        |       |       | 3.11  | 6.37  | 7.76  | 12.77 | 4.12  | 7.22  | 6.44  | 7.32        |
|          |        |       |       | 8.63  | 31.73 | 26.42 | 32.02 | 41.98 | 11.63 | 25.19 | 25.37       |
| CM104    |        |       |       |       | 6.25  | 7.26  | 15.51 | 6.54  | 9.99  | 8.88  | 9.47        |
|          |        |       |       |       | 23.10 | 41.00 | 30.10 | 19.24 | 22.01 | 24.84 | 28.18       |
| FR9      |        |       |       |       |       | 2.29  | 14.46 | 5.19  | 8.71  | 4.19  | 6.74        |
|          |        |       |       |       |       | 15.14 | 16.29 | 41.15 | 21.49 | 18.30 | 24.76       |
| PH9      |        |       |       |       |       |       | 9.16  | 10.12 | 13.44 | 5.71  | 11.43       |
|          |        |       |       |       |       |       | 29.27 | 35.08 | 25.26 | 31.47 | 31.79       |
| Oh51A    |        |       |       |       |       |       |       | 2.70  | 6.68  | 4.18  | 6.47        |
|          |        |       |       |       |       |       |       | 4.40  | 19.41 | 12.10 | 21.99       |
| B14A     |        |       |       |       |       |       |       |       | 6.14  | 8.14  | 8.37        |
|          |        |       |       |       |       |       |       |       | 9.41  | 16.53 | 19.59       |
| Va35     |        |       |       |       |       |       |       |       |       | 3.64  | 6.42        |
|          |        |       |       |       |       |       |       |       |       | 13.39 | 24.13       |

Low P; Grand mean = 7.70, Parent = 4.52,  $F_1$  = 8.49

High P; Grand mean = 24.13, Parent = 14.15,  $F_1$  = 26.35

Table 13. Analyses of variance for seedling P concentration, and total P uptake for corn grown at two levels of P, planted in the winter (mean data in Tables 11 and 12, respectively)

| Source    | df  | Mean squares |          |
|-----------|-----|--------------|----------|
|           |     | P conc.      | P uptake |
| Rep       | 2   | .0284        | 568.0    |
| P         | 1   | .1597        | 22079.0* |
| Error (a) | 2   | .0312        | 366.9    |
| G         | 54  | .0062**      | 216.6**  |
| G x P     | 54  | .0046**      | 146.5**  |
| Error (b) | 216 | .0024        | 51.2     |

mean. However, the inbreds did not rank in the same order as their array means.

The grand means for P uptake under low P and high P were 7.77 mg/4 plants and 24.13 mg/4 plants, respectively. Large differences in P uptake of inbreds between low and high P were observed in CI21E, CM104, FR9 and Va35. Four parental lines, PH9, CM104, B14A, and Mp68:616, had comparatively high P uptake under low P. The highest P uptake under low and high P was observed in PH9. Line FR9, a derivative of Wf9, had the lowest P uptake under low P but this line showed a 6.6 fold increase in P uptake when grown under the high P. Line Oh51A, a small inbred, had very low P uptake under both levels of P. These two lines, FR9 and Oh51A, had rather low P concentrations.

#### 4.1.3 Combining Ability Studies

Phosphorus concentration in corn seedlings. The genotypes used in this experiment were found to interact with P levels when analyzed in a split-plot design (Section 4.1.2). The data were analyzed at each

level of P for GCA (general combining ability) and SCA (specific combining ability) following Griffing's method 2, using parent data, model 1.

Later, the combined analysis of GCA and SCA over P levels was performed (Table 14). The GCA and SCA mean squares at each level of P were significant or highly significant, indicating that both additive and non-additive genes were important in controlling P concentration in corn seedlings. In the combined analysis, the GCA mean square was highly significant. Both GCA x P and SCA x P interaction mean squares were highly significant.

General and specific combining ability effects for this 10-entry diallel are summarized in Table 15. The GCA effects were generally very small, but differed widely among inbreds. Four inbreds, CI21E, Ky226, CM104, and PH9 had positive GCA effect under both low and high P, indicating a good combiner for increasing P concentration in the seedling. However, inbreds Mp68:616 and FR9 had positive GCA effects under the high P treatment, indicating that they are good combiners for P concentration when grown under high P. Four inbreds, Tx601, Oh51A, B14A, and Va35, had negative GCA effects under both low and high P, indicating that these inbreds generally reduced the P concentration in hybrids.

The coefficient of linear determination ( $R^2$ ) between the parental average and their GCA effects was high and accounted for 78.0% and 73.4% of the variation in low and high P, respectively. These  $R^2$  values were highly significant and significant, indicating that selecting for P concentration in inbreds would utilize their GCA value effectively.

The specific combining ability effects of hybrids (Table 15) indicate whether the hybrids were relatively better or worse than values predicted on the basis of GCA effects. The high positive value indicated

Table 14. Combining ability analyses of variance of P concentration based on Griffing's method 2, model 1

| Source | df  | Mean squares |         | Combined analysis |     |              |
|--------|-----|--------------|---------|-------------------|-----|--------------|
|        |     | Low P        | High P  | Source            | df  | Mean squares |
| GCA    | 9   | 3.279**      | 3.644** | GCA               | 9   | 2.444**      |
| SCA    | 45  | .839*        | 2.096** | SCA               | 45  | .756         |
| Error  | 108 | .533         | 1.114   | GCA x P           | 9   | 4.478**      |
|        |     |              |         | SCA x P           | 45  | 2.178**      |
|        |     |              |         | Error             | 216 | .824         |

Table 15. Estimates of general and specific combining ability effects for P concentration under low P (upper value) and high P (lower value) based on Griffing's method 2, model 1

| Parents  | CI21E         | Ky226         | Tx601         | CM104         | FR9           | PH9            | Oh51A         | B14A           | Va35           | GCA effects    |
|----------|---------------|---------------|---------------|---------------|---------------|----------------|---------------|----------------|----------------|----------------|
| Mp68:616 | .002<br>-.038 | .016<br>-.026 | .002<br>-.000 | .035<br>.009  | -.022<br>.077 | -.026<br>.028  | .041<br>-.021 | -.002<br>.028  | .004<br>.064   | -.005<br>.004  |
| CI21E    |               | -.029<br>.087 | .013<br>-.018 | .055<br>-.022 | .002<br>-.075 | -.006<br>.017  | .046<br>.030  | -.007<br>.038  | -.002<br>-.013 | .000<br>.026   |
| Ky226    |               |               | .045<br>.023  | .011<br>.058  | .014<br>-.040 | .027<br>.011   | .008<br>-.045 | -.037<br>.037  | .000<br>.072   | .011<br>.005   |
| Tx601    |               |               |               | -.034<br>.023 | .039<br>.014  | .004<br>.003   | .028<br>.071  | -.026<br>-.023 | .018<br>-.010  | -.009<br>-.009 |
| CM104    |               |               |               |               | -.005<br>.035 | -.012<br>-.037 | -.014<br>.003 | .030<br>-.024  | .014<br>.032   | .006<br>.011   |
| FR9      |               |               |               |               |               | .043<br>-.067  | -.008<br>.054 | .052<br>.042   | .005<br>.053   | -.002<br>.007  |
| PH9      |               |               |               |               |               |                | .032<br>.050  | .011<br>.007   | -.023<br>.010  | .037<br>.014   |
| Oh51A    |               |               |               |               |               |                |               | -.031<br>.009  | -.001<br>-.053 | -.011<br>-.014 |
| B14A     |               |               |               |               |               |                |               |                | .006<br>-.034  | .000<br>-.036  |
| Va35     |               |               |               |               |               |                |               |                |                | -.027<br>-.009 |

$se_d$  of GCA effect for low P and high P = 0.009 and 0.014, respectively

$se_d$  of SCA effects of two crosses having one parent line in common = 0.031 for low P and 0.045 for high P

$se_d$  of SCA effects of two crosses having no parent line in common = 0.029 for low P and 0.049 for high P

$se_d$  in this and subsequent tables refer to standard error of difference

a good combination of nonadditive genes in the parents. The SCA effects indicated that Ky226 x Tx601 and FR9 x PH9 utilized the nonadditive genes effectively at low P. Two out of nine hybrids involving Tx601 had negative SCA effects under low P, indicating that inbred Tx601 was a good source of nonadditive genes among this set of inbreds for increasing P concentration under a low level of P. Under a high P level, hybrid CI21E x Ky226 had the highest SCA effect, followed by FR9 x Mp68:616. These two hybrids had a very low SCA effect under the low P condition. The hybrid FR9 x PH9 which had the highest SCA effect under low P had the next to lowest SCA effect under the high P.

Phosphorus uptake. Phosphorus uptake is the product of P concentration in the plant and dry matter yield. The genotypes evaluated for P uptake were found to interact with P levels (Section 4.1.2). The P uptake data were analyzed at each level of P for GCA and SCA following Griffing's method 2, model 1. The combined analysis of GCA and SCA over levels of P was also performed (Table 16). The results of combining ability analyses showed that GCA and SCA mean squares were highly significant at both levels of P and also in the combined analysis, indicating that both additive and nonadditive genes were important in determining P uptake in corn seedlings. However, GCA x P and SCA x P interaction mean squares were also highly significant.

General and specific combining ability effects for P uptake for this 10-entry diallel are summarized in Table 17. The GCA effects differed widely among inbreds. Five inbreds, PH9, Oh51A, CM104, Mp68:616, and B14A, had positive GCA effects under the low P condition. The same set of inbreds except Oh51A had a positive GCA effect under the high P condition. The GCA effect of inbred Va35 was negative under low P but

Table 16. Combining ability analyses of variance of P uptake based on Griffing's method 2, model 1

| Source | df  | Mean squares |         | Combined analysis |     |              |
|--------|-----|--------------|---------|-------------------|-----|--------------|
|        |     | Low P        | High P  | Source            | df  | Mean squares |
| GCA    | 9   | 27.34**      | 137.3** | GCA               | 9   | 64.20**      |
| SCA    | 45  | 6.36**       | 105.9** | SCA               | 45  | 30.49**      |
| Error  | 108 | 3.48         | 30.6    | GCA x P           | 9   | 100.52**     |
|        |     |              |         | SCA x P           | 45  | 81.77**      |
|        |     |              |         | Error             | 216 | 17.04        |

Table 17. Estimates of general and specific combining ability effects for P uptake under low P (upper value) and high P (lower value) based on Griffing's method 2, model 1

| Parents  | CI21E  | Ky226 | Tx601 | CM104 | FR9    | PH9    | Oh51A  | B14A  | Va35  | effects |
|----------|--------|-------|-------|-------|--------|--------|--------|-------|-------|---------|
|          | .42    | 4.18  | -.56  | 4.70  | -1.49  | -1.47  | 3.08   | .49   | .24   | 1.07    |
| Mp68:616 | -11.55 | -3.31 | .33   | 3.15  | 11.00  | 8.73   | -6.51  | 5.78  | 22.02 | 2.18    |
|          |        | .19   | 1.23  | 1.87  | -.73   | 1.10   | 2.86   | -.47  | 1.02  | -.05    |
| CI21E    |        | 17.74 | -.20  | -4.26 | -4.63  | 5.26   | 3.16   | 3.70  | -4.65 | -.89    |
|          |        |       | 3.31  | -.25  | .00    | .27    | .08    | -1.48 | 1.13  | -.61    |
| Ky226    |        |       | 4.63  | 8.85  | -10.04 | 11.50  | -11.99 | 3.19  | 12.64 | -1.56   |
|          |        |       |       | 1.92  | 2.07   | 2.61   | -1.38  | -.15  | 1.06  | -.77    |
| Tx601    |        |       |       | 4.56  | 2.77   | 1.34   | 21.54  | -7.23 | 2.21  | -.26    |
|          |        |       |       |       | -.48   | 3.29   | -1.01  | .58   | 1.44  | 1.29    |
| CM104    |        |       |       |       | 13.82  | -4.12  | -4.74  | -.39  | -1.68 | 3.28    |
|          |        |       |       |       |        | 4.85   | .24    | 1.90  | -.65  | -1.31   |
| FR9      |        |       |       |       |        | -14.42 | 20.68  | 2.60  | -4.71 | -.23    |
|          |        |       |       |       |        |        | .69    | 2.15  | -3.61 | 3.16    |
| PH9      |        |       |       |       |        |        | 7.57   | -.31  | 1.42  | 6.81    |
|          |        |       |       |       |        |        |        | .05   | -.46  | 1.50    |
| Oh51A    |        |       |       |       |        |        |        | 3.73  | -7.70 | -3.43   |
|          |        |       |       |       |        |        |        |       | 1.63  | .36     |
| B14A     |        |       |       |       |        |        |        |       | -1.69 | 5.01    |
|          |        |       |       |       |        |        |        |       |       | -1.61   |
| Va35     |        |       |       |       |        |        |        |       |       | .90     |

$se_d$  of GCA effect for low P and high P = 0.76 and 2.26, respectively

$se_d$  of SCA effects of two crosses having one parent line in common = 2.53 for low P and 7.49 for high P

$se_d$  of SCA effects of two crosses having no parent line in common = 2.41 for low P and 7.15 for high P

this inbred had a positive GCA effect under high P. These positive GCA effect indicates a good combiner for increasing P uptake in hybrid combinations. Inbreds CI21E, Ky226, Tx601, FR9, and Va35 had a negative GCA effect under low P conditions. All of these inbreds had small seedlings which reflects the P uptake of these inbreds. On the high P treatment, inbred FR9, Tx601, CI21E, Ky226, and Oh51A had a negative GCA effect, indicating that these inbreds reduced the P uptake in hybrid in general.

The coefficient of linear determination ( $R^2$ ) between the parental averages and their GCA effects was high. It accounted for 59% and 44% for the variation in low and high P, respectively. These high  $R^2$  values indicated that the P uptake of inbreds can be used for predicting their GCA effects.

Specific combining ability effects of the hybrids (Table 17) varied widely under both P levels. The SCA effect indicated the relative performance of hybrids with the predicted value based on the GCA effect of their respective parents. It also indicated the deviation from the additive gene action model. Thus, the high positive SCA effect denotes a good combination of nonadditive genes in the parents. The results showed that hybrids CM104 x Mp68:616, Ky226 x Mp68:616, FR9 x PH9, Ky226 x Tx601, Mp68:616 x Oh51A, and CM104 x PH9 were good combinations which make use of nonadditive genes for P uptake under the low P condition. Under the high P condition, several hybrids including Mp68:616 x Va35, Oh51A x Tx601, and FR9 x Oh51A had high positive SCA effects.

Grain yield. Grain yields of a 10-entry diallel cross evaluated under two levels of P are presented in Table 18. Among the

Table 18. Grain yield in metric tons/ha of a 10-entry diallel grown under low P (upper values) and high P (lower values), summer planting

| Parents  | Mp<br>68:616 | CI21E         | Ky226          | Tx601          | CM104          | FR9           | PH9            | Oh51A          | B14A           | Va35          | Array<br>means |
|----------|--------------|---------------|----------------|----------------|----------------|---------------|----------------|----------------|----------------|---------------|----------------|
| Mp68:616 | 6.14<br>7.28 | 9.01<br>12.17 | 9.64<br>12.65  | 10.44<br>11.11 | 10.33<br>13.06 | 5.50<br>9.68  | 10.61<br>11.52 | 8.85<br>10.74  | 8.84<br>9.58   | 7.61<br>10.20 | 8.70<br>10.80  |
| CI21E    |              | 3.94<br>5.35  | 10.15<br>10.27 | 9.54<br>13.04  | 12.60<br>12.98 | 6.06<br>6.30  | 7.77<br>7.98   | 8.07<br>9.63   | 6.99<br>8.00   | 6.19<br>7.39  | 8.03<br>9.31   |
| Ky226    |              |               | 2.55<br>3.71   | 12.83<br>13.35 | 12.34<br>12.67 | 6.34<br>6.83  | 7.40<br>10.32  | 7.26<br>9.97   | 10.62<br>11.54 | 7.82<br>8.88  | 8.69<br>10.02  |
| Tx601    |              |               |                | 2.78<br>4.99   | 9.96<br>14.06  | 8.48<br>11.37 | 10.83<br>11.66 | 10.27<br>10.18 | 8.01<br>10.79  | 9.69<br>10.86 | 9.28<br>11.14  |
| CM104    |              |               |                |                | 7.86<br>7.70   | 8.88<br>10.84 | 10.57<br>9.94  | 9.50<br>9.68   | 8.52<br>9.61   | 8.70<br>11.31 | 9.93<br>11.19  |
| FR9      |              |               |                |                |                | .82<br>5.12   | 4.98<br>7.21   | 4.62<br>7.14   | 4.17<br>9.01   | 2.65<br>5.96  | 5.25<br>7.95   |
| PH9      |              |               |                |                |                |               | 3.09<br>6.30   | 7.03<br>7.79   | 6.25<br>7.91   | 5.66<br>8.51  | 7.42<br>8.91   |
| Oh51A    |              |               |                |                |                |               |                | 1.79<br>2.79   | 6.46<br>8.71   | 4.25<br>6.97  | 6.81<br>8.36   |
| B14A     |              |               |                |                |                |               |                |                | 2.71<br>3.09   | 6.57<br>8.06  | 6.91<br>8.63   |
| Va35     |              |               |                |                |                |               |                |                |                | 1.71<br>2.35  | 6.08<br>8.05   |

BLSD 0.05 G x P = 2.43, Mean heterotic effect = 166% for low P and 115% for high P

parental inbreds used in this diallel, inbreds CM104 and Mp68:616 had high yields under low P condition. Inbred FR9 had the lowest yield under low P condition but its yield increased tremendously and ranked fifth under the high P. The low yield in inbred FR9 under low P was partly due to disease infestation in this inbred. A slight drop of yield which was not significant was observed in CM104.

The heterotic effects, based on the mid-parental value, of these 45 hybrids were calculated. Very high heterotic effects, over 300%, were observed in Ky226 x Tx601, FR9 x Tx601, Oh51A x Tx601, and B14A x Ky226 in the low P. The mean heterotic effect of this 10-entry diallel were 166% under low P and 115% under high P.

This set of genotypes was found to interact with levels of P in grain yield (Section 4.1.2). Grain yield data were analyzed at each level of P for GCA and SCA following Griffing's method 2, model 1. The combined analysis of GCA and SCA over P levels was also performed (Table 19). The results of combining ability analyses showed that GCA and SCA mean square were highly significant in all cases, indicating that both additive and nonadditive genes were important in determining grain yield of corn. However, both GCA x P and SCA x P interaction mean squares were highly significant in combined analysis.

Table 19. Combining ability analyses of variance of grain yield based on Griffing's method 2, model 1.

| Source | df  | Mean squares |          | Combined analysis |     |              |
|--------|-----|--------------|----------|-------------------|-----|--------------|
|        |     | Low P        | High P   | Source            | df  | Mean squares |
| GCA    | 9   | 22.698**     | 16.393** | GCA               | 9   | 18.958**     |
| SCA    | 45  | 5.991**      | 6.353**  | SCA               | 45  | 5.791**      |
| Error  | 108 | .385         | .555     | GCA x P           | 9   | 20.124**     |
|        |     |              |          | SCA x P           | 45  | 6.553**      |
|        |     |              |          | Error             | 216 | .470         |

The GCA effect of parental inbreds and the SCA effect of 45 hybrids are presented in Table 20. The five inbreds, CM104, Tx601, Mp68:616, Ky226, and CI21E, had a positive GCA effect for yield under low P, indicating that these inbreds were good general combiners for yield under low P condition. Similar results were obtained for high P except that PH9 was a good combiner instead of CI21E which had a negative GCA effect. At both P levels, inbred FR9 had the lowest negative GCA effect.

The coefficient of linear determination ( $R^2$ ) between inbred yield and their GCA effect was high, 68.0% for low P and 58.6% for high P, indicating that inbred yield can be used for predicting the GCA effect of inbreds.

The SCA effects varied widely for both P levels. The hybrid Ky226 x Tx601 and B14A x Ky226 had a large SCA effect for both levels of P. Hybrid CI21E x Ky226 also had a large SCA effect in the high P condition.

