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The influence of oxygen and carbon dioxide levels in the substrate upon potassium absorption by plants

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THE INFLUENCE OF OXYGEN AND CARBON
DIOXIDE LEVELS IN THE SUBSTRATE UPON POTASSIUM
ABSORPTION BY PLANTS

by
Luther Carlisle Hammond

A Dissertation Submitted to the
Graduate Faculty in Partial Fulfillment of
The Requirements for the Degree of
DOCTOR OF PHILOSOPHY

Major Subject: Soil Fertility

Approved:

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1949
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INTRODUCTION

Soil aeration has long been recognized as an agricultural problem, and the beneficial effects to plant growth of certain tillage practices have been attributed to better aeration of the soil. Although the better aeration value of tillage was questioned by Leather (114), recently Bower, et al (20) have found that certain tillage practices even on so-called well drained soils resulted in increased yields of corn and increased nitrogen and potassium absorption by the plants. These investigators felt that the nitrification process and the process of potassium accumulation were stimulated by an increased oxygen supply due to good tillage of the soil. This was considered to be in agreement with the findings of others (88, 137) that potassium absorption was dependent on oxygen supply.

Later Hoffer (91, 92, 93) and Lawton (112, 113) have also given evidence pointing to the fact that many soils may be so poorly aerated (low in oxygen) due to compaction and high moisture content as to preclude the normal process of nutrient absorption (especially potassium) by the roots of crops.

It is of interest in this regard that Chang and Loomis (57) have indicated that toxic carbon dioxide concentrations
of 10 to 20% are probably more common in soils than limiting oxygen concentrations of 1 to 2%. Their work showing the detrimental effects of carbon dioxide in culture solutions on the water and mineral absorption of plants has stimulated interest in carbon dioxide as a possible factor in soil aeration.

In view of the above findings it seems there is a definite need for clarification of the actual aeration conditions in soils (low oxygen tension or high carbon dioxide concentrations or both) which may be related to the growth and nutrition of crop plants. The research here reported was inaugurated toward that end with the following lines of investigation in mind: (1) to determine the effects of oxygen and carbon dioxide levels in the soil upon plant growth and potassium absorption under field and greenhouse conditions; (2) to investigate the possibility of supplying oxygen from oxygen-carrying chemicals to soils under conditions of poor aeration, especially when water-logged; and (3) to attempt the separation of low oxygen tension and high carbon dioxide effects on plant growth and nutrition through the employment of controlled soil and nutrient culture aeration with gases of known oxygen and carbon dioxide content.
HISTORICAL

General

Boussingault and Lewy (19), in 1853, were probably the first to measure the air composition of the soil and Sachs (152), in 1860, first noted the beneficial effects on plant growth of aeration of culture solutions. During the passage of almost a century since these men initiated the study of substrate aeration and its effects on the roots and tops of plants, there have been hundreds of scientific and popular papers written on this subject. Two excellent monographs [Clements (61), and Cannon (55)] review the greater part of this literature up to 1925. Therefore, this review will largely concern the literature since that time. In this connection there have been recent reviews of a limited nature (63, 71, 103, 168, 179, 181).

Effects of Oxygen and Carbon Dioxide
Levels in the Substrate upon the Physiology of Plants

The almost absolute necessity for the presence of oxygen in the substrate of most plants to assure their normal growth and development is a fairly well proven fact. Numerous re-
ports are in the literature to indicate the beneficial effects on plant growth of increased oxygen supply to the plant roots, or the removal of the carbon dioxide, or both. First we shall consider the literature having to do with oxygen supply.

Cannon (38, 40, 41, 43, 45, 55) in studying the effect of oxygen tension in the soil air on the rate of root growth of a number of plant species, found that the concentration of oxygen which will just permit a normal rate of root growth at a given temperature may be as low as 1.2% for oranges and as high as 10% for corn. At higher temperatures a higher percent oxygen in the soil atmosphere around the roots was necessary for normal growth. Boynton (21), working with one year old apple trees growing in crocks sealed to varying degrees to allow controlled diffusion of the atmospheric oxygen into the crocks, found that there was a marked reduction in the formation of new rootlets if the oxygen fell much below 15% in the soil atmosphere. When the percent oxygen was below 10% in the soil air and the carbon dioxide varied from 5 to 10%, then the reduced root growth was serious enough to affect the growth of the tops of the apple trees. Cannon (36) has also found that the effects of aeration appear more quickly on root than on top growth of plants.

Another soil aeration study having to do with the growth of roots of apple tree seedlings was reported by DeVilliers
(67) who used various mixtures of oxygen and nitrogen as the aerating gases. He found that root growth at 15% oxygen was about 80% of the growth at 20.6% oxygen and that below 15% oxygen in the aerating gas the root growth was almost directly proportional to the oxygen content. On the other hand Seeley (155) found that the total dry weight of roses was not significantly lowered until the oxygen content of the aerating gas was reduced to 5%. Twelve liters of gas per day were passed through 4 by 7 inch cans of soil in this work. Reduction of the oxygen in the aerating gas to 2 to 3% resulted in the appearance of oxygen deficiency symptoms in the tops and the death of the roots.

In the light of these studies of Seeley, it is difficult to understand how Boicourt and Allen (18) were able to get almost double the linear growth of roses in beds aerated one hour daily through tile (10 inches below surface) as in un-aerated beds, when the soil air compositions under the two treatments were quite similar. In the unaerated beds the soil atmosphere at 8 inch depths contained 18.8 to 19.3% oxygen and 1.5 to 1.9% carbon dioxide, while the soil atmosphere in the aerated beds contained 20.2 to 20.3% oxygen and 0.3 to 0.6% carbon dioxide. These authors mention the possibility that the composition of the soil atmosphere does not reveal the true aeration condition.

Boynton, et al (25) have postulated different critical
concentrations of oxygen for the different phases of root activity of apple trees as follows:

1. Subsistence - 0.1 to 3.0% oxygen
2. Initiation of new roots - 12% oxygen
3. Normal growth of existing root tips - 10% oxygen
4. Absorption and accumulation - 15% oxygen

Shive (156) reports that on the basis of dry weight yields the maximum requirements for dissolved oxygen in culture solutions for soybeans was 6 ppm., for oats 8 ppm., and for tomatoes 16 ppm. Gilbert and Shive (74) suggest, on the basis of the high oxygen requirement of tomatoes, the possibility that the dissolved oxygen in equilibrium with the atmosphere is not enough for maximum growth of some species of crop plants. The production of new rootlets and the growth of the tops of apples, prunes and peaches was found by Boynton and Compton (23) to be retarded if the nutrient cultures were aerated with gases containing oxygen percentages below that of the atmosphere.

Seeley (155) in connection with the soil aeration studies referred to above also grew roses in nutrient cultures which were aerated with 10 liters of gas per day. The dry weights of the roots and tops were reduced significantly when there was 10% oxygen in the aerating gas. When the oxygen was reduced to 5% in the aerating gas the reduction in dry weight of the tops and roots was highly significant and most of the
roots died. It will be noted in comparing Seeley's results in soil aeration with those in nutrient solution that roses did not grow as well in nutrient culture as in soil when aerated with gas containing 5% oxygen. He indicates that this apparent difference in oxygen requirement may be partly explained by the fact that the light conditions were better for growth in the experiment with nutrient culture and more growth took place than in the soil experiment.

Not only may growth be retarded by an insufficient oxygen supply, but also the roots may be damaged or death may occur. The nature of the root damage, reported many times (55, 61, 71) is typified by the description of Curtis and Zantmyer (64, 65). They observed that the roots of avocado and citrus seedlings became darkened and constricted just back of the root tip when the dissolved oxygen in solution was less than 0.7 ppm.

The fact that a few plants have very low oxygen requirements is well known. The willow tree (53) and rice plants (113, 174) are examples. Taylor (167) has shown that rice may even germinate under anaerobic conditions. Laing (108) found that the rhizomes of certain semiaquatic plants could respire anaerobically for long periods of time without damage.

Some plants having low oxygen requirements may become injured if supplied with too much oxygen. Laing (109) found this to be true with certain semiaquatic plants when the water
in which they were growing was aerated with air. Detrimental effects due to high oxygen or to high aeration rates may be obtained also on plants with normally high oxygen needs.

Loehwing (119) observed injury to soybeans and sunflowers in soils when aeration was very rapid, and Gilbert and Shive (74) found that soybeans in nutrient cultures were injured if the dissolved oxygen was 8 to 16 ppm. The symptoms were chlorosis and leaf distortion. The growth of tomato roots was decreased when Erickson (71) bubbled 100% oxygen through the nutrient solution and Leonard and Pinckard (117) found cotton roots and tops were restricted in growth where 90 and 100% oxygen was used to aerate the nutrient culture. Hoagland (87) has indicated that if an oxygen supply is made available to plants at high temperatures the rapid oxidation of carbohydrates may actually be injurious to the plants. It is also possible that oxygen toxicity may be related to a reduced availability of iron and manganese due to the highly oxidized state of the substrate.

At times the diffusion of oxygen into the soil or into nutrient cultures may not be rapid enough to maintain the level of oxygen at the value for maximum growth. For this reason the artificial aeration of both soils (2, 4, 5, 34, 59, 66, 84, 96, 101, 110, 112, 119, 155) and nutrient cultures (4, 5, 8, 60, 62, 69, 77, 138, 155) has been found to increase the growth of plants.
Carbon dioxide has been found to be directly toxic to both plant and animal protoplasm. Literature relative to this point is reviewed by Chang and Loomis (57) who have recently created interest in the possible detrimental effects on plant growth and mineral nutrition of the carbon dioxide in soils.

Cannon (35, 37, 53) concluded that most plants, could tolerate rather high concentrations of carbon dioxide if adequate oxygen was available. Leonard (116) obtained almost normal growth of cotton roots in nutrient cultures aerated with a gas containing 30% carbon dioxide and 21% oxygen. On the other hand Vlamis and Davis (175) found that 20 to 30% carbon dioxide in the aerating gas was toxic to barley even when the oxygen was as high as 70 to 80%. The growth of the roots of citrus seedlings was shown by Birton (77) to be inhibited when aerated in sand cultures with 37 to 55% carbon dioxide and 20% oxygen. In experiments of Knight (101) with corn plants sealed into soil with paraffin, the plants died when the carbon dioxide in the soil air accumulated to 11.4%. In general high carbon dioxide in the root zone of plants results in the cessation of root growth, followed by the wilting and death of the whole plant (55, 72, 175, 179).

The old question of which becomes limiting first, oxygen or carbon dioxide, has evidence for both sides. Erickson (71) grew tomatoes in culture solutions some of which were exposed
to normal diffusion from the atmosphere and others which were artificially aerated. Careful measurements of the dissolved oxygen and carbon dioxide in the solutions were made periodically. At the end of five weeks the dissolved oxygen in the solution was practically zero and carbon dioxide had reached 6 m.e. per liter. He concluded that effects of poor aeration on the growth of the tomato plants appeared before the carbon dioxide reached this value and that the dissolved oxygen had become critically low before this time. With the dissolved oxygen held at 1 m.e. per liter and the carbon dioxide increased by steps to 18.9 m.e. per liter (23.9% carbon dioxide) a significant reduction in growth occurred only at the highest CO₂ level (18.9 m.e. per liter). Whether or not this was due to the low pH (4.5) of the solution was questioned.