Estimates of heritabilities. The fixed model has been used in the interpretation of data, reflecting the specific interest in this set of inbreds. However, the inbreds used in the diallel cross represent a rather wide range of germplasm, therefore, the random model was applied to this set of inbreds. In the random model, the value of all mean squares and the test of significance of SCA mean square were the same as in the fixed model except that the GCA mean square was tested against the SCA mean square as the error term. The level of significance of all GCA and SCA mean squares of P concentration, P uptake, and grain yield are summarized in Table 21. The GCA mean squares under low P were highly significant for all characters. Under high P, the GCA for grain yield was significant but the GCA mean square for P concentration and P

Table 20. Estimates of general and specific combining ability effects for grain yield under low P (upper value) and high P (lower value) based on Griffing's method 2, model 1

| Parents  | CI21E       | Ky226       | Tx601        | CM104        | FR9          | PH9          | Oh51A        | B14A         | Va35         | GCA effects    |
|----------|-------------|-------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|----------------|
| Mp68:616 | .33<br>1.87 | .52<br>1.89 | .80<br>-.69  | -.26<br>1.00 | -.60<br>.57  | 2.50<br>1.47 | 1.36<br>1.44 | 1.18<br>.03  | .73<br>1.23  | 1.06<br>1.34   |
| CI21E    |             | 1.76<br>.92 | .65<br>2.64  | 2.75<br>2.33 | .69<br>-1.41 | .40<br>-.67  | 1.31<br>1.74 | .08<br>-.14  | .05<br>-.18  | .32<br>-.06    |
| Ky226    |             |             | 3.05<br>2.50 | 2.05<br>1.56 | .53<br>-1.34 | -.40<br>1.22 | .07<br>1.62  | 3.27<br>2.94 | 1.24<br>.86  | .75<br>.40     |
| Tx601    |             |             |              | -.83<br>1.91 | 2.16<br>2.16 | 2.52<br>1.52 | 2.57<br>.79  | .15<br>1.15  | 2.59<br>1.80 | 1.26<br>1.44   |
| CM104    |             |             |              |              | 1.60<br>1.37 | 1.30<br>-.47 | .84<br>.03   | -.30<br>-.29 | .65<br>1.99  | 2.22<br>1.70   |
| FR9      |             |             |              |              |              | .19<br>-.25  | .45<br>.43   | -.17<br>2.60 | -.91<br>-.78 | -2.26<br>-1.24 |
| PH9      |             |             |              |              |              |              | .86<br>.15   | -.08<br>.02  | .10<br>1.20  | -.26<br>.31    |
| Oh51A    |             |             |              |              |              |              |              | .74<br>1.57  | -.69<br>.41  | -.88<br>-1.06  |
| B14A     |             |             |              |              |              |              |              |              | 1.46<br>1.25 | -.72<br>-.81   |
| Va35     |             |             |              |              |              |              |              |              |              | -1.49<br>-1.39 |

$se_d$  of GCA effect for low P and high P = 0.25 and 0.30, respectively

$se_d$  of SCA effects of two crosses having one parent line in common = 0.84 for low P and 1.09 for high P

$se_d$  of SCA effects of two crosses having no parent line in common = 0.80 for low P and 0.96 for high P

Table 21. A summary of significance levels of general combining ability (GCA) and specific combining ability (SCA) mean squares based on Griffing's method 2, model 2 (values of mean squares were the same as in model 1)

| Characters      | Low P |     | High P |     |
|-----------------|-------|-----|--------|-----|
|                 | GCA   | SCA | GCA    | SCA |
| P concentration | **    | **  | ns     | **  |
| P uptake        | **    | **  | ns     | **  |
| Grain yield     | **    | **  | *      | **  |

uptake was not significant. All SCA mean squares were highly significant while mean squares for P concentration under the low P condition was significant.

The effects in the expected mean squares for model 1 were equated to the variances for model 2. The additive genetic variance ( $V_A$ ), nonadditive genetic variance ( $V_D$ ), and environmental variance ( $V_E$ ) were estimated from these values (Table 22). The narrow-sense and broad-sense heritabilities were estimated as  $V_A/(V_A + V_D + V_E)$  and  $(V_A + V_D)/(V_A + V_D + V_E)$ , respectively (Table 22).

The additive genetic variance for P concentration was highly significant under low P and not significant under high P. The non-additive genetic variance was highly significant at both levels of P. The estimates of narrow-sense and broad-sense heritabilities for P concentration are given in Table 22. The narrow-sense heritability for P concentration under low P was 32.7% and only 10.9% under high P. The broad-sense heritability estimated under both levels of P was similar with values of 57.5% and 52.7% for low P and high P, respectively.

Table 22. Estimates of variance components and narrow-sense and broad-sense heritability for several characters under low and high P

| Character                | Additive |        | Nonadditive |         | Error    |        | Heritability |       |
|--------------------------|----------|--------|-------------|---------|----------|--------|--------------|-------|
|                          | $V_A$    |        | $V_D$       |         | $V_E$    |        | narrow       | broad |
|                          |          |        |             |         |          |        | %            |       |
| P concentration (Low P)  | .406 ±   | .016   | .304 ±      | .036    | .533 ±   | .005   | 32.7         | 57.5  |
| P concentration (High P) | .258 ±   | .021   | .982 ±      | .218    | 1.110 ±  | .023   | 10.9         | 52.7  |
| P uptake (Low P)         | 3.496 ±  | 2.332  | 2.878 ±     | 2.025   | 3.486 ±  | .225   | 35.4         | 64.6  |
| P uptake (High P)        | 5.232 ±  | 65.140 | 75.301 ±    | 516.266 | 30.645 ± | 17.392 | 4.7          | 72.4  |
| Grain yield (Low P)      | 2.784 ±  | 1.612  | 5.606 ±     | 1.598   | .385 ±   | .003   | 31.7         | 95.6  |
| Grain yield (High P)     | 1.674 ±  | .854   | 5.798 ±     | 1.800   | .555 ±   | .006   | 20.8         | 93.1  |

The additive genetic variance for P uptake under low P was highly significant while it was not significant under high P. This suggests that the narrow-sense heritability would be substantial under low P and smaller under high P. The estimates of narrow-sense heritabilities for P uptake were 35.4% under low P and merely 4.7% under high P. However, broad-sense heritability for P uptake was 64.6% under low P and 72.4% under high P.

Similarly, the estimates of the narrow-sense and broad-sense heritabilities for the grain yield were higher under low P than high P. The narrow-sense heritability estimated under the low P was 31.7% while it was 20.8% under the high P. This difference was substantial. On the other hand the estimate of broad-sense heritability for grain yield under low and high P was 95.6% and 93.1%, respectively.

#### 4.2 Summary

The important results from the experiment on genotypic response to P were the significance of genotype by P interactions which were observed for seedling dry weight, days to anthesis, grain yield, ear weight, ear length, number of kernels per row, kernel depth, 100 kernel weight, P concentration in the plant, and total P uptake. These results provided further evidence of differential P uptake and differential yield response to P in corn. However, the nature of this study did not allow conclusions to be drawn about the causes of these differential responses of genotypes to P. One possible cause of the differential response of corn genotypes to levels of P may be due to their rooting habit. The lack of root data from this experiment does not allow evaluation of the effect of different rooting habits on the response to P. Therefore, genotypes which differ

in differential increase in seedling dry weight such as inbred CM104, Ky226, PH9 should be tested for root weight and rooting pattern, rate of P absorption, and relative growth rate under low P and high P. Some genotypes; such as inbreds CM104, PH9 and their hybrids, should also be tested for their yielding ability under several levels of P. These further tests should help explain some of the questions with regard to the differential response of genotypes.

Genetic variations in corn with respect to mineral nutrition offer several possibilities for improving such traits as nutrient content, total nutrient uptake, and efficiency in fertilizer utilization. Corn improvement in these traits might lead to better quality feed, an increase in efficiency of fertilizer usage, reduced cost of production, and increased corn productivity in acid or alkaline soils. In this study the P concentration in the seedling stage was used as the criterion for estimating P concentration and analysis was made for combining abilities. The results showed that the differences among the 10 inbreds and 45 hybrids were highly significant. Since genotypes showed significant interaction with P, they were discussed separately under low P and high P. Inbred PH9 was found to be a good source of genes for increasing P concentration under low P. In the combining ability analyses of variance the GCA mean square was larger than the SCA mean square and the (GCA:SCA) ratio was 3.91 in low P and 1.74 in high P, indicating that additive genes were more important than nonadditive genes in the inheritance of P concentration. In this study, the expression of additive genes in relation to nonadditive genes was greater under P stress which resulted in a greater estimate of narrow-sense heritability under low P than high P.

The estimate of heritability was substantial enough to encourage recurrent selection. The significance of the coefficient of linear determination between the P concentration in the inbreds and their GCA effects suggests that selection of inbreds for high P concentration would utilize the GCA value.

In this study, P uptake by corn seedlings grown without P fertilization was used as a measure of the efficient use of soil P. Differences in P uptake were observed in the 10-entry diallel. Inbred PH9 had a high P uptake during the seedling stage which indicated that PH9 was a good source of genes for increasing P uptake. In the combining ability analyses of variance, the GCA mean square was greater than the SCA mean square under low P but not significantly greater under high P, suggesting that additive gene action was more important than the nonadditive genes in the inheritance of P uptake under low P. However, they appear equally important under high P. These results suggest that selection for P uptake should be done under low P in order to utilize additive genes more effectively. The estimate of narrow-sense heritability under low P was low but substantial enough for recurrent selection.

Evaluation of hybrids for grain yield in breeding programs has been done largely on well-fertilized soils. The present study provides additional evidence of genotype by soil fertility interactions. High P fertility is not always obtained in corn production. The significance of genotype and P interaction observed in the present study suggested that corn might be bred specifically for soils with low P levels, frequently found in developing countries. In this study, the difference in grain yield among genotypes was found to be highly significant. Inbreds CM104 and Mp68:616 performed well under low P, and their array

means were also high, suggesting that these inbreds could be used as a parent of hybrids to be grown in areas of low soil P. Although inbred Tx601 yielded poorly, its array mean was high under low P. In the combining ability analyses of variance the GCA mean square was significantly greater than the SCA mean square and the GCA:SCA ratio was 3.78 for low P and 2.58 for high P. Specific combining ability effects also appear to be important. Inbred B14A which had a relatively poor GCA effect had a good SCA effect when combined with Ky226. Thus, B14A should be tested further to maximize its superior hybrid combination. Inbred Tx601, a low yielding inbred, had a very high array mean under low P which suggests that Tx601 can produce good hybrids and should be tested thoroughly to maximize its use in hybrid combinations.

## 5. EXTERNAL PHOSPHATE REQUIREMENT FOR CORN CULTIVARS

The external phosphate requirement is defined here as the estimated P concentration in solution which is sufficient for corn to produce near maximum yield. As a matter of practical application and for convenience in graphical determinations, the estimation is usually made at 95% of maximum attainable yield. The external P requirement of 12 corn cultivars was estimated from this experiment. The levels of P established in the field were 0.003, 0.006, 0.012, 0.025, 0.05, 0.1, 0.2, 0.4, 0.8, and 1.6 ppm P in solution. The 0.012, 0.025, 0.05, and 0.1 ppm P were replicated 3 times. The P levels were arranged in an augmented block design and cultivars were treated as sub-plots. The experimental site was formerly a slope which had been graded to two bench terraces, resulting in each plot having a "cut end" and "filled end".

### 5.1 Results and Discussion

#### 5.1.1 Response of 12 Corn Cultivars to 10 Levels of Phosphate

Phosphate deficiency symptoms were obvious in the low P plots; the symptom being most severe in the 0.003 ppm P plot. At each level, the P deficiency symptoms were most severe in the 0.003 ppm P plot. At each level, the P deficiency symptoms were most severe in the cut ends of the plots. This was to be expected since the level of P in solution was lower in the cut end than in the filled end (Table 2). The symptoms appeared with different degrees of severity. The most affected cultivars were Mp68:616 x Tx601, Yellow Carimagua, and CI21E x Ky226. Some plants of Mp68:616 x Tx601 died of acute P deficiency. Deficiency symptoms associated with 0.006 ppm P were severe for Mp68:616 x Tx601 and moderate

for other cultivars. Deficiency symptoms disappeared when the P level reached 0.1 ppm P.

Growth in response to P levels of 4 cultivars at age 5 weeks is summarized in Table 23. There were large responses to P by all cultivars. The dry matter of two cultivars, H788 and CI21E x Ky226, decreased as the P level increased from 0.8 to 1.6 ppm. This drop in dry matter at 5 weeks was probably due to P toxicity. A log-log plot of average dry matter yield of 4 cultivars against levels of P in solution is presented in Figure 2. The relationship was approximately linear.

Table 23. Dry matter production at 5 weeks by 4 cultivars under 10 levels of P

| Cultivars     | Adjusted P in solution (ppm) |       |       |       |      |      |      |       |       |       |
|---------------|------------------------------|-------|-------|-------|------|------|------|-------|-------|-------|
|               | 0.003                        | 0.006 | 0.012 | 0.025 | 0.05 | 0.1  | 0.2  | 0.4   | 0.8   | 1.6   |
|               | gm/plant                     |       |       |       |      |      |      |       |       |       |
| H788          | .60                          | .85   | 2.31  | 6.31  | 3.42 | 6.59 | 5.98 | 10.73 | 15.32 | 11.37 |
| X304C         | .44                          | .41   | 2.52  | 2.25  | 2.94 | 3.56 | 2.50 | 8.31  | 17.33 | -     |
| Ky226 x Oh43  | .35                          | .82   | .59   | 1.74  | 2.85 | 4.61 | 5.11 | 10.28 | 11.02 | 21.87 |
| CI21E x Ky226 | .41                          | .51   | 1.61  | 1.97  | 1.44 | 4.13 | 7.76 | 5.90  | 14.24 | 9.51  |
| Average       | .45                          | .65   | 1.76  | 3.07  | 2.06 | 4.72 | 5.34 | 8.81  | 14.48 | 14.25 |

Grain yield of 12 corn cultivars grown in the "cut end" of plots are given in Table 24. The variety means for each P level showed that these corn cultivars responded to P fertilization. The yield of cultivars over all levels of P differed greatly and varied from 4.5 metric tons/ha by Antigua Composite to 11.4 metric tons/ha by H638. The

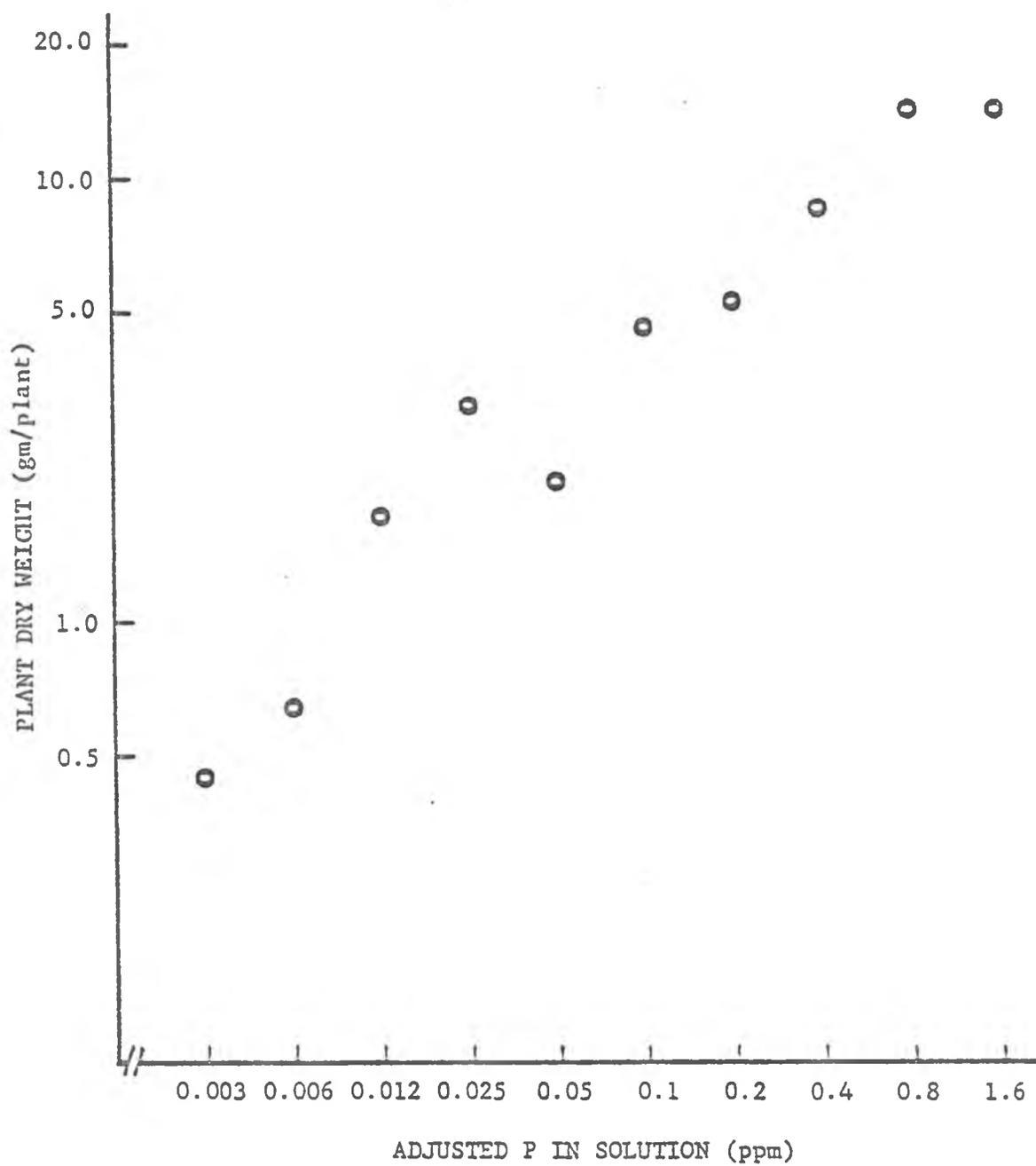


Figure 2. Relationship between mean dry matter yield of 4 corn cultivars at 5 weeks and adjusted P in solution.

Table 24. Grain yield of 12 corn cultivars grown under 10 levels of P in the field (cut end)

| Cultivars         | Adjusted P in Solution (ppm) |       |       |       |      |      |      |      |      |      | Cultivar means |
|-------------------|------------------------------|-------|-------|-------|------|------|------|------|------|------|----------------|
|                   | 0.003                        | 0.006 | 0.012 | 0.025 | 0.05 | 0.1  | 0.2  | 0.4  | 0.8  | 1.6  |                |
|                   | metric tons/ha               |       |       |       |      |      |      |      |      |      |                |
| H610              | 3.3                          | 9.0   | 9.8   | 7.7   | 10.7 | 11.3 | 11.0 | 10.8 | 13.7 | 9.8  | 9.7            |
| H788              | 5.9                          | 4.7   | 9.8   | 10.7  | 12.5 | 10.6 | 10.1 | 11.5 | 12.4 | 10.7 | 9.9            |
| X304C             | 4.5                          | 2.2   | 10.7  | 11.4  | 11.3 | 9.8  | 9.1  | 11.0 | 13.4 | 10.4 | 9.4            |
| Antigua Composite | 1.4                          | 2.2   | 4.8   | 6.4   | 5.7  | 6.3  | 4.5  | 5.4  | 4.9  | 3.4  | 4.5            |
| Ky226 x Oh43      | 0.5                          | 4.9   | 5.5   | 5.2   | 4.8  | 8.6  | 6.8  | 6.2  | 6.1  | 6.8  | 5.5            |
| Mp68:616 x Tx601  | 0.6                          | 3.1   | 11.3  | 11.6  | 8.6  | 9.7  | 11.9 | 10.7 | 10.9 | 8.5  | 8.7            |
| CM104 x Va35      | 0.6                          | 3.7   | 8.6   | 8.0   | 8.5  | 7.9  | 10.9 | 8.2  | 9.2  | 9.7  | 7.5            |
| CI21E x Ky226     | 3.4                          | 1.4   | 8.3   | 8.9   | 9.2  | 8.3  | 7.4  | 8.5  | 9.6  | 9.5  | 7.4            |
| CM104 x PH9       | 5.8                          | 3.1   | 9.4   | 6.9   | 9.1  | 10.4 | 10.4 | 10.2 | 10.5 | 10.6 | 8.6            |
| H638              | 3.7                          | 10.6  | 8.3   | 9.9   | 13.4 | 9.8  | 14.1 | 14.8 | 13.9 | 15.4 | 11.4           |
| White Carimagua   | 3.8                          | 9.1   | 9.5   | 8.8   | 9.4  | 11.5 | 12.4 | 12.1 | 11.6 | 12.2 | 10.0           |
| Yellow Carimagua  | 7.4                          | 6.1   | 10.1  | 9.0   | 11.7 | 10.2 | 12.0 | 10.3 | 10.9 | 8.1  | 9.8            |
| P means           | 3.4                          | 5.0   | 8.8   | 8.7   | 9.6  | 9.5  | 10.0 | 9.9  | 10.6 | 9.9  | 8.5            |

yields of Antigua Composite and Ky226 x Oh43 were low in almost all P levels, indicating overall poor performance by these cultivars. Cultivar Mp68:616 x Tx601 had a very low yield at 0.003 ppm but this cultivar responded to P very well. Yields were near the maximum attainable at 0.012 ppm. This cultivar should be tested further for its good response to P. Yields of H610, H788, X304C, CI21E x Ky226, CM104 x PH9, H638, White Carimagua, and Yellow Carimagua were relatively high at 0.003 ppm P. These cultivars should be tested further under low P conditions to see if this result is confirmed.