Girton (77) concluded that the beneficial effects of aeration of nutrient cultures containing citrus seedlings were due to both the increased oxygen supply and the sweeping out of the carbon dioxide. Hunter and Rich (98) observed root growth in aerated and unaerated soil, and found that in both cases the roots grew intermittently but the period of growth was longer where the soil was aerated. They discussed the possibility that the carbon dioxide concentration became narcotic around the root tip, thus stopping growth until the carbon dioxide had diffused away. In this connection McComb and Loomis (121) have suggested that the decomposition of
organic matter and respiration of grass roots in dense prairie sod produces carbon dioxide concentrations higher than can be tolerated by upland forest species, thus effectively preventing forest invasion. Also the recent work of Bibbey (15) is of interest at this point. He found that the germination of certain weed seeds which display marked environmental dormancy in the soil, was reduced by as little as 5% carbon dioxide in the germinating flask even when 19 to 20% oxygen was present.

The improved effect of aeration on the growth of corn was considered by Knight (101) to be due to the sweeping out of the small amount of carbon dioxide around the roots. Kramer (102) on the basis of the more marked effect of carbon dioxide than of nitrogen on water absorption by tomatoes and sunflowers in nutrient cultures, suggests that physical changes in permeability are caused by carbon dioxide before the effects of oxygen deficiency become noticeable.

It is evident from the above investigations that the effect of oxygen deficiency and carbon dioxide excess on the growth of plants have been recognized, but that the relation of carbon dioxide to an oxygen deficiency has not been well established.

The absorption of water by plants has also been observed [Clements (61) and Kramer (102)] to be markedly affected by the oxygen and carbon dioxide levels in the plant substrate.
Chang (56) and Chang and Loomis (57) reported that absorption of water by the roots of maize, wheat and rice was reduced 14 to 50% by bubbling pure carbon dioxide through the culture solutions ten minutes each hour. Similar aeration with nitrogen had no effect. They suggest that carbon dioxide is effective in this way due to the reduction of the cell permeability.

Childers and White (58) found that submerging in water the roots of young apple trees growing in 5 gallon cans of soil caused a reduction in transpiration in from two to seven days. Childs (59) grew young apple trees in sealed containers and varied the percent oxygen and carbon dioxide around the roots. He reported that it was necessary to reduce the oxygen below 2% to obtain a reduction in transpiration. Carbon dioxide from 0.5 to 21% was without a very noticeable effect on transpiration if oxygen was present. Henderson (85) obtained a correlation between the respiration of corn and the water absorbed. The conclusion here was that the process of water absorption by corn was accompanied by an expenditure of energy.

Also the work of Newton (127) pointed to this relationship.

The reduction in the water absorption by sunflower and tomato plants was found by Kramer (102, 103) to be very marked when carbon dioxide was passed through the water around the roots and the plants soon wilted. With tomato plants a reduction in transpiration on the order of 7.7% occurred when oxygen free nitrogen was used as compared to a reduction of
43% with carbon dioxide. Kramer (102) felt that the cell membrane was altered by carbon dioxide and therefore became less permeable to water.

Whitney (179, 180) studied both the effects of oxygen deficiency and carbon dioxide excess on the water absorption of tomato, tobacco, cotton, corn, coleus and sunflower plants in sand cultures sealed into one gallon pails. The aeration rates were 2 liters per hour per pail, and the treatments consisted of 100% nitrogen; 20% oxygen plus 20% carbon dioxide plus 60% nitrogen; 20% carbon dioxide plus 80% nitrogen; and un aerated. The oxygen deficiency caused a 10 to 70% reduction in the transpiration of tobacco, tomatoes, coleus and corn the first day. The oxygen deficiency finally resulted in the death of the roots of the tomato, coleus and tobacco plants, while there was little injury to cotton, corn and sunflowers. Where the plants were aerated with 20% oxygen plus 20% carbon dioxide there was little effect on transpiration except on the first day, when it was slightly reduced in tomatoes, coleus, tobacco and cotton. The 20% carbon dioxide aeration treatment had about the same effect as the nitrogen treatment except on the coleus and tomato plants in which case the coleus plants died after five days aeration with the 20% carbon dioxide and the transpiration of the tomato plants was less than when aerated with pure nitrogen.

In general, it would seem from the results reviewed above
that the effects of oxygen and carbon dioxide levels in the substrate upon the transpiration of plants can be attributed in part to the effect of oxygen on the respiratory activity of the roots, and in part to the effect of carbon dioxide on the permeability of the root membranes.

In regard to mineral absorption as related to oxygen, there is again a large amount of literature. Most of it is in agreement with Hoagland and Broyer (86, 88, 89) in showing the need for active aerobic metabolism and thus adequate oxygen if significant mineral accumulation is to take place (6, 8, 16, 17, 27, 30, 31, 136, 137, 138, 144, 145, 149, 153, 162, 163, 164, 165). Stewart (163) points out that aerobic respiration and salt uptake are not related quantitatively, but that the parallelism indicates that a constant fraction of energy is given to salt uptake. A general review of the interrelations of dissolved oxygen, respiration, protein synthesis and nitrogen metabolism is given by Stewart, et al (165). Robertson, et al (144, 145) have obtained complete inhibition of salt accumulation against a concentration gradient in cut carrot tissue by treatment with cyanide. This does not affect electrolytes already absorbed. They feel that the results indicate that expenditure of energy in the process of accumulation can take place only if cytochrome oxidase is uninhibited. Kramer and Wilbur (105) found that sodium azide used on mycorrhizal roots of pine limited oxygen absorption
and prevented the absorption of radioactive phosphorus.

Recently Woodford and Gregory (183) have obtained nutrient accumulation by whole barley plants sealed into solution cultures and aerated with pure nitrogen gas. It was necessary to maintain a relatively high concentration of salts in solution, and they admit of the possibility that some oxygen may have been transported to the roots from the shoots. They also found that upon increasing the concentration of salts in the culture solution there occurred an increased accumulation of salt by the plants without a corresponding increase in respiration, especially when the latter process was being limited by oxygen supply. This work is of interest in the light of the suggestion by Stewart, et al (164) of a relationship between the oxygen needs for salt accumulation and the nutrient level in the plant, and also in connection with Shive's (156) results in which soybeans were found to absorb nitrates rapidly at low oxygen tensions.

Went (178) postulated that the aeration of roots produced a growth factor more than it influenced salt absorption. This was based on his observation that nutrient deficient plants soon recovered if part of their root systems was in unaerated nutrient culture and another part in gravel or sand suspended above the nutrient solution. This, however, could hardly be an adequate basis for any theory.

The oxygen levels for maximum salt absorption have been
determined largely in solution cultures. With storage tissue
Stewart, et al (164) found salt accumulation limited below
10% oxygen and the maximum uptake was at 21% oxygen. They
found that with excised potato roots the respiration and salt
accumulation was not reduced until the oxygen in the aera-
ting gas was lowered to 10% or less. This difference in
response of tissues which are strictly aerobic and those
which develop in water led them to say, "it suggests that
metabolic factors are involved in the adaptation to an aquatic
or terrestrial environment." Pepkowitz, et al (136) estab-
lished oxygen levels for the maximum absorption of potassium,
calcium and phosphorus by soybeans at 16 ppm. and tomatoes
at 8 ppm. They (137) found that potassium uptake was much
less dependent upon the dissolved oxygen than were the ab-
sorption of calcium and phosphorus. This, however, is some-
what contrary to the findings of others [Bower, et al (20)
and Lawton (112)] on the effect of aeration upon nutrient
absorption from soils. Hoagland and Broyer (88) reported that
the maximum uptake of minerals by excised barley roots occurred
at around 10% oxygen. However, Vlamis and Davis (175) ob-
tained maximum absorption of potassium and bromine by excised
barley, tomato and rice roots at 3% oxygen.

The literature on the effect of carbon dioxide on the
mineral nutrition of plants is not so extensive. Arrington
and Shive (9) concluded that carbon dioxide in nutrient cul-
tures was without effect upon nitrogen absorption by tomato plants. Carbon dioxide if allowed to accumulate has been shown by Willaman and Beaumont (181) to reduce the respiration of apple twigs, potato tubers and wheat. Their findings are generally in agreement with the early literature as reviewed by them. Chang and Loomis (57) reported a considerable reduction in ion absorption where carbon dioxide was bubbled through nutrient cultures. They concluded that such toxic effects of carbon dioxide may also be operative under field conditions. McGeorge and Brazeale (122) believe that high carbon dioxide in the soil inactivates enzymes which normally carry on oxidative processes necessary for mineral absorption. Carbon dioxide in the soil air has been shown by Parker (129) to be of little influence on the absorption of inorganic elements by plants. Ten and 20% carbon dioxide in air was found by Hoagland and Broyer (88) to have no depressive effect upon salt accumulation by excised barley roots. However these workers later (90) found that the salt accumulating power of cells tended to be lost under the influence of nitrogen and carbon dioxide gases. The effects on cell permeability were discussed, and they concluded that permeability, metabolism and salt accumulation were so intimately interrelated as to preclude any separation of the several aspects of the phenomena.

It is probably well to point out the effect of nitrates
upon the oxygen needs of plants for growth and mineral absorption. Arnon (6, 7) observed a beneficial effect of nitrates on the growth of barley in unaerated cultures. Aeration did not seem to help in cultures where nitrogen was supplied in the nitrate form, but in cultures where the nitrogen was supplied in the ammonia form, aeration was very beneficial to growth. Gilbert and Shive (74, 156) report that oxygen may be used by some plants from nitrates when they are the sole source of nitrogen at low oxygen tensions. They (75) found that the reduction of nitrate was apparently associated with carbon dioxide production in culture solutions of low oxygen tension. Similar results were reported by Hammer (82). Haas (81) suggests oxygen may be available from nitrates in connection with beneficial effects he obtained with nitrates upon the rooting of citrus cuttings. These views are also supported by Melsted, et al (125) who found no beneficial effect of aeration on soybean yields where high applications of nitrates were made to lysimeter plots.

There are, however, at least three reports of no beneficial effects from nitrate fertilizer under conditions of poor aeration. Bain and Chapman (11) were unable to get beneficial effects with the addition of nitrates to waterlogged soils, and Vlamis and Davis (175) found that barley grown under anaerobic conditions in nutrient cultures could not use nitrates as a source of oxygen. The minimum oxygen
concentration for the growth of cotton roots, according to Leonard and Pinckard (117) was not affected by the use of nitrates.

These data on nutrient absorption suggest that the effects of aeration on salt accumulation may be influenced by at least four factors: (1) the oxygen level, (2) the carbon dioxide level, (3) the salt concentration in the substrate and in the plant and (4) the source of nitrogen.

The effect of limited aeration on the anatomy of roots is well known. There are numerous references to the increased development of large air spaces in the root cortex of unaerated roots (5, 14, 32, 68, 157) and to the fact that such roots do not develop root hairs (54, 65, 70, 176, 180). McPherson (123) concluded that the death of groups of cells due to oxygen deficiency resulted in the presence of large cortical spaces in the roots.