Other plant growth characteristics and components of yield were measured for the 12 cultivars growing in the cut end of the plots. These data which included days to silking, ear and plant height, and ear length are presented in Appendix A8 to A11.

Grain yield of 12 corn cultivars grown under 10 levels of P in the "filled end" of plots are summarized in Table 25. Grain yields in this part of the plots were generally higher than grain yields in the cut ends of plots. It should be pointed out that the levels of P in solution in the phosphate adsorption curves in the filled ends were greater than those in the cut ends in most cases (Table 2) and some levels of P were still higher than the desired levels; 0.003, 0.006, and 0.012 ppm. As a result, a very small response was observed in the filled ends.

#### 5.1.2 Estimates of External Phosphate Requirement

Data from the cut-ends of subplots gave evidence of response to P. These data were subjected to regression analysis using a square root model and a linear-response-plateau model. The means of all cultivars at each level of P were regressed on coded P. For the square root model,

Table 25. Grain yield of 12 corn cultivars grown under 10 levels of P in field condition (filled end)

| Cultivars         | Adjusted P in Solution (ppm) |       |       |       |      |      |      |      |      |      | Cultivar means |
|-------------------|------------------------------|-------|-------|-------|------|------|------|------|------|------|----------------|
|                   | 0.003                        | 0.006 | 0.012 | 0.025 | 0.05 | 0.1  | 0.2  | 0.4  | 0.8  | 1.6  |                |
|                   | metric tons/ha               |       |       |       |      |      |      |      |      |      |                |
| H610              | 10.1                         | 8.7   | 11.7  | 11.5  | 12.1 | 11.0 | 13.9 | 14.0 | 9.2  | 14.6 | 11.7           |
| H788              | 11.3                         | 10.7  | 12.9  | 11.6  | 14.1 | 13.8 | 13.7 | 13.2 | 13.9 | 12.8 | 12.8           |
| X304C             | 10.8                         | 11.9  | 12.3  | 13.2  | 12.7 | 14.1 | 13.0 | 12.5 | 15.1 | 13.9 | 13.0           |
| Antigua Composite | 6.8                          | 7.1   | 7.2   | 6.0   | 7.1  | 6.8  | 8.6  | 6.5  | 9.8  | 4.9  | 7.1            |
| Ky226 x Oh43      | 6.3                          | 7.7   | 4.4   | 5.4   | 9.9  | 6.0  | 5.8  | 9.3  | 6.5  | 6.8  | 6.8            |
| Mp68:616 x Tx601  | 11.8                         | 14.4  | 10.9  | 11.2  | 11.1 | 10.6 | 10.7 | 12.0 | 9.3  | 9.4  | 11.1           |
| CM104 x Va35      | 7.9                          | 8.1   | 7.8   | 8.9   | 9.6  | 11.7 | 9.4  | 6.2  | 9.9  | 11.9 | 9.1            |
| CI21E x Ky226     | 5.9                          | 13.4  | 9.9   | 9.6   | 10.8 | 11.2 | 9.5  | 10.7 | 11.9 | 10.3 | 10.3           |
| CM104 x PH9       | 12.1                         | 12.3  | 9.8   | 9.9   | 10.1 | 10.3 | 8.9  | 9.0  | 11.2 | 9.6  | 10.3           |
| H638              | 13.2                         | 12.7  | 12.4  | 11.1  | 10.2 | 12.0 | 10.5 | 14.2 | 14.9 | 12.5 | 12.4           |
| White Carimagua   | 10.1                         | 10.1  | 10.4  | 12.9  | 14.0 | 12.8 | 13.8 | 12.7 | 14.2 | 14.5 | 12.6           |
| Yellow Carimagua  | 10.3                         | 11.6  | 10.7  | 12.3  | 11.7 | 12.7 | 8.4  | 14.9 | 14.9 | 14.1 | 12.2           |
| P means           | 9.4                          | 10.7  | 10.0  | 10.3  | 11.1 | 11.1 | 10.5 | 11.3 | 11.7 | 11.3 |                |

it was necessary to transform P levels to a linear scale. This was done by taking the logarithm of 1000 times P concentration. The coded P in the linear-response-plateau model were 1, 2, 3, 4, 5, 6, 7, 8, 9, and 10, respectively.

The regression equation of grain yield on the transformed values of P in solution are given for each cultivar in Table 26. This table includes multiple correlation coefficients (R), estimated maximum yields, estimated P levels at maximum yield, and at 95% of maximum yield. All equations had a negative intercept indicating that interpolating to a P level lower than 0.001 ppm would be unrealistic. The lowest P concentration in this experiment was 0.003 ppm. The multiple correlation coefficient was highly significant for H788, X304C, Ky226 x Oh43, Mp68:616 x Tx601, CM104 x Va35, CM104 x PH9, H638, and White Carimagua and it was significant for H610 and CI21E x Ky226. The coefficients of determination ( $R^2$ ) for these equations were low, indicating a poor fit of the data to the square root model. A very small increase in  $R^2$  was obtained if the higher degree polynomials were included in the equation. It is also suggested that a further test of these materials is needed and the interpretations which follow are tentative until verification of these results is obtained.

Estimated maximum yields varied considerably among varieties. The highest yield, 15.0 metric tons/ha, was attained by H638. The lowest maximum yield, 6.0 metric tons/ha, was attained by Antigua Composite. Cultivars H638 and Antigua Composite were respectively the most responsive and least responsive to levels of P in solution. The estimated yields appear to be high; probably because of upward bias by the square root

Table 26. Regression equation for the square root model, multiple correlation coefficient (R), maximum yield, and estimated P in the adjusted solution for each of the 12 corn cultivars (cut end)

| Cultivars         | Regression equations                         | R      | Maximum yields<br>metric tons/ha | Estimated P       |             |
|-------------------|--|--------|----------------------------------|-------------------|-------------|
|                   |  |        |                                  | Max. <sup>a</sup> | 95% of Max. |
|                   |  |        |                                  | ppm               |             |
| H610              | $Y = -9.12 - 7.74P^b + 24.96P^{\frac{1}{2}}$ | .567*  | 11.0                             | 0.40              | 0.06        |
| H788              | $Y = -9.66 - 9.00P + 27.84P^{\frac{1}{2}}$   | .635** | 11.9                             | 0.30              | 0.05        |
| X304C             | $Y = -14.34 - 11.52P + 34.44P^{\frac{1}{2}}$ | .625** | 11.4                             | 0.23              | 0.04        |
| Antigua Composite | $Y = -4.62 - 5.34P + 15.06P^{\frac{1}{2}}$   | .356   | 6.0                              | 0.10              | 0.02        |
| Ky226 x Oh43      | $Y = -7.92 - 4.26P + 16.50P^{\frac{1}{2}}$   | .666** | 8.0                              | 1.60              | 0.35        |
| Mp68:616 x Tx601  | $Y = -26.28 - 18.84P + 53.04P^{\frac{1}{2}}$ | .695** | 11.0                             | 0.08              | 0.03        |
| CM104 x Va35      | $Y = -15.77 - 11.04P + 33.00P^{\frac{1}{2}}$ | .660** | 8.9                              | 0.15              | 0.05        |
| CI21E x Ky226     | $Y = -12.42 - 9.30P + 28.38P^{\frac{1}{2}}$  | .545*  | 9.2                              | 0.20              | 0.04        |
| CM104 x PH9       | $Y = -2.56 - 2.92P + 12.81P^{\frac{1}{2}}$   | .611** | 11.0                             | 1.60              | 0.38        |
| H638              | $Y = -4.98 - 2.98P + 16.43P^{\frac{1}{2}}$   | .652** | 15.0                             | 1.60              | 0.80        |
| White Carimagua   | $Y = -5.39 - 4.73P + 18.28P^{\frac{1}{2}}$   | .637** | 12.3                             | 1.60              | 0.35        |
| Yellow Carimagua  | $Y = -1.33 - 4.14P + 13.86P^{\frac{1}{2}}$   | .352   | 10.3                             | 0.70              | 0.05        |

<sup>a</sup>Max. = Maximum yield

<sup>b</sup>P = log (1000 P); P is the adjusted P concentration in the soil solution

model and sometime also because a very few plants were harvested (sometimes less than 10 plants) in the high P treatments. Yield estimates were adjusted to a stand of 60,000 plants/ha. Estimates of P in the adjusted solution for maximum yield ranged from 0.08 ppm to 1.6 ppm, a twenty fold range. The performance of cultivar Mp68:616 x Tx601 was especially impressive. The maximum yield of this cultivar was 11.0 metric tons/ha which was comparable to maximum yields of H610, H788, X304C, and Cm104 x PH9. However, the P requirement of Mp68:616 x Tx601 to attain its maximum yield was only 0.08 ppm which was the lowest among all cultivars.

Estimates of P required for maximum yields were high and may not be optimal for corn production. In addition it is difficult to define maximum yield when yields approach a plateau. In this respect, the level of P associated with 95% of maximum yield, the external P requirement, is preferred.

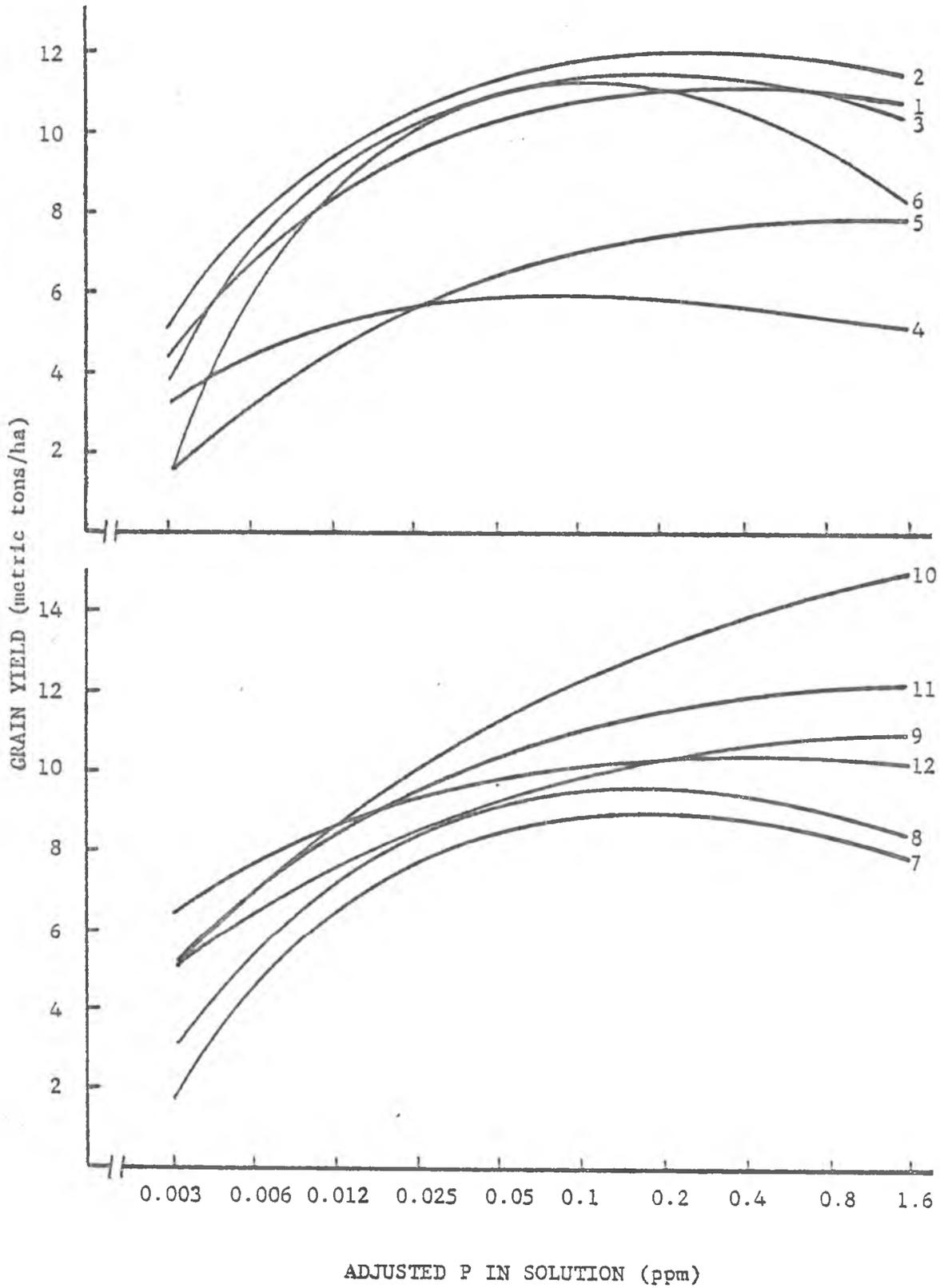
The external P requirement varied widely. The lowest requirement (0.02 ppm P) was for Antigua Composite and the highest (0.80 ppm P) was for H638. Six of the cultivars tested had external P requirements in the range of 0.04 to 0.06 ppm P. The cultivar Antigua Composite had the lowest external P requirement and its yield was also lowest. It would not be recommended for corn production. Cultivar Mp68:616 x Tx601 had a low external P requirement and its yield was high.

Plots of the fitted yield curves gave different response patterns. Yield of one cultivar, Mp68:616 x Tx601 dropped sharply at the high levels of P (Figure 3).

The linear response equations in the linear-response-plateau model for each cultivar are given together with its maximum yield (the

Figure 3. Relationship between grain yield and adjusted P in solution for 12 corn cultivars (fitted curves based on the square root model)

- 1 H610
- 2 H788
- 3 X304C
- 4 Antigua Composite
- 5 Ky226 x Oh43
- 6 Mp68:616 x Tx601
- 7 CM104 x Va35
- 8 CI21E x Ky226
- 9 CM104 x PH9
- 10 H638
- 11 White Carimagua
- 12 Yellow Carimagua



plateau) in Table 27. This table also includes the estimated P requirement at maximum yield and at 95% of maximum yield.

The estimated maximum grain yield of each cultivar in the linear-response-plateau model (Table 27) was slightly less than the maximum grain yield estimated from the square root model. The maximum grain yield of H638 was the highest, 14.5 metric tons/ha. This was similar to the maximum yield predicted by the square root model. The average external P requirement (P requirement at 95% of maximum yield) of 12 cultivars was 0.05 ppm in solution with a range of 0.02 ppm to 0.16 ppm. Except for the lower estimated external P requirement and lower grain yields, other conclusions based on the linear-response-plateau model were similar to those based on the square root model.

The linear-response-plateau model curve of each cultivar is presented in Figure 4. The slopes of the linear portion of the response curves were not tested for statistical differences; however, a large response to P was observed in Mp68:616 x Tx601, X304C, CM104 x Va35, CI21E x Ky226, and Antigua Composite. According to this model, these 5 cultivars fail to respond to P if the P concentration is higher than 0.3 ppm. The other 7 cultivars showed a smaller response but the response continued to higher P concentrations, 0.35 ppm in the case of H638.

According to this model, the cultivars Yellow Carimagua and White Carimagua performed quite well under the low P condition. These two open-pollinated varieties were selected under low P and high aluminum conditions in Colombia. The Hawaiian hybrid H638 (CM111 x Oh545) also performed well under the low P condition. These were in contrast to very poor performance of cultivars Mp68:616 x Tx601, CM104 x Va35, CI21E x Ky226, and Antigua Composite under the low P condition.

Table 27. The linear equation of the response portion of the linear-response-plateau model, maximum yield, and estimated P in the adjusted solution for each of the 12 corn cultivars (cut end)

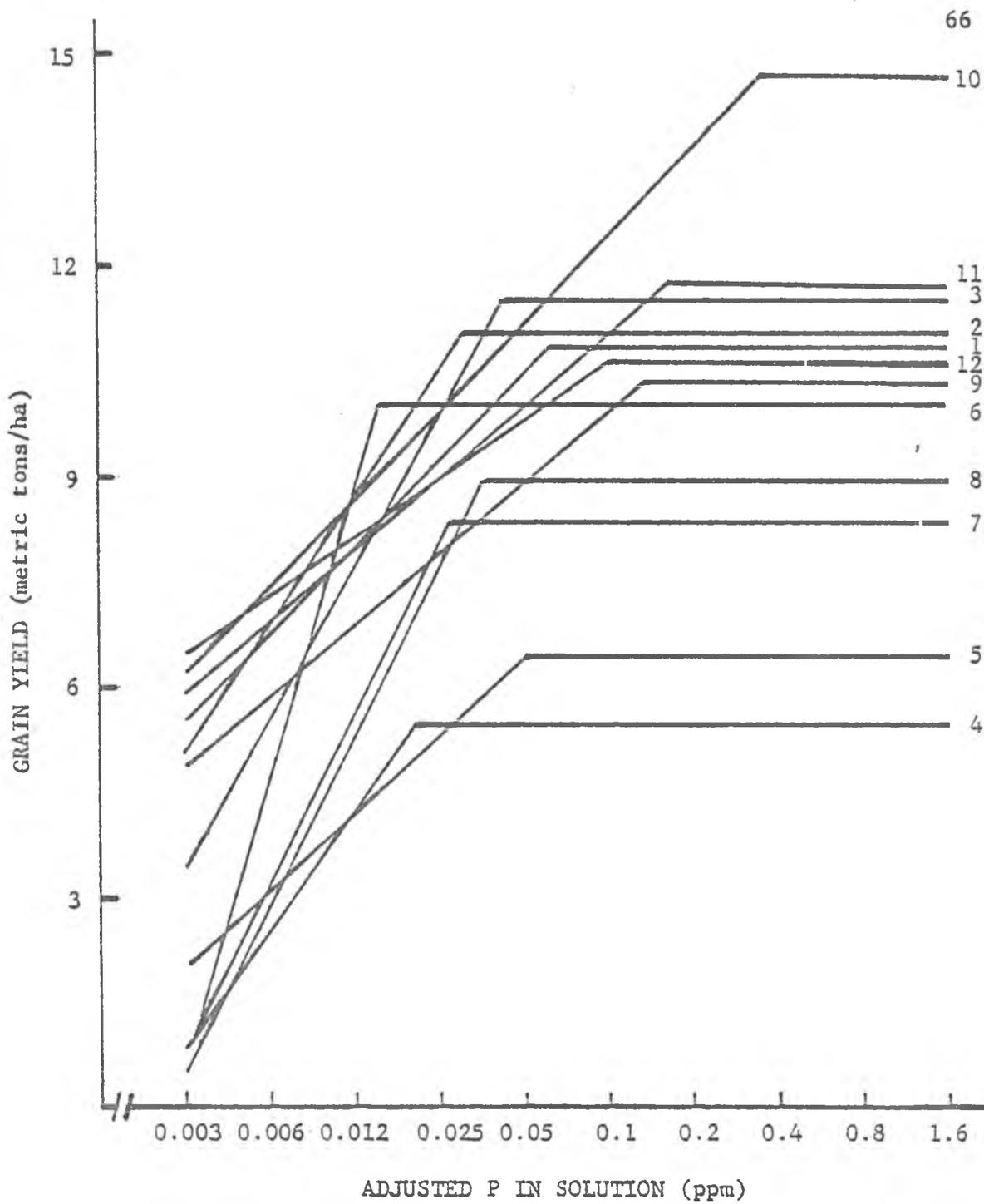
| Cultivars         | Regression equations | Maximum yields | Estimated P       |             |
|-------------------|----------------------|----------------|-------------------|-------------|
|                   |                      |                | Max. <sup>a</sup> | 95% of Max. |
|                   |                      | metric tons/ha | ppm               |             |
| H610              | $Y = 4.26 - 1.26P^b$ | 10.9           | .06               | .05         |
| H788              | $Y = 3.06 + 1.86P$   | 11.0           | .03               | .02         |
| X304C             | $Y = 1.14 + 2.28P$   | 11.5           | .04               | .04         |
| Antigua Composite | $Y = 0.84 + 1.80P$   | 5.5            | .02               | .02         |
| Ky226 x Oh43      | $Y = 0.90 + 1.14P$   | 6.5            | .05               | .04         |
| Mp68:616 x Tx601  | $Y = 3.66 + 4.14P$   | 10.3           | .02               | .01         |
| CM104 x Va35      | $Y = 1.56 + 2.40P$   | 8.4            | .03               | .02         |
| CI21E x Ky226     | $Y = 0.50 + 1.92P$   | 9.0            | .04               | .03         |
| CM104 x PH9       | $Y = 3.84 + 1.02P$   | 10.4           | .13               | .04         |
| H638              | $Y = 5.04 + 1.26P$   | 14.5           | .35               | .16         |
| White Carimagua   | $Y = 4.86 + 1.08P$   | 11.8           | .12               | .06         |
| Yellow Carimagua  | $Y = 5.64 + 0.84P$   | 11.0           | .06               | .05         |