In connection with the observed anatomical differences in roots depending upon the aeration status of the substrate, there is evidence that at least part of the oxygen needs of roots may be supplied from the atmosphere via the shoot [Cannon (44, 46, 47, 48, 49, 50, 51, 52)]. In general Cannon found that when plants were placed in sunlight after being in darkness the sudden photosynthetic activity liberated internal oxygen which moved from the shoot to the root in quantities greater than the needs of the roots. The inter-
nal oxygen was, therefore, expelled into the solution sur-
rounding the roots when it was measured by Cannon.

More recently Laing (107) has found by actual measure-
ment of the gases in the rhizomes of water plants that during
photosynthesis oxygen diffuses into the rhizome from the
shoot at the same time that carbon dioxide diffuses in the
opposite direction. That the shoot of Cladium Mariscus
supplies oxygen to its roots has been demonstrated by Con-
way (63). Brown (29) has observed gaseous exchange between
the root and shoot of the seedling of Cucurbita pepo. The
gaseous transfer was thought to occur by active translocation
in solution, the cotyledons and roots of the plant showing
the most active participation in this process. Lin (118)
observed that there was no difference in the response of
rice to aeration with oxygen and with nitrogen when the tops
were exposed to the atmosphere. Raalte (140) analyzed the
gas in the intercellular spaces of rice roots and found that
the oxygen remained around 6 to 9% even if the oxygen level
was reduced in the surrounding media.

In studies with whole plants and with excised roots,
Vlamis and Davis (175) found that rice, barley and tomato
roots reacted alike to oxygen tensions when excised, but
when attached to the plants rice roots showed little response
to varying oxygen tensions. This indicates that the rice
plant roots were like other roots when cut off from the oxy-
gen supply from the shoot. Glasstone (79) was able to pass large volumes of gas through plant tissues of 17 different species by the application of a small pressure. Age, size and moisture condition of the plants were considered to be factors in the amount of air passage.

Consideration must, therefore, be given to these possible gas movements through plants from shoot to root and vice versa when substrate aeration effects are studied. Evidence has been given that such gas movements may be an important factor in controlling the aeration conditions at the root surface. This may in part account for the fact that soil air composition measurements have not been easily correlated with plant growth responses to soil aeration practices.

The Problem of Soil Aeration

The application of the results, found in the literature thus far reviewed, to the aeration of the soil in the field is not easily made, or the problem would be nearer to solution. Kramer (104) in a short review of the recent work on soil aeration discusses the lack of knowledge of the subject at hand and especially concerning the growth of plants under waterlogged conditions. The growth of plants in wet soils has also been considered recently in a review by Conway (63). Woodford and Gregory (183), on the basis of their findings that mineral absorption may not be so dependent upon oxygen
if the minerals are of sufficient concentration in the nutrient culture, suggest that poor plant growth in soils which are water-logged may be due to a mineral starvation. The effect of the reducing conditions on the accumulation of toxic substances is also to be considered (115, 146, 168).

The soil is aerated by the interchange of gases between the soil and the atmosphere. Buckingham (33) has shown that the process of diffusion accounts for most of this gaseous interchange, while temperature, wind and pressure changes play only minor roles. Later work has been in agreement with this finding, for example Romell (148) states: "En résumé, la diffusion est sans doute l'agent principal de l'aération du sol."

Buckingham (33) also studied the rate of diffusion and derived an equation relating the diffusion rate to the square of the porosity of the soil. Penman (134, 135) has revised Buckingham's equation, finding that in the normal range of porosities encountered in soil the rate of diffusion is directly proportional to the porosity. His equation is

\[ \frac{D}{D_0} = 0.66 S \]

where \( D \) is the rate of diffusion in the soil, \( D_0 \) is the diffusion in free space, and \( S \) is the porosity.

It is surprising that the rate of diffusion of oxygen or of carbon dioxide for that matter, has not received the attention that the composition of the soil air has had for so
many years, especially since the value of the latter as a
criterion of soil aeration has been questioned (18, 151).
Cannon (39, 42, 55) observed that where certain low oxygen
gases were allowed to stream by plant roots, growth would
occur, but where the air was static there would be no growth.
He also found that, due to the more rapid rate of diffusion
of oxygen in helium gas than in nitrogen gas, there was a
much better root growth response to low oxygen values if
helium was used as the diluting gas rather than nitrogen.
Cannon was thus lead to conclude, "It is the rate of supply
and not the partial pressure of the gas that is of moment."

Hutchins (97) and Hutchins and Livingston (98) have
since then developed apparatus for studying the oxygen
supplying power of the soil, but it has evidently not been
generally used because of its bulk and rather inconvenient
adaptation for field use. More recently Taylor (168, 169)
has developed a diffusion well which may be buried in the
soil and the rate of oxygen diffusion into it measured. This
apparatus has been adapted for field use by Raney (141) and
promising results have been obtained from tillage plots.
Russell (151) has discussed these and other methods of
characterizing soil aeration. It is apparent that a revival
of the rate of supply idea concerning soil aeration has been
long overdue.

Various other methods of characterizing soil aeration
have been used. The total oxygen in a soil sample was
determined by Karsten (99) by the use of a dropping mercury
electrode. Lundegardh (120) used the rate of diffusion of
carbon dioxide as a measure of the aeration status of the
soil. He considered, however, that 1% carbon dioxide or
above in the soil gas was an indication of poor aeration.
Webley (177) has attempted to use bacteria to determine the
oxygen availability in soil, and thus to serve as an index
of soil aeration. Hardy (83) considered a soil was well
aerated if the pore space occupied by air was 12%. Schuster
and Stephenson (154) reported that roots of walnut trees
penetrated the subsoil and were adequately aerated if the
non-capillary pore space was 10 to 12% by volume. The non-
capillary porosity was used by Baver (13) as a criterion of
soil aeration. Hoffer (91, 93) has described qualitative
tests which are easily made in the field and may indicate
the aeration needs of the soil.
Oxidation-reduction potentials, especially on water-
logged soils, have been used by some to indicate the soil
aeration status (28, 76, 131, 132, 133, 139, 161), however
Taylor (168) concluded that this measurement was not generally
useful for this purpose. Malloch, et al (124) failed to find
any correlation between oxidation-reduction potentials and
yields or composition of crops in the field.
The composition of the soil atmosphere has long been
the most popular method of ascertaining the aeration needs of soils (22, 24, 61, 80, 84, 147, 150, 173). These studies have their value and it might be well to consider the range of gaseous concentrations which have been found in various soils. Albert and Armstrong (1) obtained poor aeration conditions on Norfolk fine sand by flooding, and soil air samples taken at six inch depths showed a low of 3.6% oxygen and a high of 7.82% carbon dioxide. Usually, however, the oxygen was above 10% and the carbon dioxide below 5%. Boicourt and Allen (18) in obtaining much better linear growth of roses where the soil was aerated felt that the air composition in aerated and unaerated soils did not reveal the true aeration condition of the soil since the oxygen value (20.2%) in the aerated soil was only slightly higher than the oxygen value (19%) in the unaerated soil. The average respective carbon dioxide values were 0.4% and 1.7%.

Boynton, et al (21, 22, 23) obtained wide seasonal fluctuations in the composition of the air of orchard soils. They also stressed the fact that the sum of the oxygen and carbon dioxide values may deviate widely from 20.8%. Others (73, 150, 173) have also found this to be true. Boynton (21) observed that carbon dioxide was rarely above 12% regardless of how low the oxygen was. Carbon dioxide tended to increase with depth. Others have found high carbon dioxide values between 15 and 20% (61, 84, 173), especially near the roots.
of plants [Leather (114)].

Moisture conditions have a marked influence on the composition of the soil atmosphere aside from reducing the volume of air. Vine, et al (173) obtained 20% oxygen in a dry soil and 16.4% oxygen when it was wet. Oxygen was found by Ray and Shanks (142) to drop to a minimum of 14% and carbon dioxide rose to a maximum of 3% six to nine hours after water was added to a soil. Humfield (95) found an increase in the carbon dioxide production following a rain.

There is the possibility that other factors than aeration may be operative in certain soils where the effect of tillage practices on plant growth has been observed. Bower, et al (20) have attributed the superior growth and potassium nutrition of corn to the better aerated conditions of plowed plots. However, no gas analyses were made. This is an old claim for the beneficial effects of tillage, but actual soil air measurements supporting this claim are not available.

It is interesting that soil compaction effects other than on aeration are receiving increasing attention (94, 128, 151, 158, 159, 166, 168, 184, 185). Veihmeyer and Hendrickson (171, 172) found that lack of root penetration into soils of high density was not due to oxygen deficiency. On the other hand some workers have obtained better growth and root penetration of compacted soils when artificially aerated [Knight (100)].
In concluding this review it might be well to mention the fact that a recent approach to the problem of supplying the oxygen needs of plants in the soil has been through the application of oxygen carrying fertilizers. The work with nitrates has already been reviewed. Zimmerman (186) used potassium permanganate and hydrogen peroxide effectively in solutions for the rooting of cuttings. And more recently Melsted et al (125) have applied hydrogen peroxide to soils in lysimeter plots with a resulting increase in yield of corn and soybeans comparable to the effects of forced aeration.

In summary, it is apparent that the problem of soil aeration is affected by all the interrelated factors controlling the aeration conditions in culture solutions. In addition to these, certain factors peculiar to the soil itself become important. Among these may be mentioned:

1) The rate of gaseous interchange between the soil and the atmosphere as affected by soil porosity and moisture content.
2) The accessibility to roots of plant nutrients in compacted or poorly aerated soil zones.
3) The possible formation of toxic substances in poorly aerated soils.
4) The effect of oxygen on the mobility of certain plant nutrients especially iron and manganese.
Summary

The literature in the field of aeration is probably not any more contradictory than in any other field, but due to the fact that we are dealing with the soil (complicated enough within itself) and with nutrient cultures, there is apt to be more apparent confusion and contradiction than usual. It should be emphasized that a considerable part of the work on aeration, and especially of the older work, cannot be scientifically evaluated and therefore does not represent a valuable contribution to the field. For this reason it is difficult to enumerate any generalities on aeration.

Suffice to say, however, that the oxygen needs of most plants, and the toxicity of carbon dioxide to most plants, have been shown. For example, work with whole plants, excised roots and storage tissue has established the need of aerobic respiration for the active accumulation of salt by cells against a concentration gradient. Too, the toxic effect of carbon dioxide has been demonstrated against various tissues, even the roots of plants like rice which normally live under somewhat anaerobic conditions. Both low oxygen and high carbon dioxide concentrations have been found to influence the growth, and water and mineral absorption of plants.

The numerous reports in the literature concerning the beneficial effect on the physiology of plants of the
artificial aeration of soils and nutrient cultures attest to the favorable adjustment of either or both the oxygen and carbon dioxide in the substrate by the process of aeration. The relative importance of an oxygen deficiency, a carbon dioxide toxicity, and a carbon dioxide-oxygen interaction as contributing factors to the reduced growth and mineral uptake by plants on poorly aerated soils, has not been clearly elucidated. The work here reported was designed to fit this need in the general field of plant substrate aeration.
INVESTIGATIONS

The Influence of Oxygen Carrying Fertilizers Added to Soils at Three Moisture Tensions upon the Growth of Corn

Experimental

The reasons for poor growth of crop plants on water-logged soils are not clearly understood. The general belief, however, is that the lack of an adequate oxygen supply to the roots is the main factor. In this connection Bain and Chapman (11) have attempted without success to supply the oxygen needs of avocado and grapefruit by supplying nitrates to water-logged soils. Melsted, et al (125) have reported beneficial effects on the yields of corn and soybeans by the application of hydrogen peroxide to soils (not water-logged) in lysimeter plots.

In view of these investigations it was decided to test other oxygen-carrying chemicals on the growth of corn at various moisture levels including water-logging. A survey of the chemicals which might be used for this purpose resulted in the choice of barium peroxide and ammonium persulphate. Barium peroxide reacts with water according to the following equation to liberate hydrogen peroxide which
probably disintegrates rapidly in the soil liberating oxygen:

$$\text{Ba O}_2 + 2\text{H}_2\text{O} = \text{Ba (OH)}_2 + \text{H}_2\text{O}_2$$

Ammonium persulphate also yields hydrogen peroxide when reacting with water thus:

$$(\text{NH}_4)_2 \text{S}_2\text{O}_8 + 2\text{H}_2\text{O} = 2 (\text{NH}_4)_2 \text{SO}_4 + \text{H}_2\text{O}_2$$

These chemicals were used in preference to hydrogen peroxide in the hope that oxygen-carrying chemicals might be found which could be applied to the soil during ordinary cultural practices and which would later release oxygen.

An experiment was conducted to determine the effects, on the growth of corn, of these chemicals when applied to soils of varying levels of aeration and potassium supply. The levels of soil aeration were established by varying the moisture contents of the soil. The treatments used were as follows:

Main treatments—potassium fertilization
- No potassium
- 100 pounds of potassium per acre\(^1\)
- 200 pounds of potassium per acre

Sub-treatment—moisture levels
- Field capacity (19.72%)
- Moisture holding capacity (28.20%)
- Saturation (49.50%)

\(^1\)Pounds per acre as used throughout this thesis refers to parts per 2,000,000.
Sub-sub treatments—oxygen-carrying fertilizers

No fertilization

Barium peroxide (6.03 grams per pot)

Ammonium persulphate (8.15 grams per pot)

These treatments were applied in three replications to corn grown in 1 gallon glazed pots of Carrington soil (4 kilograms per pot).

The rates of oxygen-carrying fertilizers were calculated to yield about 400 ml. of oxygen per pot if all of the material reacted to form more stable compounds. This was approximately equal to the calculated air-filled pore space in a 1 gallon pot of soil at field capacity. Ammonium sulphate was added to the necessary treatments to bring the ammonium to the same level as in the ammonium persulphate pots and calcium carbonate was added in amounts equivalent to the sulphate to prevent acidity. The barium peroxide fertilizer was prepared by mixing one part of plaster of paris with 15 parts of barium peroxide, passing it through a 4 mesh sieve and allowing it to harden into pellets. It was expected that this treatment might allow a slower release of the oxygen to the surrounding soil and that the sulphate would be beneficial in precipitating the barium.

All of the above fertilizer materials were mixed and applied in a band about two inches below the soil surface. After the plants (4 per pot) were up, phosphorus was applied
in solution to all pots at the rate of 100 pounds of P₂O₅ per acre.

At the end of six weeks the tops were harvested, dried in an oven at 60°C and the dry weights recorded.

Results and discussion

The yields of corn in this experiment are given in Table 1. The most obvious yield effect is due to moisture level, the highest yields in all cases being at the medium moisture level. Potassium was effective in increasing the yields only at this moisture level. The results of the oxygen fertilizer treatments were highly inconsistent in the three replications and even at different moisture levels. It is interesting to note, however, that where the soil was saturated the ammonium persulphate increased the yields by approximately 28 and 45 percent at the low potassium and high potassium levels respectively.

This would seem to indicate that further investigation of these materials, and any others which might release oxygen in the soil, would be desirable. Further work of this nature should probably first seek to determine the amounts and rates of oxygen release from these materials when used under various environmental conditions.
Table 1. The effect of oxygen-carrying fertilizers, when applied at varying moisture and K levels, on the dry weight of corn grown in Carrington soil.

<table>
<thead>
<tr>
<th>Moisture percent</th>
<th>No K fertilization</th>
<th>100 lbs. K/acre</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(NH₄)₂S₂O₃</td>
<td>B₂O₃</td>
</tr>
<tr>
<td>19.72 (field capacity)</td>
<td>: 3.05 : 4.13 : 3.18 : 4.62 : 2.97 : 3.16</td>
<td></td>
</tr>
<tr>
<td>49.30 (saturation)</td>
<td>: 3.18 : 2.27 : 2.48 : 3.65 : 2.51 : 2.38</td>
<td></td>
</tr>
</tbody>
</table>

1 Average of three pots
2 On the dry weight basis
Greenhouse Studies with Variable Oxygen and Carbon Dioxide Levels in the Soil.

Soil aeration experiment no. 1. The influence of restricted and forced aeration on the growth of corn at three potassium levels

Experimental A preliminary experiment was conducted to establish techniques for growing corn plants in soils under controlled aeration conditions, and to determine the composition of the soil atmosphere under both forced and restricted aeration which might be related to plant growth. High rates of potassium fertilization were included in view of Lawton's (113) observation that potassium seemed to slightly overcome the detrimental effects of poor soil aeration.

In this experiment corn was grown in a mixture of Carryington soil and sand at three potassium levels and with three aeration treatments applied in a split plot design as follows:

Main treatment-aeration

- No aeration (tops of pots open to the atmosphere)
- Forced aeration (4 liters of air per pot per day - tops partially closed)
- Restricted aeration (tops of pots closed with parafilm)
Sub treatments—potassium fertilization

No potassium

100 pounds of potassium per acre

200 pounds of potassium per acre

The experiment was replicated four times. All pots received a blanket application of 100 pounds of nitrogen per acre as ammonium nitrate, 100 pounds of P₂O₅ per acre as calcium dihydrogen phosphate, 5 pounds of borax per acre and 50 pounds of magnesium sulphate per acre. Each fertilizer material was added in solution to the top of the soil after the seeds were planted and water had been added to bring the soil to field capacity. Maintenance of the soil at this moisture level was accomplished with frequent weighing of the pots.

The tops of the pots in the restricted aeration treatment and in the forced aeration treatment, were closed before the leaves had emerged from the coleoptile by the fastening of sheets of parafilm to the sides of the pot with melted paraffin. Petrolatum was used as a seal between the parafilm and the plants only in the restricted aeration treatment. Aeration was begun immediately after the top seals were installed and was continuous at a rate of four liters per pot per day. The aeration apparatus is shown in Figure 1.

Essentially the air was forced from four liter bottles into a distribution copper coil in the bottom of the pot by the
Figure 1. Apparatus used to aerate soils with air. The major parts are: a, 50 liter reservoir; b, float valve; c, constant level reservoir; d, calibrated siphon which discharges the water from the constant level reservoir at a constant rate; and e, siphons which carry the water collected in a central glass tube from the calibrated siphon into the 4 liter bottles.

Figure 2. Comparison of corn leaves of plant grown with normal aeration (left) and with restricted aeration (right).
controlled flow of water into the four liter bottle. In Figure 1 the major parts of the apparatus are: a, the 50 liter carboy used as a supply reservoir; b, the float valve which allows water to be siphoned from the carboy at a rate to maintain a constant water level in the reservoir, c; d, the calibrated siphon which discharges the water from the constant level reservoir into a glass tube from which siphons, e, carry the water to the four liter bottles. The water level is then the same in all the bottles and rises at the same rate. Equal volumes of air are discharged if the bottles are of the same diameter.

The composition of the soil atmosphere in the pots was determined periodically by the use of a Haldane type gas analysis apparatus. The air samples were taken directly from the soil into the analysis apparatus through a short piece of capillary tubing which was forced into the soil. At the end of seven weeks the tops and roots were harvested, dried in an oven at 60°C and their dry weights recorded.

Results and discussion  The dry weights of the corn (tops and roots) are presented in Table 2. The reduction in growth of both tops and roots in the closed pots at all potassium levels is highly significant. The forced aeration treatment even at the relatively slow rate tended to increase the yields at all potassium levels. Potassium fertilization
Table 2. Yield of corn grown in a Carrington soil-sand mixture at three potassium levels and three aeration treatments.

<table>
<thead>
<tr>
<th>Aeration</th>
<th>Treatment</th>
<th>No K</th>
<th>100 lbs. K/acre</th>
<th>200 lbs. K/acre</th>
<th>Total all K</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>tops: roots: total</td>
<td>gms</td>
<td>gms</td>
<td>gms</td>
<td>gms</td>
</tr>
<tr>
<td>No aeration (closed top)</td>
<td>5.20: 2.05: 7.25: 5.75: 2.90: 8.65: 4.32: 2.05: 6.37: 15.27: 7.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
was not effective in reducing the ill effects due to poor aeration; this does not agree with the findings of Lawton (113). The reduced yields at the high level of fertilizer application was unexpected in view of the fact that the unfertilized plants showed potassium deficiency symptoms at the close of the experiment.

The analyses of the soil atmosphere (Table 3) do not indicate significant differences between the pots with forced aeration and the unaerated pots with open tops. It is possible, however, that the parafilm covers (which were left open around the plants) on the aerated pots did significantly slow down the diffusion of carbon dioxide into the atmosphere. The soil atmosphere of the unaerated sealed pots had a significant decrease in percent oxygen. These soil air composition values would not ordinarily be expected to influence plant growth to the degree found in this experiment. Numerous investigators, however, notably Cannon (39, 42, 55) have found that plants respond differently to static and to streaming gases in the root zone. In the latter case to obtain retardation of plant growth it was usually necessary to have greater extremes in the gaseous composition than in the former case.

In this experiment it is possible that the air composition around the roots was more deficient in oxygen or higher in
Table 3. Oxygen and carbon dioxide percentages in the soil atmosphere under corn grown in the greenhouse under different aeration conditions.

<table>
<thead>
<tr>
<th>Aeration treatment</th>
<th>Time of sampling (days from planting)</th>
<th>Average soil air composition</th>
<th>No K</th>
<th>100 lbs. K/acre</th>
<th>200 lbs. K/acre</th>
</tr>
</thead>
<tbody>
<tr>
<td>No aeration (open top)</td>
<td>28-30</td>
<td>CO₂</td>
<td>O₂</td>
<td>CO₂</td>
<td>O₂</td>
</tr>
<tr>
<td>Aerated with air</td>
<td>28-30</td>
<td>0.10(1)</td>
<td>20.60(1)</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>No aeration (closed top)</td>
<td>28-30</td>
<td>0.80(1)</td>
<td>20.22(1)</td>
<td>0.51(1)</td>
<td>20.45(1)</td>
</tr>
<tr>
<td>(closed top)</td>
<td>42-43</td>
<td>2.28(4)</td>
<td>18.91(4)</td>
<td>1.80(5)</td>
<td>19.10(5)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3.38(3)</td>
<td>17.84(3)</td>
<td>3.63(2)</td>
<td>17.21(2)</td>
</tr>
</tbody>
</table>

1 Figures in parenthesis indicate the number of analyses represented in the average given.
carbon dioxide than these analyses indicate. A 10 milliliter air sample comes from a total space in the soil which is three to four times larger than the air sample, and therefore, the composition must represent the average of conditions in the particular volume sampled.