<sup>a</sup> Max. = Maximum yield

<sup>b</sup> P was a coded value of 1, 2, ....., 10, respectively

Figure 4. Relationship between grain yield and adjusted P in solution for 12 corn cultivars (fitted curves based on the linear-response-plateau model)

- 1 H610
- 2 H788
- 3 X304C
- 4 Antigua Composite
- 5 Ky226 x Oh43
- 6 Mp68:616 x Tx601
- 7 CM104 x Va35
- 8 CI21E x Ky226
- 9 CM104 x PH9
- 10 H638
- 11 White Carimagua
- 12 Yellow Carimagua



Mean grain yield overall cultivars for each P level were plotted as a function of P concentration in solution (Figure 5). The regression equation for this relationship on the linear-response-plateau model was  $Y = 2.55 + 1.52P$  where P was coded from 1 to 10 consecutively. The mean maximum yield was 10.0 metric tons/ha. The P requirement for this yield level was 0.05 ppm which agrees with the median of the P requirement at maximum yield of all cultivars. The external P requirement (P requirement at 95% of maximum yield) for corn using the mean of all cultivars was 0.04 ppm.

## 5.2 Summary

The experiment for estimating external P requirement was conducted with 12 corn cultivars. These corn cultivars had different yield potentials as indicated by maximum attainable yield (Table 26). The external P requirements of these corn cultivars were estimated by two regression models, a square root model and a linear-response-plateau model. The results of the square root model were generally higher than those of the linear-response-plateau model. On both models, external P requirements of corn cultivars differed.

Based on the square root model, 6 out of 12 cultivars had external P requirements in the range of 0.04 to 0.06 ppm P which was similar to the value reported earlier. Two of these cultivars, H610 and H788, were used previously in the same type of experiment. The other four cultivars were from other corn producing areas. Six cultivars out of 12 had either lower or higher external P requirements than the first group. The results of this experiment suggest that cultivars with high yield have high external P requirements. This relationship was not strong because

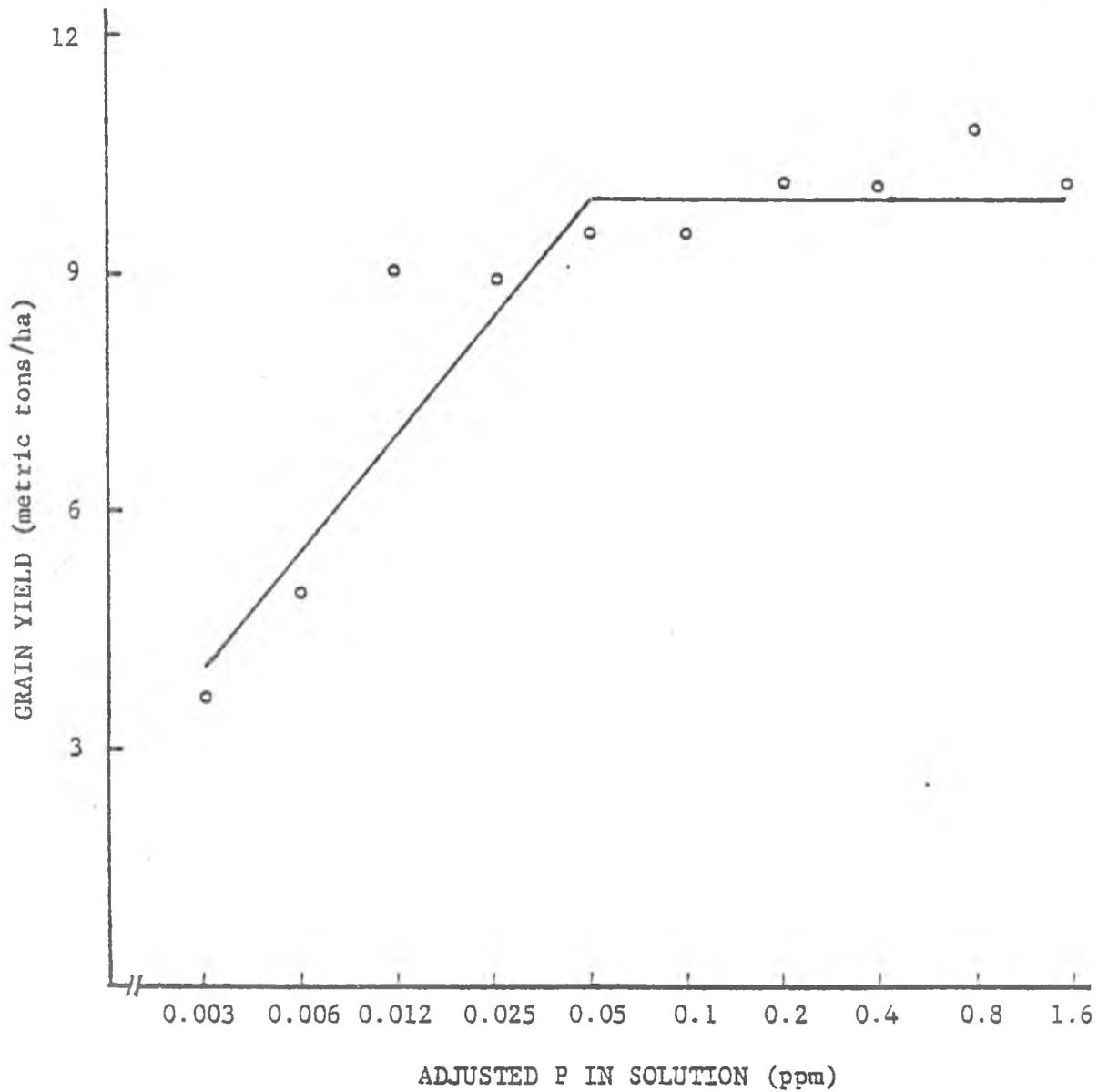


Figure 5. Relationship between average grain yield of 12 corn cultivars and adjusted P in solution (fitted curve based on the linear-response-plateau model).

cultivar Mp68:616 x Tx601 had high yield with a low external P requirement while cultivar Ky226 x Oh43 had low yield with a high external P requirement. These results suggest that it is possible to select a corn cultivar with high yield and a low external P requirement. However, the level of P in the adjusted solution should be equal to or greater than 0.05 ppm to ensure good corn yield.

## 6. ACID PHOSPHATASE ACTIVITY AND ALUMINUM STRESS

Plants are able to utilize organic phosphate in the growth media via the action of acid phosphatase (AP) activity. AP activity in roots of corn plants may have a significant role in making organic phosphate available. Genotypic differences in AP activity in root extracts and intact roots of corn inbreds and hybrids were studied.

### 6.1 Results and Discussion

#### 6.1.1 Acid Phosphatase Activity of Root Extracts

Studies of AP activity were conducted on extracts of roots of corn seedlings which were germinated in the laboratory. AP activities of 25 inbreds were expressed on the basis of fresh weight of roots ( $\mu$ moles pNP/gm of root/hr) and on the basis of amount of protein ( $\mu$ moles pNP/mg of protein) "specific activity" and are presented in Table 28. Inbreds are arranged in order of decreasing AP activity on a fresh weight basis. There were large differences among inbreds in their AP activity when expressed either on the fresh weight basis or as specific activity. Highest AP activities were obtained in the related inbreds A632 and B14A which were about 3 times greater than that of CM109 which had the lowest activity. These large differences in AP activities among inbreds were highly significant (Table 29). The correlation coefficient between AP activity based on fresh weight and AP activity based on specific activity was highly significant ( $r = 0.81^{**}$ ). These results indicate that corn inbreds differ in their AP activity and the activity can be measured as specific activity or based on fresh weight of roots. Therefore subsequent data will be expressed on the fresh weight basis.

Table 28. Acid phosphatase activity of extracts from corn roots of 10-day old seedlings of 25 corn inbreds germinated under laboratory conditions

| Inbreds  | Acid phosphatase activities                 |                               |
|----------|---|-------------------------------|
|          | Fresh weight basis                          | Specific activity             |
|          | $\mu$ moles pNP <sup>a</sup> /gm of root/hr | $\mu$ moles pNP/mg protein/hr |
| A632     | 243   | 2.2                           |
| B14A     | 234   | 1.8                           |
| Ky226    | 223   | 1.5                           |
| Ga203    | 193   | 1.7                           |
| Oh51A    | 190   | 1.0                           |
| N28      | 183   | 1.8                           |
| C123     | 182   | 1.4                           |
| 38-11    | 179   | 1.5                           |
| H95      | 175   | 1.5                           |
| CI21E    | 167   | 1.3                           |
| Va35     | 164   | 1.6                           |
| W64A     | 160   | 1.5                           |
| Oh43     | 157   | 1.2                           |
| H93      | 154   | 1.4                           |
| FR9      | 150   | 1.5                           |
| Mp68:616 | 148   | 1.1                           |
| B37      | 144   | 1.2                           |
| PH9      | 135   | 1.0                           |
| Mo17     | 123   | 1.2                           |
| CM104    | 122   | 1.0                           |
| CM111    | 121   | 1.1                           |
| Oh545    | 105   | 1.0                           |
| SC301    | 96  | .8                            |
| Tx601    | 95  | 1.1                           |
| CM109    | 92  | .6                            |
| BLSD .05 | 61  | .7                            |

<sup>a</sup> pNP = p-nitrophenol

Table 29. Analyses of variance of acid phosphatase activity of extracts from corn roots of 10-day old seedlings of 25 corn inbreds germinated under laboratory conditions (Table 28)

| Source | df | Mean squares       |                   |
|--------|----|--------------------|-------------------|
|        |    | Fresh weight basis | Specific activity |
| Rep    | 3  | 9224**             | 1.25**            |
| Inbred | 24 | 6917**             | .52**             |
| Error  | 72 | 1852               | .19               |

A genetic study of AP activity of root extracts was carried out on genotypes from a 6-entry diallel. Plants were germinated as described for inbred materials and AP activity based on fresh weight of roots is summarized (Table 30). In this 6-entry diallel, variation in AP activity of genotypes was found to be highly significant (Table 31). The highest and lowest AP activities were obtained from inbreds B14A and Tx601, respectively. The mean heterotic effect based on the mid-parental value for this set of genotypes was -11.82% indicating that generally the  $F_1$  hybrids had lower activity than the mid-parental value. Negative heterotic effect in enzyme activity has been reported for AP of corn leaves (Rigo, 1966) and for nitrate reductase (Schrader et al., 1966).

Genotypes in the 6-entry diallel were found to differ in their AP activities (Table 31). This significant difference among genotypes was necessary for a computation of general and specific combining ability analysis. The analysis of variance for combining ability of AP activity of root extracts was performed based on method 2 (parents and  $F_1$  included), model 1 (Table 32). Both GCA (general combining ability) and SCA (specific combining ability) mean squares were highly significant, indicating that both additive and nonadditive genes were important in determining AP activity of the root extracts. Several studies on other enzymes indicated that additive genes were important in controlling enzyme activities (Schrader, 1974; Sorawat, 1975). The results from this study provide additional information on the genetic variation in AP activity in corn populations.

General and specific combining ability effects of genotypes in the 6-entry diallel for their AP activity were estimated by Griffing's method 2 (parents and  $F_1$  included), model 1 and are presented in Table 33.

Table 30. Acid phosphatase activity of extracts from corn roots of 10-day old seedlings of genotypes in a 6-entry diallel germinated under laboratory conditions

| Parents  | Tx601              | Mp68:616 | CM104  | Va35   | Hy226  | B14A   |
|----------|--------------------|----------|--------|--------|--------|--------|
| Tx601    | 92.89 <sup>a</sup> | 143.78   | 109.64 | 136.20 | 110.16 | 135.11 |
| Mp68:616 |                    | 113.16   | 150.13 | 159.89 | 165.71 | 137.91 |
| CM104    |                    |          | 128.31 | 138.49 | 149.01 | 160.54 |
| Va35     |                    |          |        | 184.02 | 139.47 | 186.84 |
| Ky226    |                    |          |        |        | 213.65 | 135.82 |
| B14A     |                    |          |        |        |        | 304.29 |

BLSD<sub>.05</sub> = 23.79; Grand mean = 152.14; Parental mean = 172.71;

F<sub>1</sub> mean = 143.91; Mean heterotic effect = -11.82%

<sup>a</sup>  $\mu$ moles pNP/gm root weight/hr

Table 31. Analysis of variance of acid phosphatase activity of extracts from corn roots of 10-day old seedlings of genotypes in a 6-entry diallel germinated under laboratory conditions (Table 30)

| Source | df | Mean squares |
|--------|----|--------------|
| Rep    | 2  | 1594.5**     |
| G      | 20 | 6127.6**     |
| Error  | 80 | 273.7        |

Table 32. Combining ability analysis of acid phosphatase activity of extracts from corn roots of 10-day old seedlings of genotypes in a 6-entry diallel based on Griffing's method 2, model 1 (Table 30)

| Source | df | Mean squares |
|--------|----|--------------|
| GCA    | 5  | 4510.69**    |
| SCA    | 15 | 1167.48**    |
| Error  | 80 | 91.23        |

Table 33. Estimates of general and specific combining ability effects for acid phosphatase activity of extracts from corn roots of 10-day old seedlings of genotypes in a 6-entry diallel based on Griffing's method 2, model 1 (Table 30)

| Parents  | Tx601 | Mp68:616 | CM104 | Va35 | Ky226 | B14A  | GCA effects |
|----------|-------|----------|-------|------|-------|-------|-------------|
| Tx601    |       | 27.2     | 1.8   | 7.2  | -18.8 | -24.0 | -31.2       |
| Mp68:616 |       |          | 20.7  | 10.1 | 16.1  | 36.1  | -10.1       |
| CM104    |       |          |       | -9.3 | 1.7   | -17.6 | -12.7       |
| Va35     |       |          |       |      | -28.9 | -11.2 | 7.9         |
| Ky226    |       |          |       |      |       | -62.2 | 7.9         |
| B14A     |       |          |       |      |       |       | 38.2        |

$se_d$  between any two GCA effect = 4.8

$se_d$  between effects of two crosses having one parent line in common = 12.6

$se_d$  between effects of two crosses having no parent line in common = 11.7

The general combining ability (GCA) effect of inbreds varied widely. Inbreds Mp68:616, Tx601, and CM104 had negative GCA effects, indicating that these inbreds combined poorly for AP activity. On the other hand, inbreds Ky226, Va35, and B14A had positive GCA effects, indicating that these inbreds were good general combiners for high AP activity.

The coefficient of linear determination ( $R^2$ ) between AP activity of the parents and their respective GCA effects was 94% which was highly significant. This suggests that selecting for AP activity of the inbreds will utilize its GCA value effectively.

The specific combining ability (SCA) effect for AP activity of hybrids indicated whether the AP activity of a hybrid is relatively better or worse than would be expected on the basis of the GCA effect of the parents involved. The highest SCA effect was observed in the hybrid Mp68:616 x Tx601, indicating a good combination of nonadditive genes for high AP activity. On the other hand, hybrid B14A x Ky226 had the lowest SCA effect.

#### 6.1.2 Acid Phosphatase Activity of Intact Corn Roots

The genotypes from a 4-entry diallel grown under two levels of aluminum were evaluated for AP activity of their intact roots. AP activities, expressed on the dry weight of roots, are summarized in Table 34. The analysis of variance of week one data showed that genotype and genotype x aluminum interaction mean squares were highly significant (Table 35). These results suggest that genotypes differ in their AP activity and also differ in their response to aluminum as measured by AP activity. Inbred Va35 had the lowest AP activity with or without added aluminum. Based on the BLSD test, aluminum treatment significantly

Table 34. Acid phosphatase activity of intact roots of corn seedlings of a 4-entry diallel. The seedlings were grown in complete nutrient solution with two levels of aluminum (Al) for one and two weeks.

| Genotypes  | Week one |        | Week two |       |
|--|----------|--------|----------|-------|
|  | -Al      | +Al    | -Al      | +Al   |
| ————— $\mu$ moles pNP/gm dry weight of root/hr ————— |          |        |          |       |
| <u>INBREDS</u>                                       |          |        |          |       |
| Mp68:616   | 110.33   | 115.11 | 66.68    | 83.95 |
| Ky226  | 125.68   | 140.46 | 69.95    | 94.82 |
| Tx601  | 103.81   | 109.72 | 87.03    | 99.52 |
| Va35   | 58.42    | 89.42  | 56.89    | 72.12 |
| <u>F<sub>1</sub> HYBRIDS</u>                         |          |        |          |       |
| Mp68:616 x Ky226                                     | 147.08   | 129.18 | 60.95    | 69.83 |
| Mp68:616 x Tx601                                     | 116.19   | 126.76 | 74.06    | 74.57 |
| Mp68:616 x Va35                                      | 150.92   | 123.05 | 75.31    | 73.73 |
| Ky226 x Tx601  | 156.61   | 129.48 | 68.02    | 83.78 |
| Ky226 x Va35   | 110.77   | 96.94  | 62.13    | 62.44 |
| Tx601 x Va35   | 132.78   | 131.86 | 60.62    | 70.44 |
| Mean   | 121.27   | 119.19 | 68.66    | 78.52 |
| B LSD .05 G x Al                                     | 24.64    |        | 11.95    |       |

Table 35. Analysis of variance of acid phosphatase activity of intact roots of corn seedlings of a 4-entry diallel. The seedlings were grown in complete nutrient solution with two levels of aluminum (Al) for one and two weeks (Table 32)

| Source          | df  | Week one<br>Mean squares | Week two<br>Mean squares |
|-----------------|-----|--------------------------|--------------------------|
| Rep             | 1   | 18630.2**                | 17928.4**                |
| G               | 9   | 7251.0**                 | 12527.3**                |
| Al              | 1   | 171.8                    | 3885.4**                 |
| G x Al          | 9   | 1476.7**                 | 305.0**                  |
| Treatment x Rep | 19  | 963.9                    | 1013.4                   |
| Error           | 120 | 526.5                    | 118.1                    |

increased AP activity of inbred Va35 and significantly decreased the AP activity of hybrid Mp68:616 x Va35. Differences in AP activity between the two aluminum treatments in other genotypes were not significant.