The parafilm covers were not as effective as had been expected. Upon exposure to greenhouse conditions for a period of three weeks the covers became brittle and were easily punctured. All covers had to be replaced at least once before the experiment was completed. In subsequent experiments it was found that diffusion of atmospheric air into the pot could be very effective even through small cracks around the edge of paraaffin covers.

The plants under restricted aeration began to show abnormal growth after five to six days of treatment. Splotches and bands of chlorotic areas appeared on the leaves. Some plants became stunted, and others grew short and stocky with twisted leaves, the bases of which were usually chlorotic. Figure 2 shows a typically banded leaf in comparison to a healthy one. These symptoms on corn plants had not previously been observed and no references regarding them have been found in the literature. These symptoms were not observed in any subsequent experiments where aeration was restricted.

The root systems under the restricted aeration were definitely less extensive and less fibrous than those under
aeration. The appearance of the roots in the forced and normally aerated pots were essentially the same.

The possibility of nitrite accumulation was checked by extracting a soil sample with Morgan's (126) universal soil extracting solution (pH 4.8) on which nitrites were determined by the method of Rider and Mellon (143). Between 0.02 and 0.04 ppm of nitrites were found, which is in agreement with others (1, 65) who have also found nitrite values below the toxic range in flooded soils and in nutrient solutions kept under anaerobic conditions.

Soil aeration experiment no. 2. The growth of corn as influenced by the amount of oxygen and carbon dioxide in the aerating gas and the level of potassium fertilization.

Experimental In view of the results in the last experiment where it was noted that the soil air composition may not reflect the true aeration conditions around the plant roots, an experiment was conducted in which an attempt was made to control the aeration conditions in the soil. This consisted of sweeping a relatively porous soil with large volumes of different gases. It was felt that by this technique a greater uniformity of aeration conditions within the soil around the plant roots might be attained.

The first experiment of this nature was designed to get
extreme effects, if possible, by using as the aerating gases 100% nitrogen, 100% carbon dioxide and a 40%-oxygen-60% nitrogen mixture. Ten liters of each of these gases were passed through a 1 gallon pot of a mixture of equal parts of Carrington soil and sand. Four corn plants were grown in each pot. The treatments, replicated four times, were applied in a split plot design as follows:

Main treatments-potassium fertilization

No potassium
100 pounds of potassium per acre

Sub-treatments-aeration

No aeration (tops of pots open to the atmosphere)
100% nitrogen
100% carbon dioxide
40% oxygen, 60% nitrogen

The gases were distributed in the bottom of the pot in the same manner as in the last experiment.

The mixing of the gases and the control of the flow rate was accomplished by the use of calibrated capillaries constructed as shown in Figure 3. Preparation and calibration of the capillaries consisted of the following steps. A short piece of 5 mm. glass capillary tubing was heated in a small "focusing" type oxidizing flame from a blast lamp and drawn out as indicated in Figure 3. The two capillaries were then broken apart and each was calibrated to allow a known volume
Figure 3. Stages in the preparation of glass capillaries for controlled gas flow.

Figure 4. The Haldane type gas analysis apparatus used throughout this work, showing the method of inserting the gas sample from a 10 milliliter syringe through a hypodermic needle which has been plunged into the rubber tube side arm. Mercury fills the gas burette, the rubber side arm and up to a stopcock (just out of the photograph) before the gas sample is entered.
of gas to pass through per unit time and at the gas pressure to be used in the experiment. This was accomplished by placing the capillary in a compressed air line in which the pressure was controlled at the same value to be used later. The volume of gas then passing through the capillary was collected and measured by the displacement of water in a burette. The tip of the capillary was broken back until the desired volume of gas per unit time was obtained. Once a capillary was made as a standard for a certain gas flow, others of the same flow rate could be made easily and rapidly by the use of a bubble counter as described by Bartholomew and Broadbent (12).

The capillary was protected by fastening it into a short piece of glass tubing with sealing wax as indicated in Figure 3. Ordinary red sealing wax was found to be unsatisfactory under greenhouse conditions. Fischer's "Pyseal" gave better results but still separated from the outer glass tube in some cases.

A diagrammatic sketch showing the use of the capillaries in the complete system is shown in Figure 5. In this case the rate of flow of gases through the pots was 10 liters per 24 hours. This means that capillaries placed in the manifold distributing gases to the pots were each calibrated at 100 cm. of water pressure to allow the passage of 10 liters of gas per 24 hours. The compressed gas was delivered from the tank at 200 cm. of water pressure and passed through other cap-
illaries into the mixing chamber. The pressure differential on these capillaries controlling the flow rate to the mixing chambers was then 100 cm. of water. To obtain the desired percentages of gas, the capillaries entering the mixing chamber were calibrated to deliver the proper ratios of the components of the mixed gas. The total delivery from all the capillaries entering a mixing chamber was equal to the number of replications times the flow rate through each pot. The installation of the apparatus for this experiment is shown in Figure 6.

The following fertilizers were applied in solution to all pots: 100 pounds of nitrogen per acre as ammonium nitrate, 200 pounds of P₂O₅ per acre as calcium dihydrogen phosphate and 50 pounds of magnesium sulphate per acre. The soil moisture was maintained at field capacity by frequent weighing of the pots.

The prevention of gaseous diffusion from the atmosphere into the soil was attempted by the application of 400 grams of ball-milled white quartz sand to the soil surface in each pot after the plants emerged.

The soil atmosphere was sampled for analysis through small copper tubes placed in the soil at the beginning of the experiment. Two tubes were installed in each pot at about four and six inch depths. Soldered on to each tube were two copper baffle plates to aid in holding the tubes stationary
Figure 6. General view of apparatus used in the first aeration experiment with controlled gas mixtures.
in the soil and to prevent the flow of gases from the atmosphere along the tube when air samples were withdrawn. A small square of fine mesh bronze screen was folded over the end of the tubes to prevent their becoming plugged with soil. The Haldane type gas analyzer was connected directly to the sampling tubes by means of a piece of glass capillary tubing. The air sample was then drawn from the soil into the gas burette by lowering the mercury leveling bulb.

The entire plants were harvested, and the heights to blade tips and the green weights of the tops were obtained. The roots and tops were then dried in an oven at 60°C and their dry weights recorded.

Results and discussion The heights, green yield of tops and dry yields of tops and roots of corn in this study are given in Table 4. The dry weights are shown graphically in Figure 7. The striking effect of the carbon dioxide on root growth at both potassium levels is best observed in the photographs of the plants (Figures 8 and 9). Most of the roots were found in the top half of the pots aerated with carbon dioxide. When 100 pounds of potassium per acre were applied the carbon dioxide aeration had little effect on the top growth. This indicates the possibility that there was a sufficient supply of potassium remaining in the upper levels of the pot in contact with the small root
Table 4. Yield and height of corn grown in a soil-sand mixture with and without potassium fertilizer and aerated continuously with various gas mixtures. Average of four replications.

<table>
<thead>
<tr>
<th>Aerating gas</th>
<th>Height to blade tip</th>
<th>Green weight of tops</th>
<th>Dry weights</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Tops</td>
</tr>
<tr>
<td>No K : K/acre</td>
<td>cms : gms</td>
<td>cms : gms</td>
<td>cms : gms</td>
</tr>
<tr>
<td>100% NO₂</td>
<td>77.7 : 83.9</td>
<td>52.0 : 76.1</td>
<td>5.96 : 9.04</td>
</tr>
<tr>
<td>100% CO₂</td>
<td>48.0 : 75.5</td>
<td>17.5 : 62.6</td>
<td>2.55 : 8.94</td>
</tr>
<tr>
<td>40% O₂, 60% N₂</td>
<td>75.5 : 89.0</td>
<td>46.0 : 78.5</td>
<td>5.33 : 9.16</td>
</tr>
<tr>
<td>No aeration</td>
<td>71.8 : 84.3</td>
<td>46.0 : 71.0</td>
<td>5.36 : 8.45</td>
</tr>
</tbody>
</table>
Figure 7. The effect of continuous aeration with various gases on the dry weight of corn tops and roots at different potassium levels.
LEGEND:

- TOPS
- ROOTS

COMPOSITION OF AERATING GASES

<table>
<thead>
<tr>
<th></th>
<th>DRY WEIGHT GRAMS/POT</th>
</tr>
</thead>
<tbody>
<tr>
<td>O-K N_2</td>
<td></td>
</tr>
<tr>
<td>K</td>
<td></td>
</tr>
<tr>
<td>O-K CO_2</td>
<td></td>
</tr>
<tr>
<td>K</td>
<td></td>
</tr>
<tr>
<td>O-K 40% O_2</td>
<td></td>
</tr>
<tr>
<td>K</td>
<td></td>
</tr>
<tr>
<td>O-K CHECK</td>
<td></td>
</tr>
<tr>
<td>K</td>
<td></td>
</tr>
</tbody>
</table>
Figure 8. Corn plants grown in one gallon pots without potassium fertilization and aerated continuously at the rate of 10 liters per day with the following gases: No. 1 - 100% N₂, No. 2 - 100% CO₂, No. 3 - 40% O₂ and No. 4 - no aeration, check.
Figure 9. Corn plants grown in one gallon pots with potassium fertilization and aerated continuously at the rate of 10 liters per day with the following gases: No. 1 - 100% N₂, No. 2 - 100% CO₂, No. 3 - 40% O₂, and No. 4 - no aeration, check.
system to allow almost normal growth of the corn. The plants under the latter treatment were observed to develop phosphorus deficiency symptoms quite suddenly during the last few days of the experiment. Where there was no application of potassium to the carbon dioxide aerated pots the plants appeared generally stunted and showed poor growth throughout the experiment. The high oxygen aeration treatment had apparently little beneficial effect on the growth of corn over the unaerated treatment and the nitrogen aeration treatment was not detrimental. The potassium fertilizer obviously benefitted the growth under all conditions.

The average oxygen and carbon dioxide content of the soil atmosphere under the various treatments is given in Table 5. These values show the ineffectiveness of the surface layer of sand in preventing diffusion of gases from the atmosphere. In fact, this shows in a surprising fashion the effectiveness of gaseous diffusion in the replenishment of the soil atmosphere.

The actual flow rates of the gases were found to differ slightly from the expected 10 liters per pot per 24 hours. The average flow rate of the nitrogen was 10 liters per 24 hours. However, the average carbon dioxide flow rate was 11½ liters per 24 hours and the average flow rate of the high oxygen gas was about 9½ liters per 24 hours. This at least partly accounts for the fact that the percent oxygen
Table 5. Oxygen and carbon dioxide percentages in the soil atmosphere under corn grown in the greenhouse under continuous aeration with different gases.

<table>
<thead>
<tr>
<th>Aerating gas</th>
<th>Depth of sample (inches)</th>
<th>Average soil air composition</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>CO₂</td>
</tr>
<tr>
<td>100% N₂</td>
<td>4</td>
<td>---</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>---</td>
</tr>
<tr>
<td>100% CO₂</td>
<td>4</td>
<td>30.93(3)</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>30.05(16)</td>
</tr>
<tr>
<td>40% O₂, 60% N₂</td>
<td>4</td>
<td>0.20(2)</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>0.25(2)</td>
</tr>
<tr>
<td>No aeration</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

¹Figures in parenthesis indicate the number of analysis represented in the average given.
is higher in the nitrogen aerated pots than in the carbon
dioxide aerated pots. The differences in the viscosity of
the gases accounts for the differences in the flow rates.
The viscosities (micropoises) of several gases at approximately
19°C are given below.¹

<table>
<thead>
<tr>
<th>Gas</th>
<th>Viscosity (μP)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Air</td>
<td>182.7</td>
</tr>
<tr>
<td>N₂</td>
<td>175</td>
</tr>
<tr>
<td>O₂</td>
<td>201.8</td>
</tr>
<tr>
<td>CO₂</td>
<td>149.9</td>
</tr>
</tbody>
</table>

The Poiseuille equation [Glasstone (78)] for the vis-
cosity of gases or liquids is

\[ \eta = \frac{Fr^4t}{8vL} \]

where \( \eta \) is the coefficient of viscosity of the gas or liquid
flowing at a uniform velocity at a rate \( v \) milliliters per
second \( t \) through a narrow tube of radius \( r \) cm, and length \( L \)
\( \text{cm} \), under a pressure gradient of \( P \) dynes per square cm. The
equation can be written

\[ v = \frac{Fr^4t}{8\eta L} \]

to indicate the inverse relationship between the volume of
gas flowing per unit time and the coefficient of viscosity.
This equation is applicable only to "streamlined" flow at
low rates in tubes of small diameters.

¹Handbook of Chemistry and Physics. 30th ed. Cleveland.
Since the capillaries were calibrated with compressed air the flow of carbon dioxide through these capillaries would naturally be more rapid than air due to the former's lower viscosity. It is seen that capillaries for the control of nitrogen can for practical purposes be calibrated with compressed air. In subsequent experiments it was found most practical to calibrate all capillaries with compressed air and then adjust the flow rate to the desired values by making minor adjustments in the pressures of the different gases. This also has the advantage that all capillaries are interchange able and different combinations of gas mixtures can be obtained by simply changing the gas source at the capillaries leading to the mixing chambers.

The control of the gas pressures at 200 cm. is difficult unless a series of at least two needle valves are used in reducing the high pressure in the tank. Changes in temperature cause the most trouble where only one needle valve is used.

Although capillary flowmeters have long been used for the mixing of gases and the control of flow rates, the type of glass capillaries described above were apparently first developed and used by investigators in the Iowa State College Soil Bacteriology Department. Details of apparatus designed for aeration in bacteriological work are given by Broadbent (26) and Bartholomew and Broadbent (12).
In the analysis of the soil atmosphere using the "buried-well" technique, it was found that the necessity of disposing of 3 or 4 milliliters of the gas first withdrawn was a distinct disadvantage. Too, the connection between the gas analysis apparatus and the copper tube leading into the soil is not always easily made and requires special precautions to avoid leaks.

The Pauling (130) oxygen analyzer manufactured by Beckman was tested during this experiment. It was found that the air sample required was too large for work with 1 gallon pots. Also, it was found that considerable sweeping of the apparatus was necessary if two successive samples were very different in composition. Carbon dioxide especially was found to linger in the oxygen analyzer. It was concluded that soil gases could be more accurately measured by the introduction of small samples directly into a Haldane type gas analyzer. A satisfactory method of accomplishing the latter was developed and used in later experiments.

The gains from this experiment were largely in experimental methods. However, the results indicate that under the conditions of this experiment root growth was inhibited by high carbon dioxide levels and that oxygen levels considerably below atmospheric values had no effect on the growth of corn. These findings are in agreement with those of Cannon (55) and several others (77, 116).
Soil aeration experiment no. 3. The influence of oxygen and carbon dioxide levels in the soil upon water and potassium absorption by corn and soybeans

Experimental The fact that carbon dioxide gave the predominant effect on the growth of corn in the last experiment prompted major attention to be turned to this factor in the next experiment. It also seemed desirable to use as uniform plant material as possible with short periods of aeration during which time water and potassium absorption would be determined. In this way the confounding of the absorption effects with growth effects would be minimized. The experiment was designed to include two tests, one with corn and one with soybeans, the treatments being the same in both cases. The soybeans were therefore planted a few days later than the corn to allow the use of the same aeration apparatus. A general description of the experiment followed by a more detailed explanation of the equipment and the procedures used is given below.

The two sets of plants were grown for four weeks in a 1:1 mixture of Carrington soil and sand as in the previous experiment. The pots were arranged on the greenhouse bench in a randomized block design (four replications). All pots were treated alike, each receiving 100 pounds of nitrogen per acre as ammonium nitrate, 200 pounds of P₂O₅ per acre as treble superphosphate and 50 pounds of magnesium sulphate
per acre, added in solution to the top of the soil after the plants had emerged. The soil was maintained at field capacity by frequent weighing of the pots.

At the end of four weeks six different aeration treatments were applied with each pot receiving 10 liters of gas per 24 hours distributed through a copper coil in the bottom of the pot as in previous experiments. The six gas mixtures used were as follows:

1. 100% N₂
2. 20% O₂, 80% N₂
3. 20% O₂, 5% CO₂, 75% N₂
4. 20% O₂, 10% CO₂, 70% N₂
5. 20% O₂, 20% CO₂, 60% N₂
6. 20% O₂, 50% CO₂, 30% N₂

Prior to the start of the aeration four pots were harvested, and during the aeration four other pots were left un-aerated (tops open) and unfertilized with potassium. These two treatments, especially the latter, served as a basis of comparison for the effect of the different aerating gases on the accumulation of added potassium. The potassium (150 pounds per acre) was added to all aerated pots after the aeration had been in progress for 24 hours and then 48 hours later the plants (tops and roots) from all the aerated and from the four unaerated pots were harvested.

The design of the capillary control apparatus for the
aeration of the pots is shown in Figure 10. The numbers on the mixing chambers correspond to the six gas mixtures already listed. All the tubing was made from Pyrex glass tubing, and glass to glass connections were made where possible. Ordinary rubber tubing was used in the first experiments but was replaced later by neoprene tubing which was found to be more resistant to greenhouse weather conditions. Fischer's "Celloseal" was used to increase the tightness of the seal between the glass and rubber tubings. The mixing chambers consisted of small round flasks with necks large enough for number 8 rubber stoppers. By inserting inlet, outlet and 100 cm. water pressure control tubes into holes in the rubber stoppers, the amount of glass blowing was cut to a minimum. In practice the number one mixing chamber was not used, a glass t-joint sufficing. The diagram in Figure 10 may be compared with the one in Figure 5 for a better understanding of the basic principles underlying the construction and use of this type of apparatus.

Photographs of the apparatus as actually set up in the greenhouse are shown in Figures 11 and 12. Major parts of the equipment are indicated by the following letters in both pictures: a, b, and c are the 200 cm. water pressure control towers for oxygen, carbon dioxide and nitrogen respectively. The mixing chambers, d, are arranged in a group in such a manner that the three distribution manifolds, e, f, and g,
Figure 10. Diagram of apparatus for the aeration of soil in greenhouse pots at controlled rates and with six gases of composition as follows:
No. 1 - 100% N₂; No. 2 - 20% O₂, 80% N₂;
No. 3 - 20% O₂, 5% CO₂ and 75% N₂; No. 4 -
20% O₂, 10% CO₂, and 70% N₂; No. 5 - 20% O₂,
20% CO₂ and 60% N₂; and No. 6 - 20% O₂,
50% CO₂ and 30% N₂.
Figures 11 and 12. Two views of the aeration apparatus as used for the distribution of six different gas mixtures through four pots for each gas. Lettering in both photographs refer to the following parts of the apparatus: a, b, and c are the 200 cm. water pressure control towers for oxygen, carbon dioxide and nitrogen, respectively; d, mixing chambers consisting of small round flasks; e, f, and g, distribution manifolds for oxygen, carbon dioxide and nitrogen respectively; h, capillaries for controlling the proportions of the different gases; j, connecting tubes from the mixing chambers to the 100 cm. water control tower, k; m, outlet tubes through which the mixed gases flow to the pot manifolds, n; o, capillaries controlling the rate of gas flow into the pots; and p, moisture chambers.
for oxygen, carbon dioxide and nitrogen respectively form a compact triangular arrangement. The capillaries, h, which control the proportions of the various gases are placed in the tubes connecting the manifolds to the different mixing chambers. Glass tubes, j, lead from the mixing chambers to the 100 cm. water pressure control tower, k. Outlet tubes, m, connect the mixing chambers to the pot manifolds, n. The gases then pass through the capillaries, o, which control the flow into pots, bubble through small moisture chambers, p, and into the bottom of the pot. The small moisture chambers were used largely as bubble counters to check on the flow of the gases.

At the time the aeration was begun the tops of the pots in which corn was grown were closed with plastic cloth. A layer of paraffin-vaseline mixture was used for closing the pots in which soybeans were grown. The plastic cloth was fastened to the top rim of the pot with plastic cement. Cotton and paraffin were used around the corn plants to make a tighter contact with the plastic cloth. The paraffin-vaseline covers for the soybeans were prepared by melting 135 grams of paraffin and 15 grams of petrolatum together, allowing it to cool almost to the solidifying point and then pouring it around the soybeans on the soil surface. This material made a cover varying from one quarter to one half inch in thickness. Small rings of cotton were placed around
the soybeans to protect the plants from the heat. In earlier preliminary studies it was found that paraffin covers of this type contracted during the cool nights and pulled away from the side of the pot. A mixture of one part of petrolatum and four parts of red sealing wax when melted together and allowed to cool could be rolled into strings about the size of a lead pencil and applied between the pot and the edge of the paraffin cover. This material remained soft and pliable and maintained the seal between the pot and the paraffin even under wide temperature fluctuations.

With the covers thus installed the aeration of the pots was continued for 24 hours to allow the soil atmosphere to be brought into equilibrium with the aerating gases. Thirty milliliters of potassium chloride solution (equivalent to 150 pounds of potassium per acre) was then applied through the covers in three different locations by using a 10 milli-liter medical syringe and a 4 inch hypodermic needle. Water necessary to bring the soil to field capacity was added in the same manner.