The analysis of variance of AP activity of week two data showed that genotype, aluminum, and genotype x aluminum interaction mean squares were highly significant (Table 35). These results suggested that genotypes differ in their AP activities and their response to aluminum stress as measured by AP activity. In week two, AP activities of corn grown under aluminum stress were generally higher than AP activities of corn grown without aluminum stress. Based on the BLSD test, aluminum stress significantly increased AP activity in all inbreds and one hybrid, Ky226 x Va35. The result of these experiments indicate that corn genotypes differ in their AP activity which might result in differences in their ability to extract organic phosphate from soils.

The genotypes in the 4-entry diallel were found to differ in their AP activity, therefore a combining ability analysis was performed based on method 2, model 1. The analysis was performed separately for each aluminum treatment and each week.

Combining ability analyses of AP activity of intact corn roots are summarized in Table 36. The general combining ability (GCA) and specific combining ability (SCA) mean squares were highly significant in all cases, indicating that both additive and nonadditive genes were important in determining AP activity of intact corn roots. The GCA to SCA ratio was slightly greater than unity in all cases except in the solution without aluminum at week one.

General combining ability effects for AP activity of the 4 parental inbreds are given in Table 37. In week one inbred Va35 had the

Table 36. Combining ability analyses (based on Griffing's method 2, model 1) of acid phosphatase activity of intact roots of corn seedlings of a 4-entry diallel grown in two levels of aluminum (Al) for one and two weeks (Table 34)

|       |    | Week one     |          | Week two     |          |
|-------|----|--------------|----------|--------------|----------|
|       |    | Mean squares |          | Mean squares |          |
|       |    | -Al          | +Al      | -Al          | +Al      |
| GCA   | 3  | 746.50**     | 345.77** | 124.23**     | 177.71** |
| SCA   | 6  | 869.98**     | 224.85** | 57.82**      | 118.27** |
| Error | 60 | 72.49        | 24.26    | 15.69        | 13.82    |

Table 37. Estimates of general combining ability effects (based on Griffing's method 2, model 1) for acid phosphatase activity of intact roots of corn seedlings of a 4-entry diallel grown in two levels of aluminum (Al) for one and two weeks (Table 34)

|                                   | General combining ability effects |        |          |       |
|-----------------------------------|-----------------------------------|--------|----------|-------|
|                                   | Week one                          |        | Week two |       |
|                                   | -Al                               | +Al    | -Al      | +Al   |
| Mp68:616                          | 4.75                              | 2.21   | .48      | -1.09 |
| Ky226                             | 9.93                              | 6.76   | -1.64    | 2.18  |
| Tx601                             | 1.15                              | 1.92   | 5.99     | 5.87  |
| Va35                              | -15.83                            | -10.89 | -4.83    | -6.96 |
| $se_d$ between any<br>two effects | 4.91                              | 2.84   | 2.29     | 2.15  |

lowest GCA effect, indicating that Va35 was a poor combiner for high AP activity. Inbreds Ky226, Mp68:616, and Tx601 had positive GCA effects. The high GCA effect in Ky226 indicated that Ky226 was generally a good combiner for AP activity. In week two, inbred Tx601 had the highest GCA effect while inbred Va35 had the lowest GCA effect.

Estimates of the SCA effect of AP activity of intact corn roots of the 4-entry diallel are presented in Table 38. SCA effects differed widely under different aluminum treatment. In almost all cases, hybrid Mp68:616 x Va35 had the highest SCA effect, indicating a good combination of nonadditive genes in these two parents for high AP activity of intact roots.

#### 6.1.3 Genotypic Response to Aluminum Stress

The shoot and root weights of corn plants grown for one and two weeks in nutrient solution with 2 levels of aluminum (0 and 6 mg Al/liter) were studied for the effects of aluminum stress and are summarized in Tables 39 and 41, respectively. The analyses of variance of shoot weight using a randomized block design with two replications showed that both genotype and aluminum caused significant difference in shoot growth (Table 40). During the first week, genotypes did not interact significantly with aluminum treatments, but this interaction was highly significant in the second week, indicating that the response of shoot dry weight to aluminum differed with genotype. Based on the BLSD of interaction, shoot weights of inbreds Tx601 and Ky226 were significantly decreased by aluminum whereas decrease in shoot weight with increasing aluminum in the other genotypes was not significant.

Root weights are summarized in Table 41, and the analyses of variance of root weights are presented in Table 42. The roots of

Table 38. Estimates of specific combining ability effects (based on Griffing's method 2, model 1) for acid phosphatase activity of intact roots of corn seedlings of a 4-entry diallel grown in two levels of aluminum for one and two weeks (Table 34)

| Hybrids                    | Specific combining ability effects |        |          |        |
|----------------------------|------------------------------------|--------|----------|--------|
|                            | Week one                           |        | Week two |        |
|                            | -Al                                | +Al    | -Al      | +Al    |
| Mp68:616 x Ky226           | 11.16                              | 1.02   | -6.05    | -9.78  |
| Mp68:616 x Tx601           | -10.96                             | 3.46   | -.57     | -8.73  |
| Mp68:616 x Va35            | 40.72                              | 12.57  | 11.50    | 3.26   |
| Ky226 x Tx601              | 24.26                              | 1.61   | -4.50    | -2.79  |
| Ky226 x Va35               | -4.56                              | -18.18 | .43      | -11.30 |
| Tx601 x Va35               | 26.22                              | 21.66  | -8.70    | -6.99  |
| $SE_{(s_{ij} - s_{ik})}^a$ | 10.99                              | 6.36   | 5.11     | 4.80   |
| $SE_{(s_{ij} - s_{kl})}^b$ | 9.82                               | 5.69   | 4.57     | 4.29   |

<sup>a</sup> $se_d$  between effects of two crosses having one parent line in common

<sup>b</sup> $se_d$  between effects of two crosses having no parent line in common

Table 39. Dry weight of shoots of a 4-entry diallel of corn grown for one and two weeks in complete nutrient solution with two levels of aluminum (Al)

| Genotypes                    | Week one |      | Week two |      |
|------------------------------|----------|------|----------|------|
|                              | -Al      | +Al  | -Al      | +Al  |
| ————— gm/plant —————         |          |      |          |      |
| <u>INBREDS</u>               |          |      |          |      |
| Mp68:616                     | 0.26     | 0.19 | 0.95     | 0.62 |
| Ky226                        | 0.26     | 0.18 | 0.99     | 0.45 |
| Tx601                        | 0.15     | 0.08 | 0.92     | 0.14 |
| Va35                         | 0.20     | 0.14 | 0.84     | 0.57 |
| Mean                         | 0.22     | 0.15 | 0.93     | 0.45 |
| <u>F<sub>1</sub> HYBRIDS</u> |          |      |          |      |
| Mp68:616 x Ky226             | 0.40     | 0.36 | 1.15     | 1.28 |
| Mp68:616 x Tx601             | 0.49     | 0.34 | 1.26     | 1.15 |
| Mp68:616 x Va35              | 0.34     | 0.26 | 1.06     | 0.96 |
| Ky226 x Tx601                | 0.42     | 0.23 | 1.03     | 0.83 |
| Ky226 x Va35                 | 0.45     | 0.34 | 1.17     | 1.08 |
| Tx601 x Va35                 | 0.36     | 0.24 | 1.08     | 1.08 |
| Mean                         | 0.41     | 0.30 | 1.13     | 1.06 |
| BLSD .05 G                   |          | 0.07 |          | 0.21 |
| BLSD .05 G x AL              |          | 0.34 |          | 0.34 |

Table 40. Analyses of variance of dry weight of shoots of a 4-entry diallel of corn grown for one and two weeks in complete nutrient solution with two levels of aluminum (Al) (Table 39)

| Source         | df  | Mean squares |          |
|----------------|-----|--------------|----------|
|                |     | Week one     | Week two |
| Rep            | 1   | .1402**      | .2770    |
| Treatment (19) |     |              |          |
| G              | 9   | .1478**      | .8879**  |
| Al             | 1   | .4326**      | 2.0525** |
| G x Al         | 9   | .0078        | .2840**  |
| Residual       | 19  | .0125        | .0969    |
| Error          | 120 | .0125        | .1013    |

Table 41. Root dry weight of a 4-entry diallel of corn grown for one and two weeks in complete nutrient solution with two levels of aluminum (Al)

| Genotypes                    | Week one |      | Week two |      |
|------------------------------|----------|------|----------|------|
|                              | -Al      | +Al  | -Al      | +Al  |
| ----- gm/plant -----         |          |      |          |      |
| <u>INBREDS</u>               |          |      |          |      |
| Mp68:616                     | 0.10     | 0.10 | 0.39     | 0.31 |
| Ky226                        | 0.10     | 0.08 | 0.52     | 0.25 |
| Tx601                        | 0.04     | 0.04 | 0.37     | 0.08 |
| Va35                         | 0.07     | 0.08 | 0.33     | 0.24 |
| Mean                         | 0.08     | 0.08 | 0.40     | 0.22 |
| <u>F<sub>1</sub> HYBRIDS</u> |          |      |          |      |
| Mp68:616 x Ky226             | 0.16     | 0.15 | 0.66     | 0.54 |
| Mp68:616 x Tx601             | 0.24     | 0.16 | 0.66     | 0.52 |
| Mp68:616 x Va35              | 0.12     | 0.14 | 0.52     | 0.42 |
| Ky226 x Tx601                | 0.17     | 0.14 | 0.67     | 0.40 |
| Ky226 x Va35                 | 0.17     | 0.17 | 0.59     | 0.51 |
| Tx601 x Va35                 | 0.12     | 0.12 | 0.56     | 0.49 |
| Mean                         | 0.16     | 0.15 | 0.61     | 0.48 |
| BLSD .05 <sup>G</sup>        | 0.03     |      | 0.004    |      |

Table 42. Analyses of variance of root dry weight of a 4-entry diallel of corn grown for one and two weeks in complete nutrient solution with 2 levels of aluminum (Al) (Table 41)

| Source         | df  | Mean squares |          |
|----------------|-----|--------------|----------|
|                |     | Week one     | Week two |
| Rep            | 1   | .0165**      | .0236    |
| Treatment (19) |     |              |          |
| G              | 9   | .0347**      | .2767**  |
| Al             | 1   | .0029        | .9141**  |
| G x Al         | 9   | .0026        | .0318    |
| Residual       | 19  | .0031        | .0249    |
| Error          | 120 | .0023        | .0168    |

hybrids weighed about twice as much as those of inbreds. The analysis of variance of the first-week data indicated that the aluminum effect was not significant, but that genotypes differed significantly. In the second week, aluminum and genotype mean squares were highly significant but the genotype by aluminum interaction mean square was not. The lack of significant of genotype by aluminum interaction indicated that response of roots to aluminum was the same for all genotypes.

Aluminum stress, in this experiment, affected shoots more than roots. It should be pointed out that the level of aluminum in this experiment was high but the period of treatment was relatively short. However, the high aluminum treatment for two weeks damaged the roots of corn plants. These results were similar to those in other studies with corn (Rhue and Grogan, 1977) and with other crops (Reid et al., 1969). Genetic variation in aluminum tolerance by genotypes is indicated by variation in shoot weight among genotypes during the two-week treatment period in the present study. Inbred Va35 was more tolerant to high aluminum than inbred Tx601. In the study of Rhue and Grogan (1977), Val7, a relative of Va35, was resistant to aluminum toxicity. The results of this study and that of Rhue and Grogan (1977) indicate that inbreds related to Val7 and Va35 should be tested more thoroughly for their tolerance to aluminum stress.

## 6.2 Summary

In this study, AP activity of corn root extracts and of intact corn roots were investigated. The results showed that inbreds varied widely in AP activity of root extracts. These variations were expressed on the basis of root weight or as specific activity. Genetic variation in AP

activity of corn root extracts was investigated in a 6-entry diallel. Combining ability analysis indicated that both additive and nonadditive genes were important in controlling AP activity of corn root extracts. It suggests that selection for high or low AP activity in root extracts is possible in corn populations.

AP activities of intact corn roots were found to vary among genotypes and the response of genotypes to aluminum stress, as measured by their AP activities, also differed. The increase in AP activity by aluminum was detected predominantly on inbreds in week two. Genetic interpretation of data was based on the fixed model (parents were selected). In all cases, additive and nonadditive genes were important in controlling AP activity of intact corn roots and a large proportion of genetic variation was due to nonadditive genetic variance.

## 7. CONCLUSIONS

Studies were made to evaluate response of corn genotypes to two levels of P, to determine level of genetic variation of P concentration, P uptake, and grain yield under two levels of P and acid phosphatase (AP) activity under two levels of aluminum, and to estimate the external P requirement of corn cultivars in the field.

High P fertility improves seedling vigor, maturity, grain yield, yield components, and P uptake of corn genotypes. The most important result in this study is that corn genotypes respond differently to P fertility. This differential response can be measured in seedling dry weight, days to anthesis, grain yield, yield components, P concentration, and P uptake. Genetic study of P concentration, P uptake, and grain yield reveals higher narrow-sense heritabilities under low P compared to lower narrow-sense heritabilities under high P. All narrow-sense heritabilities were low, but substantial enough to encourage recurrent selection in corn population for improving these three characters.

Estimates of external P requirements of corn cultivars used in this experiment varied from 0.02 to 0.8 ppm but most corn cultivars had external P requirements in the range of 0.04 to 0.06 ppm. This range of P concentration in solution can be tentatively recommended for corn cultivars. Cultivars with extremely low external P requirements (0.02 ppm) and high yield potential were found which suggests that it is possible to select a corn cultivar with low external P requirement and high yield for areas with soils which have low P availability.

AP activity of root extracts of corn genotypes differed. In a 6-entry diallel, additive and nonadditive genes were important in controlling AP activity of root extracts of corn genotypes suggesting that

it is possible to develop a corn population with high AP activity of root extracts. Corn genotypes also differed in AP activity of intact roots. Response of shoot weight and AP activity of intact roots to aluminum differed among corn genotypes. This indicates that there is genetic variation in response to aluminum in a corn population and suggests that aluminum tolerant genotypes can be selected. The nature of the inheritance of aluminum tolerance and AP activity of intact roots must be studied in detail.

APPENDIX A  
TABLES OF DATA

A1. Dry weights of shoots of corn plants grown for 3 weeks  
in pots with two levels of P

| Inbreds | Low P                 | High P | % Increase |
|---------|-----------------------|--------|------------|
|         | ———— gm/4 plants ———— |        |            |
| 74-1721 | 2.16                  | 3.00   | 39         |
| 74-1610 | 2.05                  | 2.26   | 10         |
| 74-1629 | 1.04                  | 2.06   | 98         |
| 38-11   | 0.86                  | 1.99   | 131        |
| B14A    | 2.04                  | 3.14   | 54         |
| B37     | 2.72                  | 3.18   | 17         |
| C123    | 2.42                  | 2.90   | 20         |
| CM104   | 2.46                  | 3.61   | 47         |
| CM105   | 1.64                  | 2.76   | 68         |
| CM109   | 2.44                  | 3.20   | 31         |
| CM111   | 1.76                  | 2.68   | 52         |
| F44     | 1.41                  | 2.52   | 79         |
| H55     | 2.14                  | 2.12   | 00         |
| H84     | 2.38                  | 3.39   | 42         |
| H91     | 1.19                  | 2.14   | 80         |
| H93     | 1.98                  | 2.97   | 50         |
| H95     | 1.81                  | 3.49   | 93         |
| K148    | 1.47                  | 1.48   | 1          |
| Mo17    | 2.30                  | 3.12   | 36         |
| N28     | 1.49                  | 2.33   | 56         |
| Oh43    | 1.40                  | 2.44   | 74         |
| Oh51A   | 0.80                  | 0.90   | 13         |
| Oh545   | 2.80                  | 3.56   | 27         |
| PH9     | 1.88                  | 3.60   | 91         |
| SC301   | 1.25                  | 1.54   | 23         |
| Tx601   | 0.96                  | 1.16   | 21         |
| Va35    | 2.57                  | 4.16   | 62         |
| W64A    | 1.68                  | 2.37   | 41         |
| Average | 1.83                  | 2.65   | 45         |

A2. Seedling dry weights of a 10-entry diallel grown under low and high P for four weeks in the field

| Genotypes                    | Winter |        |                    | Summer |        |       |
|------------------------------|--------|--------|--------------------|--------|--------|-------|
|                              | Low P  | High P | Diff. <sup>a</sup> | Low P  | High P | Diff. |
| ————— gm/4 plants —————      |        |        |                    |        |        |       |
| <u>INBREDS</u>               |        |        |                    |        |        |       |
| Mp68:616                     | 2.4    | 4.4    | 2.0                | 7.1    | 8.9    | 1.8   |
| CI21E                        | 1.9    | 4.8    | 2.9                | 2.4    | 5.6    | 3.2   |
| Ky226                        | 1.2    | 1.6    | 0.4                | 3.4    | 3.1    | -0.3  |
| Tx601                        | 1.5    | 2.6    | 1.1                | 2.3    | 2.4    | 0.1   |
| CM104                        | 2.8    | 6.2    | 3.4                | 3.4    | 9.8    | 6.4   |
| FR9                          | 1.3    | 4.6    | 3.3                | 2.0    | 4.8    | 2.8   |
| PH9                          | 2.8    | 7.5    | 4.7                | 2.7    | 7.4    | 4.7   |
| Oh51A                        | 1.3    | 1.5    | 0.2                | 0.8    | 2.5    | 1.7   |
| B14A                         | 2.5    | 3.7    | 1.2                | 5.3    | 7.3    | 2.0   |
| Va35                         | 2.1    | 4.3    | 2.2                | 3.0    | 5.0    | 2.0   |
| <u>F<sub>1</sub> HYBRIDS</u> |        |        |                    |        |        |       |
| Mp68:616 x CI21E             | 3.7    | 3.9    | 0.2                | 5.7    | 9.2    | 3.5   |
| Mp68:616 x Ky226             | 4.4    | 6.2    | 1.8                | 7.4    | 8.2    | 0.8   |
| Mp68:616 x Tx601             | 3.1    | 7.4    | 4.3                | 6.4    | 9.6    | 3.2   |
| Mp68:616 x CM104             | 5.4    | 8.6    | 3.2                | 9.3    | 18.3   | 9.0   |
| Mp68:616 x FR9               | 2.8    | 8.6    | 5.8                | 5.0    | 8.2    | 3.2   |
| Mp68:616 x PH9               | 4.1    | 10.1   | 6.0                | 5.3    | 21.9   | 16.6  |
| Mp68:616 x Oh51A             | 3.8    | 5.0    | 1.2                | 6.2    | 9.4    | 3.2   |
| Mp68:616 x B14A              | 3.8    | 7.4    | 3.6                | 6.4    | 9.8    | 3.4   |
| Mp68:616 x Va35              | 3.4    | 11.3   | 7.9                | 6.7    | 10.3   | 3.6   |
| CI21E x Ky226                | 3.0    | 8.3    | 5.3                | 3.6    | 8.4    | 4.8   |
| CI21E x Tx601                | 3.1    | 6.4    | 3.3                | 5.9    | 11.5   | 5.6   |
| CI21E x CM104                | 3.7    | 5.6    | 1.9                | 4.8    | 11.2   | 6.4   |
| CI21E x FR9                  | 2.7    | 5.8    | 3.1                | 5.2    | 8.7    | 3.5   |
| CI21E x PH9                  | 4.2    | 8.4    | 4.2                | 5.2    | 9.5    | 4.3   |
| CI21E x Oh51A                | 3.3    | 5.5    | 2.2                | 3.7    | 7.8    | 4.1   |
| CI21E x B14A                 | 3.0    | 5.6    | 2.6                | 4.4    | 8.4    | 4.0   |
| CI21E x Va35                 | 3.1    | 4.9    | 1.8                | 5.2    | 8.6    | 3.4   |
| Ky226 x Tx601                | 3.4    | 6.9    | 3.5                | 4.6    | 10.9   | 6.3   |
| Ky226 x CM104                | 3.1    | 7.2    | 4.1                | 6.2    | 8.9    | 2.7   |
| Ky226 x FR9                  | 2.3    | 3.7    | 1.4                | 5.3    | 9.5    | 4.2   |
| Ky226 x PH9                  | 3.3    | 10.5   | 7.2                | 8.4    | 10.1   | 1.7   |
| Ky226 x Oh51A                | 2.3    | 2.3    | 0                  | 4.5    | 7.6    | 3.1   |
| Ky226 x B14A                 | 2.7    | 5.8    | 3.1                | 8.1    | 9.5    | 1.4   |
| Ky226 x Va35                 | 2.9    | 7.8    | 4.9                | 2.9    | 5.5    | 2.6   |
| Tx601 x CM104                | 3.1    | 8.4    | 5.3                | 4.3    | 9.3    | 5.0   |
| Tx601 x FR9                  | 2.9    | 7.0    | 4.1                | 4.6    | 10.2   | 5.6   |
| Tx601 x PH9                  | 4.7    | 8.7    | 4.0                | 4.9    | 13.1   | 8.2   |
| Tx601 x Oh51A                | 2.2    | 10.3   | 8.1                | 4.2    | 7.7    | 3.5   |

A2. (Continued) Seedling dry weights of a 10-entry diallel grown under low and high P for four weeks in the field

| Genotypes      | Winter |        |                    | Summer |        |       |
|----------------|--------|--------|--------------------|--------|--------|-------|
|                | Low P  | High P | Diff. <sup>a</sup> | Low P  | High P | Diff. |
| gm/4 plants    |        |        |                    |        |        |       |
| Tx601 x B14A   | 3.4    | 3.9    | 0.5                | 5.6    | 10.6   | 5.0   |
| Tx601 x Va35   | 2.9    | 7.6    | 4.7                | 4.3    | 10.6   | 6.3   |
| CM104 x FR9    | 3.0    | 9.8    | 6.8                | 5.4    | 11.4   | 6.0   |
| CM104 x PH9    | 5.6    | 8.3    | 2.7                | 7.9    | 12.2   | 4.3   |
| CM104 x Oh51A  | 2.9    | 5.2    | 2.3                | 4.9    | 8.5    | 3.6   |
| CM104 x B14A   | 3.6    | 7.0    | 3.4                | 5.1    | 10.8   | 5.7   |
| CM104 x Va35   | 3.6    | 7.2    | 3.6                | 7.5    | 11.5   | 4.0   |
| FR9 x PH9      | 4.2    | 5.1    | 0.9                | 6.2    | 16.5   | 10.3  |
| FR9 x Oh51A    | 2.3    | 10.1   | 7.8                | 6.8    | 8.2    | 1.4   |
| FR9 x B14A     | 3.0    | 5.8    | 2.8                | 6.5    | 14.1   | 7.6   |
| FR9 x Va35     | 2.0    | 4.5    | 2.5                | 1.3    | 7.7    | 6.4   |
| PH9 x Oh51A    | 3.4    | 7.9    | 4.5                | 3.2    | 15.4   | 12.2  |
| PH9 x B14A     | 4.4    | 7.3    | 2.9                | 7.6    | 13.4   | 5.8   |
| PH9 x Va35     | 2.5    | 8.3    | 5.8                | 8.5    | 16.9   | 8.4   |
| Oh51A x B14A   | 3.3    | 5.9    | 2.6                | 7.2    | 12.4   | 5.2   |
| Oh51A x Va35   | 2.0    | 3.9    | 1.9                | 2.0    | 3.8    | 1.8   |
| B14A x Va35    | 3.6    | 5.2    | 1.6                | 5.9    | 12.4   | 6.5   |
| Average        | 3.1    | 6.4    |                    | 5.1    | 9.6    |       |
| BLSD .05 G x P |        |        | 2.6                |        |        | 5.5   |

<sup>a</sup> Diff. in this and subsequent tables refers to the difference between high P and low P

A3. Mean days to silking and anthesis of a 10-entry diallel cross grown under low and high P in the field

| Genotypes                    | Silking |        |        |        | Anthesis |        |       |
|------------------------------|---------|--------|--------|--------|----------|--------|-------|
|                              | Winter  |        | Summer |        | Summer   |        | Diff. |
|                              | Low P   | High P | Low P  | High P | Low P    | High P |       |
|                              | days    |        |        |        |          |        |       |
| <u>INBREDS</u>               |         |        |        |        |          |        |       |
| Mp68:616                     | 75.1    | 69.9   | 66.1   | 62.1   | 63.6     | 60.2   | 3.4   |
| CI21E                        | 76.3    | 71.8   | 71.1   | 66.3   | 66.1     | 62.3   | 3.8   |
| Ky226                        | 78.1    | 74.6   | 75.3   | 68.9   | 71.4     | 65.8   | 5.6   |
| Tx601                        | 85.4    | 79.1   | 76.3   | 72.9   | 72.9     | 69.3   | 3.6   |
| CM104                        | 75.1    | 69.4   | 70.8   | 66.0   | 67.7     | 63.9   | 3.8   |
| FR9                          | 71.4    | 66.5   | 67.1   | 59.6   | 63.7     | 57.7   | 6.0   |
| PH9                          | 67.2    | 63.5   | 62.0   | 58.3   | 60.8     | 57.5   | 3.3   |
| Oh51A                        | 74.3    | 70.2   | 66.1   | 60.6   | 63.0     | 58.3   | 4.7   |
| B14A                         | 71.6    | 70.4   | 64.7   | 59.6   | 62.5     | 58.0   | 4.5   |
| Va35                         | 68.4    | 63.6   | 58.7   | 58.1   | 56.8     | 56.5   | 0.3   |
| <u>F<sub>1</sub> HYBRIDS</u> |         |        |        |        |          |        |       |
| Mp68:616 x CI21E             | 72.8    | 69.9   | 65.3   | 63.8   | 62.6     | 60.9   | 1.7   |
| Mp68:616 x Ky226             | 67.6    | 65.7   | 64.5   | 61.6   | 62.6     | 59.4   | 3.2   |
| Mp68:616 x Tx601             | 73.8    | 68.2   | 67.0   | 64.8   | 65.1     | 63.2   | 1.9   |
| Mp68:616 x CM104             | 68.1    | 65.6   | 64.3   | 62.6   | 62.5     | 61.7   | 0.8   |
| Mp68:616 x FR9               | 66.7    | 62.0   | 61.2   | 57.1   | 58.9     | 55.8   | 3.1   |
| Mp68:616 x PH9               | 64.5    | 60.9   | 61.5   | 58.1   | 60.6     | 57.5   | 3.1   |
| Mp68:616 x Oh51A             | 65.3    | 64.0   | 60.0   | 58.3   | 58.9     | 56.9   | 2.0   |
| Mp68:616 x B14A              | 68.2    | 64.5   | 61.5   | 59.1   | 60.3     | 57.5   | 2.8   |
| Mp68:616 x Va35              | 66.8    | 61.2   | 60.9   | 57.7   | 59.8     | 56.8   | 3.0   |
| CI21E x Ky226                | 72.8    | 66.5   | 65.5   | 60.0   | 63.2     | 60.3   | 2.9   |
| CI21E x Tx601                | 72.8    | 68.6   | 67.4   | 64.6   | 64.8     | 62.3   | 2.5   |
| CI21E x CM104                | 71.5    | 68.4   | 67.2   | 63.0   | 65.0     | 60.3   | 4.7   |
| CI21E x FR9                  | 71.2    | 65.4   | 63.6   | 59.6   | 60.7     | 57.1   | 3.6   |
| CI21E x PH9                  | 67.0    | 63.8   | 61.7   | 59.7   | 60.3     | 57.9   | 2.4   |
| CI21E x Oh51A                | 67.6    | 64.6   | 62.9   | 60.0   | 60.8     | 57.7   | 3.1   |
| CI21E x B14A                 | 69.7    | 65.4   | 63.8   | 58.7   | 61.6     | 57.2   | 4.4   |
| CI21E x Va35                 | 66.9    | 66.8   | 63.5   | 59.0   | 60.9     | 57.6   | 3.3   |
| Ky226 x Tx601                | 73.6    | 69.7   | 68.1   | 64.9   | 66.1     | 63.6   | 2.5   |
| Ky226 x CM104                | 70.3    | 66.4   | 65.3   | 62.7   | 63.6     | 60.7   | 2.9   |
| Ky226 x FR9                  | 69.7    | 68.7   | 62.7   | 60.2   | 61.2     | 58.6   | 2.6   |
| Ky226 x PH9                  | 66.4    | 60.9   | 61.2   | 58.2   | 60.3     | 57.3   | 3.0   |
| Ky226 x Oh51A                | 66.4    | 65.7   | 60.3   | 58.7   | 58.4     | 57.9   | 0.5   |
| Ky226 x B14A                 | 69.8    | 65.7   | 62.9   | 60.1   | 61.6     | 58.5   | 3.1   |
| Ky226 x Va35                 | 69.4    | 63.4   | 61.0   | 59.1   | 59.8     | 57.7   | 2.1   |
| Tx601 x CM104                | 76.0    | 68.7   | 69.9   | 66.7   | 66.6     | 64.5   | 2.1   |
| Tx601 x FR9                  | 71.6    | 65.9   | 64.0   | 60.8   | 62.0     | 59.7   | 2.3   |
| Tx601 x PH9                  | 68.1    | 65.7   | 62.9   | 62.9   | 62.6     | 61.3   | 1.3   |
| Tx601 x Oh51A                | 69.4    | 66.1   | 64.4   | 61.6   | 62.5     | 60.3   | 2.2   |
| Tx601 x B14A                 | 70.8    | 65.1   | 65.8   | 60.8   | 64.5     | 58.8   | 5.7   |
| Tx601 x Va35                 | 69.7    | 65.3   | 63.2   | 59.7   | 62.0     | 58.8   | 3.2   |

A3. (Continued) Mean days to silking and anthesis of a 10-entry diallel cross grown under low and high P in the field

| Genotypes      | Silking |        |        |        | Anthesis |        |       |
|----------------|---------|--------|--------|--------|----------|--------|-------|
|                | Winter  |        | Summer |        | Summer   |        | Diff. |
|                | Low P   | High P | Low P  | High P | Low P    | High P |       |
|                | days    |        |        |        |          |        |       |
| CM104 x FR9    | 69.7    | 64.1   | 63.2   | 61.1   | 61.7     | 59.4   | 2.3   |
| CM104 x PH9    | 64.9    | 63.6   | 62.2   | 61.5   | 60.8     | 60.0   | 0.8   |
| CM104 x Oh51A  | 68.7    | 65.2   | 62.1   | 59.4   | 60.5     | 58.4   | 2.1   |
| CM104 x B14A   | 68.6    | 65.7   | 63.2   | 60.6   | 61.7     | 58.9   | 2.8   |
| CM104 x Va35   | 66.5    | 66.4   | 61.3   | 57.7   | 59.6     | 56.9   | -0.3  |
| FR9 x PH9      | 63.8    | 60.5   | 59.2   | 60.0   | 58.1     | 54.6   | 3.5   |
| FR9 x Oh51A    | 62.4    | 57.8   | 58.0   | 54.4   | 56.8     | 53.6   | 3.2   |
| FR9 x B14A     | 66.1    | 62.3   | 60.2   | 55.8   | 56.6     | 54.6   | 2.0   |
| FR9 x Va35     | 67.3    | 62.9   | 61.0   | 55.9   | 59.2     | 55.0   | 4.2   |
| PH9 x Oh51A    | 63.2    | 61.2   | 59.9   | 55.7   | 58.6     | 55.0   | 3.6   |
| PH9 x B14A     | 63.4    | 61.2   | 60.6   | 56.9   | 59.6     | 56.2   | 3.4   |
| PH9 x Va35     | 61.2    | 58.2   | 58.2   | 56.3   | 57.6     | 56.0   | 1.6   |
| Oh51A x B14A   | 66.7    | 60.9   | 59.0   | 56.0   | 57.7     | 54.7   | 3.0   |
| Oh51A x Va35   | 66.9    | 64.4   | 58.6   | 55.5   | 57.4     | 54.6   | 2.8   |
| B14A x Va35    | 65.9    | 62.7   | 58.9   | 56.3   | 58.1     | 55.3   | 2.8   |
| Average        | 69.4    | 65.5   | 63.6   | 60.3   | 61.7     | 58.7   |       |
| BLSD .05 G x P |         | ns     | ns     |        |          |        | 2.4   |

A4. Mean ear and plant height of a 10-entry diallel grown under low and high P in two seasons in the field (only inbred and hybrid means are shown)

| Genotypes                    | Ear height |        | Plant height |        |
|------------------------------|------------|--------|--------------|--------|
|                              | Winter     | Summer | Winter       | Summer |
| cm                           |            |        |              |        |
| <u>INBREDS</u>               |            |        |              |        |
| Mp68:616                     | 71         | 78     | 180          | 198    |
| CI21E                        | 64         | 74     | 149          | 197    |
| Ky226                        | 40         | 63     | 145          | 186    |
| Tx601                        | 60         | 76     | 168          | 202    |
| CM104                        | 79         | 94     | 166          | 203    |
| FR9                          | 31         | 38     | 109          | 147    |
| PH9                          | 64         | 84     | 158          | 204    |
| Oh51A                        | 31         | 40     | 98           | 148    |
| B14A                         | 48         | 61     | 149          | 177    |
| Va35                         | 42         | 41     | 136          | 170    |
| <u>F<sub>1</sub> HYBRIDS</u> |            |        |              |        |
| Mp68:616 x CI21E             | 80         | 93     | 193          | 230    |
| Mp68:616 x Ky226             | 76         | 96     | 197          | 233    |
| Mp68:616 x Tx601             | 93         | 101    | 208          | 250    |
| Mp68:616 x CM104             | 88         | 111    | 191          | 223    |
| Mp68:616 x FR9               | 61         | 78     | 177          | 213    |
| Mp68:616 x PH9               | 86         | 109    | 193          | 241    |
| Mp68:616 x Oh51A             | 68         | 92     | 181          | 226    |
| Mp68:616 x B14A              | 78         | 89     | 197          | 222    |
| Mp68:616 x Va35              | 72         | 75     | 179          | 214    |
| CI21E x Ky226                | 80         | 95     | 189          | 237    |
| CI21E x Tx601                | 87         | 110    | 216          | 250    |
| CI21E x CM104                | 93         | 109    | 202          | 235    |
| CI21E x FR9                  | 81         | 75     | 192          | 207    |
| CI21E x PH9                  | 81         | 99     | 187          | 234    |
| CI21E x Oh51A                | 72         | 78     | 187          | 221    |
| CI21E x B14A                 | 72         | 75     | 189          | 207    |
| CI21E x Va35                 | 60         | 77     | 177          | 218    |
| Ky226 x Tx601                | 95         | 116    | 212          | 266    |
| Ky226 x CM104                | 82         | 101    | 184          | 223    |
| Ky226 x FR9                  | 51         | 74     | 150          | 206    |
| Ky226 x PH9                  | 66         | 94     | 177          | 229    |
| Ky226 x Oh51A                | 59         | 76     | 168          | 215    |
| Ky226 x B14A                 | 72         | 90     | 191          | 222    |
| Ky226 x Va35                 | 57         | 72     | 169          | 218    |
| Tx601 x CM104                | 88         | 120    | 192          | 244    |
| Tx601 x FR9                  | 74         | 100    | 184          | 249    |
| Tx601 x PH9                  | 81         | 106    | 197          | 246    |
| Tx601 x Oh51A                | 80         | 99     | 189          | 241    |

A4. (Continued) Mean ear and plant height of a 10-entry diallel grown under low and high P in two seasons in the field (only inbred and hybrid means are shown)

| Genotypes     | Ear height |        | Plant height |        |
|---------------|------------|--------|--------------|--------|
|               | Winter     | Summer | Winter       | Summer |
|               | cm         |        |              |        |
| Tx601 x B14A  | 76         | 94     | 191          | 232    |
| Tx601 x Va35  | 74         | 92     | 188          | 236    |
| CM104 x FR9   | 68         | 87     | 155          | 200    |
| CM104 x PH9   | 95         | 112    | 194          | 223    |
| CM104 x Oh51A | 73         | 97     | 161          | 218    |
| CM104 x B14A  | 77         | 84     | 187          | 208    |
| CM104 x Va35  | 70         | 83     | 175          | 217    |
| FR9 x PH9     | 69         | 79     | 165          | 206    |
| FR9 x Oh51A   | 56         | 61     | 147          | 189    |
| FR9 x B14A    | 58         | 74     | 162          | 206    |
| FR9 x Va35    | 50         | 52     | 143          | 186    |
| PH9 x Oh51A   | 70         | 85     | 170          | 219    |
| PH9 x B14A    | 84         | 85     | 192          | 216    |
| PH9 x Va35    | 67         | 79     | 164          | 224    |
| Oh51A x B14A  | 65         | 72     | 154          | 200    |
| Oh51A x Va35  | 55         | 56     | 164          | 193    |
| B14A x Va35   | 53         | 68     | 168          | 214    |
| Average       | 70         | 84     | 175          | 212    |

A5. Mean grain yield and ear weight of a 10-entry diallel grown under low and high P in the fields, summer planting

| Genotypes                    | Grain yield |        |       | Ear weight |        |       |
|------------------------------|-------------|--------|-------|------------|--------|-------|
|                              | Low P       | High P | Diff. | Low P      | High P | Diff. |
| metric tons/ha               |             |        |       |            |        |       |
| <u>INBREDS</u>               |             |        |       |            |        |       |
| Mp68:616                     | 6.14        | 7.28   | 1.14  | 7.83       | 9.14   | 1.31  |
| CI21E                        | 3.94        | 5.35   | 1.41  | 4.99       | 6.73   | 1.74  |
| Ky226                        | 2.55        | 3.71   | 1.16  | 3.40       | 4.50   | 1.10  |
| Tx601                        | 2.78        | 4.99   | 2.21  | 3.89       | 6.26   | 2.37  |
| CM104                        | 7.86        | 7.70   | -0.16 | 9.16       | 9.14   | -0.20 |
| FR9                          | 0.82        | 5.12   | 4.30  | 1.24       | 2.54   | 1.30  |
| PH9                          | 3.09        | 6.30   | 3.21  | 3.68       | 7.83   | 4.15  |
| Oh51A                        | 1.79        | 2.79   | 1.00  | 2.39       | 3.41   | 1.02  |
| B14A                         | 2.71        | 3.09   | 0.38  | 3.48       | 3.95   | 0.47  |
| Va35                         | 1.71        | 2.35   | 0.64  | 2.08       | 2.86   | 0.78  |
| <u>F<sub>1</sub> HYBRIDS</u> |             |        |       |            |        |       |
| Mp68:616 x CI21E             | 9.01        | 12.17  | 3.16  | 11.18      | 15.45  | 4.27  |
| Mp68:616 x Ky226             | 9.64        | 12.65  | 3.01  | 11.78      | 15.50  | 3.72  |
| Mp68:616 x Tx601             | 10.44       | 11.11  | 0.67  | 13.06      | 14.72  | 1.66  |
| Mp68:616 x CM104             | 10.33       | 13.06  | 2.73  | 12.43      | 15.78  | 3.35  |
| Mp68:616 x FR9               | 5.50        | 9.68   | 4.18  | 6.62       | 11.78  | 5.16  |
| Mp68:616 x PH9               | 10.61       | 11.52  | 0.91  | 12.64      | 13.58  | 0.94  |
| Mp68:616 x Oh51A             | 8.85        | 10.74  | 1.89  | 10.31      | 12.54  | 2.23  |
| Mp68:616 x B14A              | 8.84        | 9.58   | 0.74  | 10.66      | 11.64  | 0.98  |
| Mp68:616 x Va35              | 7.61        | 10.20  | 2.59  | 9.02       | 12.17  | 3.15  |
| CI21E x Ky226                | 10.15       | 10.27  | 0.12  | 11.83      | 11.93  | 0.10  |
| CI21E x Tx601                | 9.54        | 13.04  | 3.50  | 11.19      | 15.08  | 3.89  |
| CI21E x CM104                | 12.60       | 12.98  | 0.38  | 14.65      | 15.09  | 0.44  |
| CI21E x FR9                  | 6.06        | 6.30   | 0.24  | 7.20       | 7.43   | 0.23  |
| CI21E x PH9                  | 7.77        | 7.98   | 0.21  | 9.11       | 9.27   | 0.16  |
| CI21E x Oh51A                | 8.07        | 9.63   | 1.56  | 9.43       | 11.10  | 1.67  |
| CI21E x B14A                 | 6.99        | 8.00   | 1.01  | 8.28       | 9.62   | 1.34  |
| CI21E x Va35                 | 6.19        | 7.39   | 1.20  | 7.42       | 8.73   | 1.31  |
| Ky226 x Tx601                | 12.83       | 13.35  | 0.52  | 14.83      | 15.58  | 0.75  |
| Ky226 x CM104                | 12.34       | 12.67  | 0.33  | 14.27      | 15.30  | 1.03  |
| Ky226 x FR9                  | 6.34        | 6.83   | 0.49  | 7.27       | 7.82   | 0.55  |
| Ky226 x PH9                  | 7.40        | 10.32  | 2.92  | 8.62       | 12.03  | 3.41  |
| Ky226 x Oh51A                | 7.26        | 9.97   | 2.71  | 8.30       | 11.35  | 3.05  |
| Ky226 x B14A                 | 10.62       | 11.54  | 0.92  | 12.35      | 13.41  | 1.06  |
| Ky226 x Va35                 | 7.82        | 8.88   | 1.06  | 9.04       | 10.44  | 1.40  |
| Tx601 x CM104                | 9.96        | 14.06  | 4.10  | 11.57      | 16.55  | 4.92  |
| Tx601 x FR9                  | 8.48        | 11.37  | 2.89  | 10.08      | 13.28  | 3.20  |
| Tx601 x PH9                  | 10.83       | 11.66  | 0.83  | 12.35      | 14.35  | 2.00  |
| Tx601 x Oh51A                | 10.27       | 10.18  | -0.09 | 11.94      | 11.80  | -0.14 |