During the period of aeration the soil atmosphere was analyzed for oxygen and carbon dioxide using the following technique: A 10 milliliter medical syringe in which the plunger had been greased slightly with "Celloseal" was filled with a few milliliters of water, connected to a 4 inch hypodermic needle and as the needle was forced through the cover and into the soil the water was forced from the syringe.
through the needle to prevent its becoming plugged. The air sample was then taken into the syringe slowly by pulling the plunger. Approximately 12 milliliters of gas was collected in this manner, the long needle then withdrawn from the soil and quickly replaced on the syringe by a short 20 gauge hypodermic needle. Excess liquid in the syringe was then slowly forced out through this small needle. The needle was then inserted into the mercury filled rubber tube sidearm on the Haldane type gas analyzer and the air sample discharged into the gas burette. This technique is illustrated in Figure 4.

Aeration was continued for an additional 48 hours after which the corn and soybean plants were cut off and the roots removed from the soil. The harvested plants were dried in an oven at 60°C, the dry weights obtained, then ground in a Christy-Norris mill and stored in air tight glass bottles for chemical analysis.

In the analysis for potassium two gram samples of the ground plant material were ashed in 50 milliliter Pyrex beakers in a muffle furnace at 550°C, the residue taken up with dilute hydrochloric acid and diluted to 100 milliliters with distilled water. Potassium was then determined on a suitable aliquot of this solution by the dipicrylamine method of Lawton (111). The total milligrams of potassium absorbed per pot was calculated. A comparison was then made between the total potassium content of the differently aerated plants.
and the unaerated, unfertilized plants which had been allowed to continue growth during the aeration period. The plants harvested just prior to the start of the aeration furnished information on the status of the plants at the beginning of the treatment, and served as a check to determine whether or not any aeration treatment completely stopped growth and absorption.

Results and discussion In most cases the corn and soybeans showed no visible effects from the aeration treatments during the three days. One exception to this was the 50% carbon dioxide aeration treatment. The corn and soybean plants under this treatment would wilt slightly in the early morning, but they would recover by noon.

The yields and potassium content of the corn are presented in Table 6. The increase in the total dry weight over the check plants harvested just prior to the application of the aeration treatments was about the same in all cases.

In comparing the percent potassium in the plants of all treatments carried through the three day aeration period against the percent potassium in the plants harvested at the start of the aeration, it is seen that a reduction in the percent potassium in the tops occurred in all treatments. There was also a reduction in the percent potassium in the
Table 6. Yield and potassium content of corn aerated for 72 hours with various gas mixtures and fertilized with potassium after the first 24 hours of aeration.

<table>
<thead>
<tr>
<th>Aerating gas</th>
<th>Average dry wt. per four plants</th>
<th>Average potassium content per four plants</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>tops:roots:total</td>
<td>tops</td>
</tr>
<tr>
<td></td>
<td>gms: gms: gms: %: mg: %: mg: mg</td>
<td></td>
</tr>
<tr>
<td>100% N₂</td>
<td>14.97: 5.66: 20.63: 1.76: 262.08: 0.96: 53.70: 315.78</td>
<td></td>
</tr>
<tr>
<td>20% O₂</td>
<td>13.66: 5.85: 19.74: 1.79: 249.05: 1.06: 62.05: 311.10</td>
<td></td>
</tr>
<tr>
<td>20% O₂, 5% CO₂</td>
<td>14.11: 6.21: 20.32: 1.79: 251.16: 0.98: 60.29: 311.45</td>
<td></td>
</tr>
<tr>
<td>20% O₂, 10% CO₂</td>
<td>13.26: 5.74: 19.00: 1.95: 258.53: 1.02: 58.87: 317.40</td>
<td></td>
</tr>
<tr>
<td>20% O₂, 20% CO₂</td>
<td>13.73: 5.83: 19.56: 1.76: 240.45: 0.99: 57.75: 298.20</td>
<td></td>
</tr>
<tr>
<td>20% O₂, 50% CO₂</td>
<td>15.15: 5.44: 20.59: 1.44: 218.93: 1.25: 67.03: 285.96</td>
<td></td>
</tr>
<tr>
<td>No aeration (Open top)</td>
<td>: : : : : : : :</td>
<td></td>
</tr>
<tr>
<td>Harvest and no K prior to aeration</td>
<td>: : : : : : : :</td>
<td></td>
</tr>
</tbody>
</table>

¹In each aerating gas the remaining percentage not given is nitrogen gas.
roots in all treatments except the 50% carbon dioxide aeration where the value remained about the same as in the early harvest. The percent potassium in the tops of the plants aerated with 50% carbon dioxide was the lowest of the treatments.

A comparison of the total milligrams of potassium in the plants yields further interesting information. All plants grown during the three day aeration period contained more potassium in the tops than the plants harvested at the start of the aeration, however, in the plants receiving no aeration and no potassium fertilizer the accumulation of potassium during the experimental period was very slight. Therefore, the main comparison is made between the aerated plants and the unaerated, unfertilized plants allowed to grow the same length of time. A statistical analysis of the total milligrams of potassium in the tops of the plants of these seven treatments revealed that certain differences between treatments were significant beyond the 5% level. If the individual aeration treatments are compared against the unaerated, unfertilized treatment all are significantly higher in total milligrams of potassium except the 50% carbon dioxide aeration treatment. The plants in this treatment failed to accumulate a significant amount of potassium from the added fertilizer.

Consider in a similar way the total milligrams of potas-
sium in the roots. The differences here are not consistent with the tops, the lowest value being under the 100% nitrogen aeration treatment and the highest value being under the 50% carbon dioxide treatment. In the case of the plants aerated with 100% nitrogen, it appears that potassium was moved rapidly from the roots into the tops. Apparently under the 50% carbon dioxide aeration treatment some potassium moved into the roots but was not transported to the tops.

An analysis of variance of the total milligrams of potassium in the whole plant revealed that there were no significant differences between the aeration treatments. A comparison of the sum of all the aeration treatments against the un-aerated, unfertilized treatments, however, reveals a significant difference beyond the 1% level. It is interesting to note that both the 20% carbon dioxide and the 50% carbon dioxide aeration treatments tended to reduce the accumulation of the added potassium.

Table 7 gives the yields and potassium content of the soybeans. Here again, there was considerable increase in the dry weight in all treatments during the three day period. Also, the percent potassium decreased. The treatment effects on the total milligrams of potassium in the tops tested significant beyond the 1% level. The 50% carbon dioxide aeration treatment was even significantly lower than the un-aerated, unfertilized treatment. It was surprising to find that only
Table 7. Yield and potassium content of soybeans aerated for 72 hours with various gas mixtures and fertilized with potassium after the first 24 hours of aeration.

<table>
<thead>
<tr>
<th>Aerating gas</th>
<th>Average dry wt. per four plants</th>
<th>Average potassium content per four plants</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>tops:roots:total (gms)</td>
<td>tops:roots:total (mg)</td>
</tr>
<tr>
<td>100% N₂</td>
<td>9.38: 2.03: 11.41: 2.13</td>
<td>199.52: 1.86: 37.88: 237.40</td>
</tr>
<tr>
<td>20% O₂</td>
<td>8.77: 2.21: 10.98: 2.30</td>
<td>201.79: 1.86: 41.11: 242.90</td>
</tr>
<tr>
<td>5% CO₂</td>
<td>8.01: 2.00: 10.01: 2.35</td>
<td>188.00: 1.89: 37.89: 225.89</td>
</tr>
<tr>
<td>20% CO₂</td>
<td>8.98: 2.04: 11.02: 2.29</td>
<td>205.45: 1.86: 37.92: 243.37</td>
</tr>
<tr>
<td>10% CO₂</td>
<td>9.04: 2.12: 11.16: 2.17</td>
<td>195.74: 1.81: 33.34: 234.08</td>
</tr>
<tr>
<td>20% CO₂</td>
<td>8.21: 2.11: 10.32: 2.19</td>
<td>179.74: 1.78: 37.24: 216.98</td>
</tr>
<tr>
<td>No aeration</td>
<td>8.54: 1.90: 10.44: 2.26</td>
<td>192.87: 1.56: 29.62: 222.49</td>
</tr>
<tr>
<td>(open top)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>No K</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Harvest prior to aeration</td>
<td>6.20: 1.77: 7.97: 2.79</td>
<td>172.86: 1.98: 34.91: 207.77</td>
</tr>
</tbody>
</table>

1 In each aerating gas the remaining percentage not given is nitrogen gas.
the 10% carbon dioxide treatment tested significantly higher than the unaerated, unfertilized treatment. The low yield and the resulting low potassium content of the plants under the 5% carbon dioxide aeration treatment is difficult to explain. The plants in all four pots of this treatment were somewhat smaller than the others even at the beginning of the aeration.

The total milligrams of potassium in roots are not very different between the various treatments, but all aeration treatments are higher than the unaerated, unfertilized treatment.

A statistical analysis of the total milligrams of potassium in the plants (tops and roots) aerated and in those left to grow the same length of time without aeration and without potassium fertilization (total of seven treatments) reveals treatment differences significant beyond the 5% level. In the case of the plants aerated with 50% carbon dioxide the potassium content (milligrams) does not differ significantly from the potassium content of the unaerated, unfertilized plants. The plants under two treatments, 20% oxygen - no carbon dioxide and 20% oxygen-10% carbon dioxide, contained significantly more potassium than the unaerated, unfertilized plants. The net potassium uptake by corn and soybeans above the unaerated, unfertilized plants as affected by aeration treatment is shown in Figure 13.
Figure 13. Net potassium uptake by corn and soybeans (total plants) as affected by the composition of the gases used to aerate the soil. (Net potassium uptake is the excess over the potassium contained in plants grown in unaerated and unfertilized pots.)
The data of these experiments with corn and soybeans indicate that high concentrations of carbon dioxide in the soil atmosphere may significantly affect the accumulation of potassium even when adequate oxygen is available. The two crops respond alike except where the soybeans were aerated with 5% carbon dioxide. In view of the fact that the soybean plants were smaller in this case even at the beginning of the aeration, the low value may not be a true aeration treatment effect, but may be due to random variation in the plant material available for the experiment. This is more evident when transpiration by the plants is considered.

The effect of the aeration treatments on transpiration by the corn and soybeans is presented in Table 8 and shown graphically in Figure 14. Since the soybeans transpired more water than the corn, more difficulty was experienced in maintaining the soil moisture under the soybeans. The reduction in transpiration due to the 50% carbon dioxide aeration treatment is significant for both the corn and soybeans. Here again, as with the dry weights and potassium content, the water transpired by the 5% carbon dioxide aerated soybeans was lower than that transpired by the plants of all the other aeration treatments except the 50% CO₂ treatment. This reflects the small size of the 5% carbon dioxide aerated plants since the water transpired per gram of dry weight of tops is practically the same for all aeration treatments except the 50% carbon dioxide treatment.
Table 8. Water transpired by soybeans and corn grown in soils in which the atmosphere was maintained at different carbon dioxide and oxygen levels.