A5. (Continued) Mean grain yield and ear weight of a 10-entry diallel grown under low and high P in the fields, summer planting

| Genotypes      | Grain yield    |        |       | Ear weight |        |       |
|----------------|----------------|--------|-------|------------|--------|-------|
|                | Low P          | High P | Diff. | Low P      | High P | Diff. |
|                | metric tons/ha |        |       |            |        |       |
| Tx601 x B14A   | 8.01           | 10.79  | 2.78  | 10.74      | 13.04  | 2.3   |
| Tx601 x Va35   | 9.69           | 10.86  | 1.17  | 11.34      | 13.02  | 1.68  |
| CM104 x FR9    | 8.88           | 10.84  | 1.96  | 10.13      | 12.77  | 2.64  |
| CM104 x PH9    | 10.57          | 9.94   | -0.63 | 12.17      | 11.32  | -0.85 |
| CM104 x Oh51A  | 9.50           | 9.68   | 0.18  | 10.82      | 11.11  | 0.29  |
| CM104 x B14A   | 8.52           | 9.61   | 1.09  | 9.92       | 11.23  | 1.31  |
| CM104 x Va35   | 8.70           | 11.31  | 2.61  | 10.27      | 13.19  | 2.92  |
| FR9 x PH9      | 4.98           | 7.21   | 2.23  | 6.02       | 8.43   | 2.41  |
| FR9 x Oh51A    | 4.62           | 7.14   | 2.52  | 5.49       | 8.16   | 2.67  |
| FR9 x B14A     | 4.17           | 9.01   | 4.84  | 5.17       | 10.51  | 5.34  |
| FR9 x Va35     | 2.65           | 5.96   | -3.31 | 3.25       | 6.60   | 3.35  |
| PH9 x Oh51A    | 7.03           | 7.79   | 0.76  | 8.06       | 8.99   | 0.93  |
| PH9 x B14A     | 6.25           | 7.91   | 1.66  | 7.38       | 9.23   | 1.85  |
| PH9 x Va35     | 5.66           | 8.51   | 2.85  | 7.24       | 9.78   | 2.54  |
| Oh51A x B14A   | 6.46           | 8.71   | 2.25  | 7.60       | 10.34  | 2.74  |
| Oh51A x Va35   | 4.25           | 6.97   | 2.72  | 5.06       | 7.98   | 2.92  |
| B14A x Va35    | 6.57           | 8.06   | 1.49  | 7.83       | 9.38   | 1.55  |
| Average        | 7.31           | 9.01   |       | 8.69       | 10.63  |       |
| BLSD .05 G x P |                |        | 2.43  |            |        | 2.71  |

A6. Mean ear length, number of kernels per row, and row number of a 10-entry diallel grown under low and high P, summer planting

| Genotypes                    | Ear length     |        |       | Kernels |        |       | Row number |        |
|------------------------------|----------------|--------|-------|---------|--------|-------|------------|--------|
|                              | Low P          | High P | Diff. | Low P   | High P | Diff. | Low P      | High P |
|                              | ————— cm ————— |        |       |         |        |       |            |        |
| <u>INBREDS</u>               |                |        |       |         |        |       |            |        |
| Mp68:616                     | 13.0           | 13.2   | 0.2   | 31.4    | 31.9   | 0.5   | 12.9       | 13.0   |
| CI21E                        | 11.2           | 12.4   | 1.2   | 26.9    | 29.1   | 2.2   | 14.7       | 14.1   |
| Ky226                        | 9.4            | 9.8    | 0.4   | 18.3    | 20.6   | 2.3   | 10.8       | 12.3   |
| Tx601                        | 8.9            | 10.8   | 1.9   | 18.5    | 24.8   | 6.3   | 10.2       | 12.2   |
| CM104                        | 14.5           | 15.5   | 1.0   | 32.3    | 30.1   | -2.2  | 14.8       | 14.9   |
| FR9                          | 5.6            | 8.1    | 2.5   | 15.8    | 20.1   | 4.3   | 9.8        | 12.3   |
| PH9                          | 10.8           | 14.2   | 3.4   | 26.8    | 31.8   | 5.0   | 12.5       | 13.3   |
| Oh51A                        | 8.8            | 9.9    | 1.1   | 17.2    | 23.3   | 6.1   | 9.7        | 10.8   |
| B14A                         | 9.5            | 9.8    | 0.3   | 15.1    | 18.1   | 3.0   | 12.5       | 12.7   |
| Va35                         | 8.2            | 8.3    | 0.1   | 19.9    | 19.3   | 0.6   | 9.9        | 10.4   |
| <u>F<sub>1</sub> HYBRIDS</u> |                |        |       |         |        |       |            |        |
| Mp68:616 x CI21E             | 14.9           | 16.9   | 2.0   | 38.8    | 41.2   | 2.4   | 14.4       | 15.4   |
| Mp68:616 x Ky226             | 14.6           | 15.1   | 0.5   | 37.7    | 39.1   | 1.4   | 13.9       | 15.0   |
| Mp68:616 x Tx601             | 15.2           | 15.9   | 0.7   | 36.9    | 35.8   | -1.1  | 13.6       | 13.5   |
| Mp68:616 x CM104             | 16.1           | 16.5   | 0.4   | 37.3    | 36.7   | -0.6  | 14.4       | 14.7   |
| Mp68:616 x FR9               | 11.4           | 15.2   | 3.8   | 30.1    | 38.2   | 8.1   | 15.1       | 14.9   |
| Mp68:616 x PH9               | 14.4           | 15.5   | 1.1   | 33.9    | 35.5   | 1.6   | 13.8       | 13.6   |
| Mp68:616 x Oh51A             | 14.4           | 15.0   | 0.6   | 35.9    | 37.9   | 2.0   | 13.6       | 14.3   |
| Mp68:616 x B14A              | 14.4           | 15.4   | 1.0   | 33.4    | 34.3   | 0.9   | 13.6       | 14.2   |
| Mp68:616 x Va35              | 14.1           | 15.9   | 1.8   | 32.9    | 37.0   | 4.1   | 13.8       | 14.5   |
| CI21E x Ky226                | 15.7           | 14.5   | -1.2  | 35.8    | 36.3   | 0.5   | 13.6       | 14.5   |
| CI21E x Tx601                | 14.5           | 16.9   | 2.4   | 36.7    | 39.7   | 3.0   | 14.2       | 14.7   |
| CI21E x CM104                | 17.5           | 16.2   | -1.3  | 34.1    | 38.3   | 4.2   | 15.3       | 16.0   |
| CI21E x FR9                  | 13.6           | 13.0   | -0.6  | 34.7    | 34.3   | -0.4  | 15.3       | 15.5   |
| CI21E x PH9                  | 14.7           | 14.5   | -0.2  | 36.4    | 35.0   | -1.4  | 12.8       | 13.4   |
| CI21E x Oh51A                | 14.8           | 15.8   | -1.0  | 37.9    | 39.5   | 1.6   | 13.7       | 14.4   |
| CI21E x B14A                 | 13.8           | 14.2   | 0.4   | 33.7    | 31.7   | -2.0  | 13.2       | 13.8   |
| CI21E x Va35                 | 12.8           | 13.8   | 1.0   | 32.3    | 34.3   | 2.0   | 14.3       | 14.6   |
| Ky226 x Tx601                | 17.3           | 16.6   | -0.7  | 46.4    | 42.8   | -3.6  | 14.1       | 14.1   |
| Ky226 x CM104                | 16.3           | 16.3   | 0     | 40.3    | 41.0   | 0.7   | 14.5       | 14.5   |
| Ky226 x FR9                  | 11.9           | 12.1   | 0.2   | 31.7    | 32.0   | 0.3   | 14.2       | 15.1   |
| Ky226 x PH9                  | 14.0           | 15.3   | 1.3   | 35.7    | 36.5   | 0.8   | 13.2       | 13.8   |
| Ky226 x Oh51A                | 12.3           | 14.6   | 2.3   | 30.7    | 37.7   | 7.0   | 13.3       | 13.7   |
| Ky226 x B14A                 | 16.3           | 16.4   | 0.1   | 38.5    | 37.9   | -0.6  | 13.6       | 13.8   |
| Ky226 x Va35                 | 13.2           | 14.2   | 1.0   | 33.1    | 35.7   | 2.6   | 13.6       | 13.9   |
| Tx601 x CM104                | 15.3           | 16.7   | 1.4   | 37.9    | 39.1   | 1.2   | 14.1       | 14.7   |
| Tx601 x FR9                  | 15.0           | 16.3   | 1.3   | 37.6    | 39.4   | 1.8   | 15.0       | 16.0   |
| Tx601 x PH9                  | 15.2           | 16.1   | 0.9   | 37.0    | 36.5   | 0.5   | 14.2       | 13.3   |

A6. (Continued) Mean ear length, number of kernels per row, and row number of a 10-entry diallel grown under low and high P, summer planting

| Genotypes      | Ear length     |        |       | Kernels |        |       | Row number |        |
|----------------|----------------|--------|-------|---------|--------|-------|------------|--------|
|                | Low P          | High P | Diff. | Low P   | High P | Diff. | Low P      | High P |
|                | ----- cm ----- |        |       |         |        |       |            |        |
| Tx601 x Oh51A  | 16.2           | 16.1   | -0.1  | 41.2    | 40.9   | -0.3  | 13.1       | 13.3   |
| Tx601 x B14A   | 14.0           | 15.4   | 1.4   | 32.4    | 34.1   | 1.7   | 13.1       | 14.2   |
| Tx601 x Va35   | 14.9           | 15.9   | 1.0   | 36.9    | 38.5   | 1.6   | 13.7       | 14.6   |
| CM104 x FR9    | 14.7           | 15.7   | 1.0   | 36.6    | 39.7   | 3.1   | 15.2       | 15.2   |
| CM104 x PH9    | 15.7           | 14.4   | 0.7   | 38.1    | 34.7   | -3.4  | 15.0       | 15.0   |
| CM104 x Oh51A  | 15.5           | 15.4   | -0.1  | 38.9    | 37.1   | -1.8  | 14.4       | 14.4   |
| CM104 x B14A   | 13.7           | 14.9   | 1.2   | 30.6    | 33.9   | 3.3   | 14.2       | 14.8   |
| CM104 x Va35   | 14.2           | 16.7   | 2.5   | 33.1    | 35.8   | 2.7   | 14.3       | 14.8   |
| FR9 x PH9      | 13.5           | 14.2   | 0.7   | 33.8    | 35.3   | 1.5   | 14.6       | 14.9   |
| FR9 x Oh51A    | 11.9           | 13.4   | 1.5   | 30.8    | 34.0   | 3.2   | 14.9       | 14.4   |
| FR9 x B14A     | 11.4           | 14.5   | 3.1   | 27.9    | 36.6   | 8.7   | 15.0       | 16.9   |
| FR9 x Va35     | 8.9            | 12.0   | 3.1   | 21.5    | 28.5   | 7.0   | 13.3       | 15.5   |
| PH9 x Oh51A    | 14.2           | 15.1   | 0.9   | 35.2    | 35.1   | -0.1  | 12.5       | 13.0   |
| PH9 x B14A     | 13.0           | 14.3   | 1.3   | 29.0    | 30.9   | 1.9   | 13.9       | 13.8   |
| Ph9 x Va35     | 13.4           | 14.7   | 1.3   | 32.1    | 34.3   | 2.2   | 13.6       | 13.2   |
| Oh51A x B14A   | 14.0           | 15.7   | 1.7   | 32.8    | 35.9   | 3.1   | 13.3       | 13.6   |
| Oh51A x Va35   | 11.5           | 14.0   | 2.5   | 29.0    | 33.7   | 4.7   | 12.2       | 14.7   |
| B14A x Va35    | 13.1           | 14.7   | 1.6   | 30.2    | 32.4   | 2.2   | 13.8       | 14.1   |
| Average        | 13.4           | 14.4   |       | 32.4    | 34.2   |       | 13.5       | 14.1   |
| BLSD .05 G x P |                |        | 1.9   |         |        | 6.9   |            | ns     |

A7. Mean kernel depth, 100-kernel weight, and number of ears per 10 plants of a 10-entry diallel grown under low and high P in the field, summer planting

| Genotypes                    | Kernel depth |        |       | Kernel weight      |        |       | Number of ears |        |
|------------------------------|--------------|--------|-------|--------------------|--------|-------|----------------|--------|
|                              | Low P        | High P | Diff. | Low P              | High P | Diff. | Low P          | High P |
|                              | - mm -       |        |       | - gm/100 kernels - |        |       | - 10 plants -  |        |
| <u>INBREDS</u>               |              |        |       |                    |        |       |                |        |
| Mp68:616                     | 10           | 11     | 1     | 22.4               | 27.7   | 5.3   | 12.9           | 12.4   |
| CI21E                        | 9            | 10     | 1     | 18.0               | 23.6   | 5.6   | 10.0           | 10.0   |
| Ky226                        | 10           | 10     | 0     | 26.7               | 31.2   | 4.5   | 8.7            | 9.6    |
| Tx601                        | 10           | 11     | 1     | 27.0               | 28.4   | 1.4   | 9.6            | 10.6   |
| CM104                        | 9            | 10     | 1     | 26.3               | 29.2   | 2.9   | 11.6           | 10.8   |
| FR9                          | 8            | 9      | 1     | 15.3               | 13.9   | -1.4  | 8.3            | 9.6    |
| PH9                          | 9            | 10     | 1     | 16.9               | 25.1   | 8.2   | 10.8           | 10.8   |
| Oh51A                        | 8            | 9      | 1     | 21.1               | 20.9   | -0.2  | 10.4           | 10.0   |
| B14A                         | 10           | 10     | 0     | 27.2               | 24.8   | -2.4  | 9.3            | 10.0   |
| Va35                         | 9            | 9      | 0     | 19.6               | 22.2   | 2.6   | 8.6            | 9.6    |
| <u>F<sub>1</sub> HYBRIDS</u> |              |        |       |                    |        |       |                |        |
| Mp68:616 x CI21E             | 11           | 11     | 0     | 28.4               | 30.0   | 1.6   | 10.5           | 12.4   |
| Mp68:616 x Ky226             | 12           | 12     | 0     | 30.3               | 33.3   | 3.0   | 10.4           | 11.9   |
| Mp68:616 x Tx601             | 11           | 12     | 1     | 31.5               | 33.3   | 1.8   | 11.3           | 11.2   |
| Mp68:616 x CM104             | 11           | 11     | 0     | 30.7               | 32.9   | 2.2   | 11.1           | 15.5   |
| Mp68:616 x FR9               | 10           | 11     | 1     | 21.3               | 28.6   | 7.3   | 10.0           | 10.0   |
| Mp68:616 x PH9               | 11           | 11     | 0     | 28.1               | 31.1   | 3.0   | 16.6           | 14.9   |
| Mp68:616 x Oh51A             | 11           | 12     | 1     | 27.8               | 30.8   | 3.0   | 11.8           | 11.1   |
| Mp68:616 x B14A              | 11           | 12     | 1     | 32.1               | 34.3   | 2.2   | 10.9           | 10.0   |
| Mp68:616 x Va35              | 10           | 11     | 0     | 27.2               | 33.8   | 6.6   | 11.0           | 10.0   |
| CI21E x Ky226                | 11           | 12     | 1     | 31.3               | 32.9   | 1.6   | 10.0           | 10.0   |
| CI21E x Tx601                | 11           | 12     | 1     | 30.8               | 34.1   | 3.3   | 10.9           | 11.6   |
| CI21E x CM104                | 11           | 11     | 0     | 29.7               | 31.6   | 1.9   | 10.7           | 12.8   |
| CI21E x FR9                  | 10           | 10     | 0     | 19.8               | 20.8   | 1.0   | 10.0           | 10.0   |
| CI21E x PH9                  | 10           | 11     | 1     | 25.6               | 27.0   | 1.4   | 12.6           | 11.8   |
| CI21E x Oh51A                | 11           | 11     | 0     | 26.3               | 30.3   | 4.0   | 10.0           | 10.0   |
| CI21E x B14A                 | 11           | 11     | 0     | 29.6               | 31.3   | 1.7   | 9.6            | 10.0   |
| CI21E x Va35                 | 11           | 11     | 0     | 23.5               | 25.5   | 2.0   | 10.0           | 10.0   |
| Ky226 x Tx601                | 12           | 12     | 0     | 31.1               | 33.0   | 1.9   | 11.8           | 12.2   |
| Ky226 x CM104                | 12           | 12     | 0     | 32.9               | 32.9   | 0     | 11.3           | 11.8   |
| Ky226 x FR9                  | 10           | 10     | 0     | 23.5               | 23.7   | 0.2   | 10.0           | 10.0   |
| Ky226 x PH9                  | 11           | 11     | 0     | 27.6               | 31.8   | 4.2   | 10.0           | 12.5   |
| Ky226 x Oh51A                | 11           | 12     | 1     | 30.0               | 33.7   | 3.7   | 10.0           | 10.0   |
| Ky226 x B14A                 | 12           | 12     | 0     | 32.5               | 35.4   | 2.9   | 11.3           | 10.7   |
| Ky226 x Va35                 | 11           | 11     | 0     | 29.4               | 31.2   | 1.8   | 10.0           | 10.0   |
| Tx601 x CM104                | 11           | 11     | 0     | 29.0               | 32.2   | 3.2   | 12.5           | 13.8   |
| Tx601 x FR9                  | 11           | 12     | 1     | 26.4               | 30.7   | 4.3   | 10.0           | 10.3   |

A7. (Continued) Mean kernel depth, 100-kernel weight, and number of ears per 10 plants of a 10-entry diallel grown under low and high P in the field, summer planting

| Genotypes      | Kernel depth |        |       | Kernel weight      |        |       | Number of ears |        |
|----------------|--------------|--------|-------|--------------------|--------|-------|----------------|--------|
|                | Low P        | High P | Diff. | Low P              | High P | Diff. | Low P          | High P |
|                | — mm —       |        |       | — gm/100 kernels — |        |       | — 10 plants —  |        |
| Tx601 x PH9    | 12           | 11     | -1    | 30.7               | 32.2   | 1.5   | 12.7           | 13.8   |
| Tx601 x Oh51A  | 12           | 12     | 0     | 31.4               | 31.3   | -0.1  | 10.0           | 10.0   |
| Tx601 x B14A   | 12           | 13     | 1     | 33.3               | 37.8   | 4.5   | 10.0           | 10.0   |
| Tx601 x Va35   | 12           | 11     | -1    | 31.4               | 33.1   | 1.7   | 10.9           | 10.0   |
| CM104 x FR9    | 11           | 11     | 0     | 26.9               | 28.4   | 1.5   | 10.0           | 10.6   |
| CM104 x PH9    | 11           | 11     | 0     | 28.3               | 27.9   | 0.4   | 11.6           | 13.6   |
| CM104 x Oh51A  | 11           | 11     | 0     | 28.1               | 30.3   | 2.2   | 11.0           | 10.4   |
| CM104 x B14A   | 12           | 11     | -1    | 33.4               | 32.0   | -1.4  | 10.0           | 10.7   |
| CM104 x Va35   | 11           | 11     | 0     | 32.1               | 32.8   | 0.7   | 10.0           | 10.4   |
| FR9 x PH9      | 10           | 11     | 1     | 16.9               | 23.6   | 6.7   | 10.5           | 10.4   |
| FR9 x Oh51A    | 10           | 11     | 1     | 18.5               | 25.9   | 7.4   | 10.0           | 10.0   |
| FR9 x B14A     | 10           | 11     | 1     | 16.6               | 28.7   | 12.1  | 10.0           | 10.0   |
| FR9 x Va35     | 9            | 11     | 2     | 16.0               | 23.3   | 7.3   | 9.3            | 9.6    |
| PH9 x Oh51A    | 10           | 11     | 1     | 25.7               | 29.8   | 4.1   | 11.7           | 11.1   |
| PH9 x B14A     | 10           | 11     | 1     | 25.5               | 32.3   | 6.8   | 10.5           | 10.4   |
| PH9 x Va35     | 10           | 11     | 1     | 25.2               | 29.2   | 4.0   | 10.0           | 11.8   |
| Oh51A x B14A   | 10           | 11     | 1     | 25.2               | 30.9   | 5.7   | 10.0           | 10.0   |
| Oh51A x Va35   | 10           | 11     | 1     | 20.6               | 26.2   | 5.6   | 10.0           | 10.0   |
| B14A x Va35    | 11           | 11     | 0     | 29.1               | 30.8   | 1.7   | 10.0           | 10.0   |
| Average        | 11           | 11     |       | 26.4               | 29.5   |       | 10.5           | 10.9   |
| BLSD .05 G x P |              |        | 1     |                    |        | 5.2   | ns             |        |

A8. Days to silking of 12 corn cultivars grown under 10 levels of P in the field (cut end)

| Cultivars         | Adjusted P in solution (ppm) |       |       |       |      |     |     |     |     |     | Cultivar means |
|-------------------|------------------------------|-------|-------|-------|------|-----|-----|-----|-----|-----|----------------|
|                   | 0.003                        | 0.006 | 0.012 | 0.025 | 0.05 | 0.1 | 0.2 | 0.4 | 0.8 | 1.6 |                |
|                   | days                         |       |       |       |      |     |     |     |     |     |                |
| H610              | 91                           | 74    | 73    | 77    | 71   | 68  | 69  | 70  | 66  | 64  | 72             |
| H788              | 88                           | 90    | 73    | 76    | 77   | 71  | 77  | 77  | 67  | 70  | 76             |
| X304C             | 90                           | 91    | 75    | 72    | 77   | 73  | 74  | 67  | 66  | 69  | 74             |
| Antigua Composite | 82                           | 82    | 79    | 75    | 74   | 78  | 76  | 80  | 74  | 78  | 77             |
| Ky226 x Oh43      | 95                           | 76    | 75    | 70    | 68   | 67  | 61  | 70  | 60  | 62  | 70             |
| Mp68:616 x Tx601  | 95                           | 95    | 72    | 71    | 76   | 73  | 73  | 72  | 70  | 70  | 75             |
| GM104 x Va35      | 95                           | 77    | 73    | 69    | 72   | 69  | 68  | 70  | 64  | 65  | 72             |
| CI21E x Ky226     | 90                           | 80    | 70    | 73    | 75   | 75  | 70  | 74  | 67  | 67  | 74             |
| GM104 x PH9       | 80                           | 80    | 71    | 74    | 72   | 71  | 67  | 74  | 67  | 65  | 72             |
| H638              | 83                           | 70    | 70    | 74    | 69   | 68  | 65  | 65  | 61  | 62  | 69             |
| White Carimagua   | 91                           | 88    | 78    | 81    | 81   | 74  | 75  | 70  | 73  | 76  | 79             |
| Yellow Carimagua  | 90                           | 91    | 75    | 81    | 79   | 74  | 75  | 81  | 73  | 71  | 78             |
| P means           | 89                           | 82    | 74    | 74    | 74   | 72  | 71  | 72  | 67  | 68  |                |

A9. Ear height of 12 corn cultivars grown under 10 levels of P in the field (cut end)

| Cultivars         | Adjusted P in solution (ppm) |       |       |       |      |     |     |     |     |     | Cultivar means |
|-------------------|------------------------------|-------|-------|-------|------|-----|-----|-----|-----|-----|----------------|
|                   | 0.003                        | 0.006 | 0.012 | 0.025 | 0.05 | 0.1 | 0.2 | 0.4 | 0.8 | 1.6 |                |
|                   | cm                           |       |       |       |      |     |     |     |     |     |                |
| H610              | 56                           | 82    | 108   | 108   | 106  | 112 | 112 | 124 | 128 | 124 | 107            |
| H788              | 57                           | 74    | 124   | 122   | 118  | 134 | 137 | 134 | 146 | 154 | 122            |
| X304C             | 49                           | 56    | 118   | 118   | 109  | 120 | 112 | 134 | 147 | 144 | 113            |
| Antigua Composite | 61                           | 74    | 108   | 103   | 105  | 120 | 104 | 110 | 136 | 129 | 106            |
| Ky226 x Oh43      | 32                           | 46    | 85    | 76    | 82   | 101 | 77  | 97  | 110 | 89  | 82             |
| Mp68:616 x Tx601  | 70                           | 61    | 118   | 122   | 106  | 130 | 116 | 144 | 152 | 144 | 117            |
| CM104 x Va35      | 45                           | 66    | 120   | 91    | 95   | 110 | 102 | 111 | 131 | 118 | 101            |
| CI21E x Ky226     | 56                           | 56    | 100   | 102   | 97   | 109 | 108 | 121 | 117 | 132 | 101            |
| CM104 x PH9       | 60                           | 65    | 119   | 106   | 116  | 118 | 109 | 129 | 139 | 129 | 111            |
| H638              | 49                           | 82    | 98    | 94    | 101  | 102 | 107 | 114 | 108 | 114 | 98             |
| White Carimagua   | 60                           | 98    | 127   | 119   | 125  | 156 | 130 | 158 | 155 | 138 | 129            |
| Yellow Carimagua  | 82                           | 95    | 136   | 117   | 120  | 147 | 127 | 168 | 182 | 135 | 130            |
| P means           | 56                           | 71    | 113   | 106   | 107  | 122 | 112 | 129 | 138 | 129 |                |

A10. Plant height of 12 corn cultivars grown under 10 levels of P in the field (cut end)

| Cultivars         | Adjusted P in solution (ppm) |       |       |       |      |     |     |     |     |     | Cultivar means |
|-------------------|------------------------------|-------|-------|-------|------|-----|-----|-----|-----|-----|----------------|
|                   | 0.003                        | 0.006 | 0.012 | 0.025 | 0.05 | 0.1 | 0.2 | 0.4 | 0.8 | 1.6 |                |
|                   | cm                           |       |       |       |      |     |     |     |     |     |                |
| H610              | 159                          | 223   | 253   | 241   | 245  | 262 | 254 | 273 | 278 | 278 | 248            |
| H788              | 183                          | 200   | 265   | 264   | 263  | 276 | 270 | 287 | 290 | 306 | 263            |
| X304C             | 172                          | 183   | 262   | 265   | 259  | 267 | 251 | 295 | 316 | 307 | 260            |
| Antigua Composite | 174                          | 152   | 220   | 222   | 221  | 236 | 210 | 230 | 253 | 235 | 218            |
| Ky226 x Oh43      | 128                          | 184   | 228   | 224   | 232  | 258 | 226 | 262 | 270 | 260 | 231            |
| Mp68:616 x Tx601  | 133                          | 202   | 277   | 279   | 260  | 290 | 275 | 312 | 330 | 322 | 272            |
| CM104 x Va35      | 132                          | 214   | 253   | 232   | 249  | 255 | 231 | 270 | 285 | 263 | 243            |
| CI21E x Ky226     | 197                          | 188   | 249   | 250   | 254  | 269 | 258 | 278 | 291 | 310 | 255            |
| CM104 x PH9       | 190                          | 191   | 252   | 240   | 251  | 257 | 266 | 263 | 288 | 280 | 249            |
| H638              | 186                          | 233   | 256   | 258   | 258  | 265 | 265 | 270 | 284 | 290 | 258            |
| White Carimagua   | 178                          | 238   | 259   | 256   | 253  | 300 | 272 | 295 | 320 | 292 | 266            |
| Yellow Carimagua  | 223                          | 240   | 278   | 248   | 257  | 290 | 282 | 305 | 326 | 297 | 272            |
| P means           | 171                          | 240   | 254   | 247   | 250  | 269 | 255 | 278 | 294 | 286 |                |

All. Ear length of 12 corn cultivars grown under 10 levels of P in the field (cut end)

| Cultivars         | Adjusted P in solution (ppm) |       |       |       |      |      |      |      |      |      | Cultivar means |
|-------------------|------------------------------|-------|-------|-------|------|------|------|------|------|------|----------------|
|                   | 0.003                        | 0.006 | 0.012 | 0.025 | 0.05 | 0.1  | 0.2  | 0.4  | 0.8  | 1.6  |                |
|                   | cm                           |       |       |       |      |      |      |      |      |      |                |
| H610              | 11.7                         | 18.2  | 19.8  | 19.6  | 20.4 | 20.3 | 17.2 | 21.0 | 21.3 | 19.9 | 19.4           |
| H788              | 15.3                         | 12.9  | 18.3  | 19.0  | 19.5 | 20.1 | 19.0 | 19.6 | 20.4 | 21.3 | 18.8           |
| X304C             | 12.6                         | 10.5  | 20.7  | 21.2  | 20.4 | 20.4 | 17.4 | 20.8 | 22.9 | 21.4 | 19.6           |
| Antigua Composite | 8.0                          | 8.8   | 13.9  | 14.6  | 15.9 | 14.9 | 12.1 | 16.1 | 14.3 | 14.9 | 13.4           |
| Ky226 x Oh43      | 9.0                          | 12.1  | 13.1  | 13.4  | 14.0 | 13.9 | 14.5 | 13.1 | 13.2 | 17.6 | 13.4           |
| Mp68:616 x Tx601  | 10.8                         | 12.4  | 18.7  | 18.7  | 16.8 | 18.9 | 18.2 | 20.0 | 19.7 | 18.7 | 17.7           |
| CM104 x Va35      | 9.5                          | 17.2  | 17.9  | 16.2  | 16.0 | 18.4 | 16.7 | 16.1 | 17.6 | 18.4 | 16.7           |
| CI21E x Ky226     | 12.9                         | 8.9   | 16.4  | 15.7  | 16.9 | 15.1 | 19.8 | 15.4 | 19.0 | 18.2 | 15.9           |
| CM104 x PH9       | 15.2                         | 13.7  | 18.4  | 15.4  | 17.7 | 17.4 | 18.1 | 18.6 | 18.2 | 18.3 | 17.1           |
| H638              | 11.2                         | 20.0  | 18.6  | 18.8  | 18.9 | 19.9 | 20.7 | 22.9 | 21.2 | 22.2 | 19.3           |
| White Carimagua   | 13.2                         | 15.5  | 17.8  | 17.6  | 15.4 | 19.3 | 18.6 | 18.2 | 20.2 | 20.8 | 17.6           |
| Yellow Carimagua  | 16.9                         | 16.1  | 18.0  | 15.3  | 17.7 | 19.0 | 17.1 | 21.3 | 19.2 | 18.6 | 17.8           |
| P means           | 12.1                         | 13.8  | 17.6  | 17.1  | 17.4 | 18.1 | 17.4 | 18.6 | 18.9 | 19.2 |                |

## APPENDIX B

### DETERMINATION OF PHOSPHORUS ADSORPTION CURVE

The phosphorus adsorption curve was determined by the method outlined by Fox and Kamprath (1970). Three gm samples of dry soil were equilibrated for 6 days in 30 ml of 0.01 M  $\text{CaCl}_2$  with varied concentrations of  $\text{Ca}(\text{H}_2\text{PO}_4)_2$ . Toluene was added to prevent microbial activity. Samples were shaken horizontally for 30 minutes each morning and evening. After 6 days the samples were centrifuged and phosphate remaining in the supernatant was determined by Murphy and Riley's method of phosphorus determination described by Watanabe and Olsen (1965). The method is outlined below:

Reagent A: Dissolve 12 gm of ammonium molybdate in 250 ml of distilled water. Dissolve 0.2908 gm of antimony potassium tartrate in 100 ml of distilled water. Add both solutions to 1000 ml of 5 N  $\text{H}_2\text{SO}_4$ , mix and make volume to 2000 ml with distilled water. Store in the dark.

Reagent B: Dissolve 1.056 gm of ascorbic acid in 200 ml of reagent A. Reagent B is used in phosphate determination.

Procedure: Pipette supernatant (contains 1-20  $\mu\text{gm}$  orthophosphate) into a 25 ml volumetric flask. Add distilled water to make volume to about 20 ml and add 4 ml of reagent B, mix and make volume to 25 ml with distilled water. After 20 minutes, read the optical density at 660 nm on a spectrophotometer. Phosphorus concentration in the supernatant is then read from a standard curve base on  $\text{Ca}(\text{H}_2\text{PO}_4)_2$ .

Phosphorus remaining in solution is calculated from phosphorus concentration in the supernatant. Phosphorus adsorbed by soils is then calculated as the difference between total phosphorus added before

equilibration and phosphorus remaining in the solution after equilibration.

The phosphorus adsorption curve was obtained by plotting on semi-log graph paper phosphate sorbed against phosphorus remaining in solution. Phosphorus remaining in solution is plotted on the log scale on the x-axis. The phosphorus adsorption curve of the soil at Waimanalo Research Station is shown in Figure 6. The amount of P fertilizer needed to bring the level of P in this soil to 0.1 ppm was read directly on the phosphorus sorbed scale.

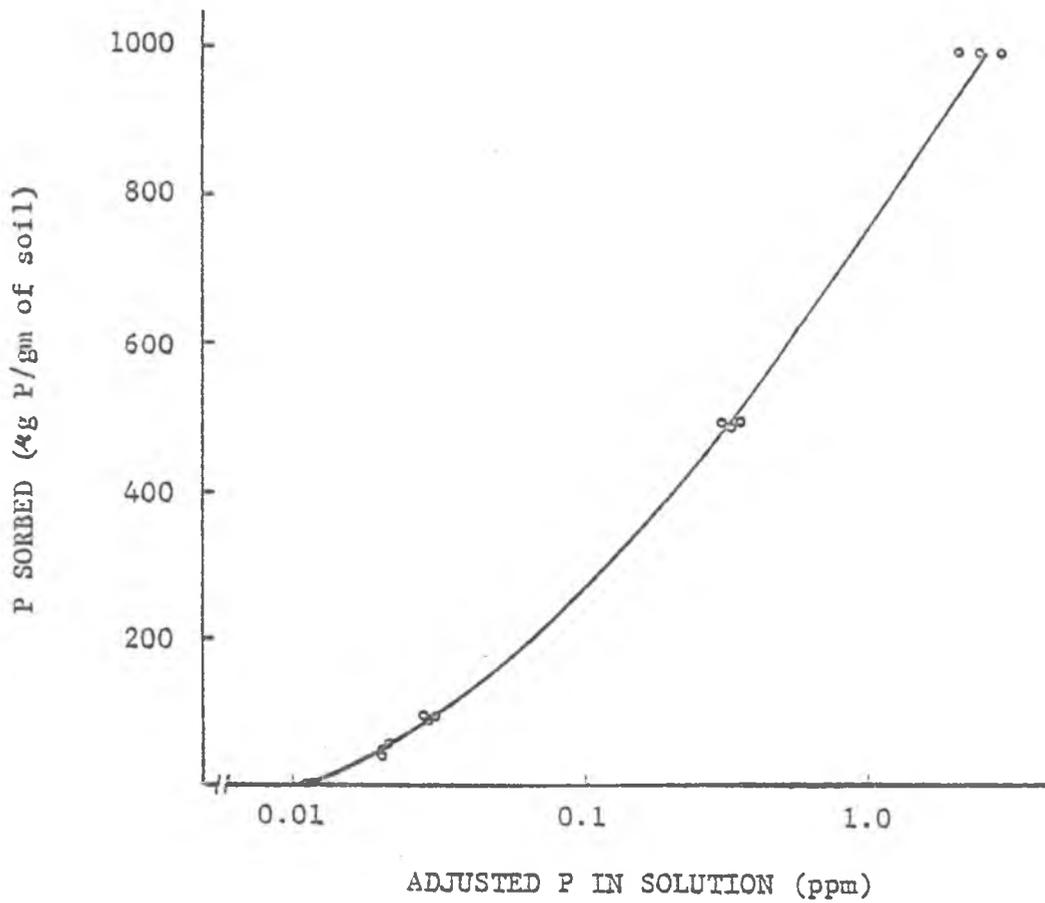


Figure 6. Phosphate adsorption curve for the soil in field A<sub>1</sub> at the Waimanalo Research Station.

## APPENDIX C

### PLANT ANALYSIS FOR PHOSPHORUS CONTENT

All plant materials to be analyzed for P content were ground in a Wiley Mill. Plant material (0.4-0.6 gm per sample) was predigested in digestion tubes in 5 ml of a 2:1 mixture of nitric-perchloric acid overnight at room temperature. Small, short-stemmed funnels were placed in the tubes to aid refluxing. After preliminary digestion, tubes were placed in a cold aluminum block digester and the temperature raised to 150C for 1 hr. The tubes were removed from the block, 1 ml of 1:1 HCl:H<sub>2</sub>O was added through the funnels and the tubes were returned to the block. A U-shaped glass rod was placed under each funnel to permit exit of volatile vapors. Temperature was slowly increased until all traces of nitric acid had disappeared, after which the U-shaped glass rods were removed and the temperature raised to 235C. The time was noted when dense white HClO<sub>4</sub> fumes appeared in the tubes. Digestion was continued for approximately 1 hr. Samples were removed from the digester, allowed to cool a few minutes, then a little distilled water was added through the funnel. After the vapors had condensed, water was added in small increments, washing down the walls of the tubes and the funnels and volume was made up to 50 ml.

The vanadate-molybdate-yellow method was used for the analysis of P in plant material (Chapman and Pratt, 1961). The reagents used were prepared as follows: Dissolve 22.5 gm of (NH<sub>4</sub>)<sub>6</sub>Mo<sub>7</sub>O<sub>24</sub>·4H<sub>2</sub>O in 400 ml of water and dissolve 1.25 gm of ammonium vanadate in 300 ml of boiling water. Add the ammonium vanadate solution to the ammonium molybdate solution and cool to room temperature. Add 250 ml of concentrated nitric

acid slowly with constant stirring. Make the volume to 1 liter with distilled water.

A 0.5 ml aliquot of the supernatant solution of the digested plant material was transferred to colorimeter tubes and 1 ml of ammonium molybdate-ammonium vanadate was added and mixed; 5 ml of water were added and mixed again. The optical density was read at 470 nm on a spectrophotometer after 30 minutes. The concentration of P in the unknown samples was read from a standard curve prepared with  $\text{KH}_2\text{PO}_4$ .

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