<table>
<thead>
<tr>
<th>Aerating gas</th>
<th>Weight of water lost per four plants (average of 4 replications)</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>corn</td>
<td>soybeans</td>
<td></td>
</tr>
<tr>
<td></td>
<td>gms</td>
<td>gms</td>
<td></td>
</tr>
<tr>
<td>100% N₂</td>
<td>659</td>
<td>945</td>
<td></td>
</tr>
<tr>
<td>20% O₂</td>
<td>603</td>
<td>912</td>
<td></td>
</tr>
<tr>
<td>20% C₂</td>
<td>616</td>
<td>800</td>
<td></td>
</tr>
<tr>
<td>5% CO₂</td>
<td>616</td>
<td>952</td>
<td></td>
</tr>
<tr>
<td>20% O₂</td>
<td>625</td>
<td>922</td>
<td></td>
</tr>
<tr>
<td>20% CO₂</td>
<td>497</td>
<td>649</td>
<td></td>
</tr>
</tbody>
</table>

In each aerating gas the remaining percentage not given is nitrogen gas.
Figure 14. Weight of water lost during three days from pots of corn and soybeans aerated continuously with various gases.
LEGEND:

- □ □ SOYBEANS
- ● ● CORN

PERCENT CO₂ IN AERATING GASES

GRAMS OF H₂O LOSS/POT

20 % O₂
The composition of the gases at the inlets to the pots and the resulting composition of the soil atmosphere are given in Table 9. These analyses were made with the syringe technique described earlier. The oxygen and carbon dioxide values of the gas mixtures did not differ greatly from the expected values. A comparison of the soil atmosphere under the corn and soybeans indicate that the plastic covers used on the corn pots were in general not as effective as the paraffin covers used on the soybean pots in preventing gaseous diffusion from the atmosphere. The surprising revelation of these analyses is the fact that 10 liters per 24 hours of gas flowing through the pot was not sufficient to prevent the accumulation of carbon dioxide or to maintain the level of oxygen. Seeley (155) obtained similar results in aeration studies with roses sealed in 4x7 inch cans and continuously aerated with 12 liters of gas per 24 hours. This emphasizes the difficulty of completely controlling the aeration condition in the soil. Even in the case of the unaerated soybean pots with no covers, diffusion from the atmosphere did not prevent a slight accumulation of carbon dioxide and a slight reduction in the percent oxygen around the roots. Watering of these latter pots had a profound effect upon the accumulation of carbon dioxide and the reduction in oxygen. These data will be presented in a later section.

The syringe method of sampling soil gases from pots was found to be very satisfactory, there being little difficulty
Table 9. Composition of aerating gases and of the resulting soil atmosphere under corn and soybeans grown in the greenhouse.

<table>
<thead>
<tr>
<th>Aerating gas</th>
<th>Composition at inlet to pots</th>
<th>Composition of soil atmosphere at depth of approximately 4 inches</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>CO₂</td>
<td>O₂</td>
</tr>
<tr>
<td>100% N₂</td>
<td>0(2)²</td>
<td>0(2)</td>
</tr>
<tr>
<td>20% O₂</td>
<td>0(2)</td>
<td>21.48(2)</td>
</tr>
<tr>
<td>5% CO₂</td>
<td>4.93(2)</td>
<td>21.91(2)</td>
</tr>
<tr>
<td>20% O₂</td>
<td>10.28(3)</td>
<td>21.59(1)</td>
</tr>
<tr>
<td>10% CO₂</td>
<td>19.49(2)</td>
<td>20.97(1)</td>
</tr>
<tr>
<td>20% O₂</td>
<td>20.52(2)</td>
<td>47.45(2)</td>
</tr>
<tr>
<td>50% CO₂</td>
<td>47.45(2)</td>
<td>20.52(2)</td>
</tr>
<tr>
<td>20% O₂</td>
<td>20.52(2)</td>
<td>47.45(2)</td>
</tr>
</tbody>
</table>

1. In each aerating gas the remaining percentage not given is nitrogen gas.
2. Figures in parenthesis indicate the number of analyses represented in the average given.
with the stoppage of the needle. It was found necessary to allow the water (or better acidulated water to prevent absorption of carbon dioxide) to drain away from the point of the needle before beginning the intake of the air sample. This prevented the withdrawal of soil particles and muddy water into the syringe proper.
Greenhouse Studies with Variable Oxygen and Carbon Dioxide Levels in Nutrient Cultures.

Culture solution experiment no. 1. The influence of the level of carbon dioxide in the aerating gas with adequate oxygen upon water and potassium absorption by corn

Experimental The variable results of the soil aeration experiments with corn and soybeans made it difficult to set forth any generalities. Further experiments were therefore planned in which nutrient cultures were used. It was felt that this technique would allow better control of environmental conditions, especially in the root zone, and the results on potassium uptake could be obtained with greater accuracy by periodic analysis of the culture solutions.

In the first experiment with nutrient cultures a group of corn plants were grown in quart Mason jars of Hoagland's (89) solution for a period of three weeks under uniform conditions without artificial aeration of the solution. Comparable sets of plants were then selected for duplicate aeration treatments with two 10 liter per 24 hour gas outlets in each jar. The aeration treatments were applied for a period of seven days during which time samples of the solution were obtained for chemical analysis. Six different gas mixtures were used as follows:
1. 100% nitrogen
2. 20% O₂, 80% N₂
3. 20% O₂, 5% CO₂, 75% N₂
4. 20% O₂, 10% CO₂, 70% N₂
5. 20% O₂, 20% CO₂, 60% N₂
6. 20% O₂, 50% CO₂, 30% N₂

These were of the same composition as those used in the greenhouse soil aeration experiment number 5. No arrangement was made for further purification of the nitrogen. The gas mixing and dispensing apparatus was that already described for the above experiment. The quart jars were wrapped with black paper to prevent the growth of algae in the nutrient solution.

The corn was germinated in sphagnum moss in the light. As soon as the hypocotyle was about three inches long, three seedlings were transferred to quart jars of Hoagland's solution. The phosphorus was not included in this solution at first so that iron could be supplied in solution. Squares of paraffin treated plywood, held in place over the jars by four shingle nails, were used to support the plants.

Iron (1 milliliter of 0.4% ferric tartrate solution added per jar each day) was supplied to the plants during the period when no phosphorus was in the solution. Phosphorus was first added after six days. On the tenth day the solutions were changed and iron again supplied to the plants for five days while there was no phosphorus in the solution.
Subsequently the nutrient solution was changed every five days and iron supplied as needed.

When the plants were three weeks old the aeration experiment was begun with the plants in a known weight of fresh Hoagland's complete nutrient solution. The two gas outlets in each jar, constructed of 5 mm. glass capillary tubing, were so arranged that a small stream of bubbles escaped from each near the bottom of the jar.

A small roll of "plasticene" was placed around the top of the jar and the plywood cover pushed down in place to seal the top on to the jar. "Plasticene" was used to seal any other openings except the "cottoned" openings immediately surrounding the plants.

Ten milliliter samples of the nutrient solution were taken every few hours at the beginning of the experiment. At later stages the nutrient solution was sampled twice each day. During each sampling the jars were weighed, the tops opened and distilled water added to bring the weight of solution back to the original weight. From these data it was possible to adjust the potassium analyses to the volume of solution present when the sample was taken and to record the water transpired. Adjustments in the apparent potassium uptake were also necessary because of the loss of potassium from the solution by previous samplings. No analysis of the dissolved gases were made in this experiment. However, fre-
quent analyses were made of the gases going into the jars.

Analysis for potassium in the solution was made by the method of Attoe (10) using the Perkin-Elmer Model 18 flame photometer. The final solution used in the above apparatus was made up to contain between 5 and 20 ppm. of potassium.

Results and discussion. The corn plants in this experiment grew very rapidly and were strong and healthy except during a few periods when iron deficiency appeared quite suddenly. A few days in a phosphorus free solution with ferric tartrate added soon corrected this condition.

During the aeration no effects on the general appearance of the plants became obvious until the close of the experiment, and then only minor differences in vigor were apparent. The plants under all aeration treatments except the pure nitrogen and the 50% carbon dioxide aeration treatments looked very much alike. In the case of these latter two, lack of vigor was evident in the light green color, slender stems and relatively short height of the plants.

Differences in guttation during the night were noticeable at the beginning of the experiment. The plants aerated with pure nitrogen, 20% carbon dioxide and 50% carbon dioxide showed little or no evidence of guttation until after about three days of treatment.
The potassium uptake by the corn is presented in Table 10 and Figure 15. The potassium and water absorption at the end of five days is shown in Figure 15. In Table 11 the water absorption during several periods is given. These values for water absorption are perhaps better defined as water lost from the culture jars. This represents losses due to absorption by the plants and due to absorption by the gases as they bubble through the solution and escape into the atmosphere. The moisture chambers helped to prevent some of the loss due to the gases, but the pressure drop of 100 cm. of water after leaving the moisture chambers increased the capacity of the gas to absorb more moisture from the nutrient solution. The expected gaseous composition and the measured composition at the inlets to the jars are presented in Table 12.

The results of the cumulative uptake of potassium by the plants aerated differently are indicated in Figure 15. The 20% oxygen, the 20% oxygen plus 5% carbon dioxide, and 20% oxygen plus 10% carbon dioxide aeration treatments are practically parallel and equal in their effect on potassium uptake. Potassium uptake was decreased soon after the aeration treatments were started by the 20% and 50% carbon dioxide aeration treatments. The effect of nitrogen was somewhat slower, probably due to delayed sweeping of the oxygen from the solution, but at the end of the experiment the uptake from the
Table 10. Cumulative uptake of potassium by corn grown in Hoagland's nutrient solution aerated continuously with gases of varying oxygen and carbon dioxide levels. (3 corn plants per quart jar of solution)

<table>
<thead>
<tr>
<th>Aerating gas</th>
<th>Days after start of aeration treatments</th>
<th>Potassium absorption per jar (Aver. of 2 reps.)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>100% N₂</td>
<td></td>
<td></td>
</tr>
<tr>
<td>20% O₂</td>
<td>18.27</td>
<td>25.02</td>
</tr>
<tr>
<td>20% O₂ 5% CO₂</td>
<td>24.60</td>
<td>65.91</td>
</tr>
<tr>
<td>20% O₂ 10% CO₂</td>
<td>27.36</td>
<td>63.87</td>
</tr>
<tr>
<td>20% O₂ 20% CO₂</td>
<td></td>
<td></td>
</tr>
<tr>
<td>50% CO₂</td>
<td>7.78</td>
<td>36.62</td>
</tr>
<tr>
<td>No aeration</td>
<td>4.80</td>
<td>17.87</td>
</tr>
<tr>
<td>N₂</td>
<td>7.41</td>
<td>25.83</td>
</tr>
</tbody>
</table>

1In each aerating gas the remaining percentage not given is nitrogen gas
Figure 15. Cumulative uptake of potassium by corn grown in Hoagland's nutrient solution aerated continuously with gases of varying oxygen and carbon dioxide levels. (3 plants per quart jar)
Figure 16. Potassium and water absorption by corn plants growing in Hoagland's nutrient solution during 5 days of continuous aeration with various gases. Culture solution experiment no. 1.
MGS. K UPTAKE/JAR

Composition of Aerating Gases

- 100% N₂
- 75% N₂
- 50% N₂
- 20% N₂

No Aeration

GMS. H₂O LOSS/JAR
Table 11. Water absorbed by corn plants in Hoagland's nutrient solution aerated continuously with gases of varying oxygen and carbon dioxide levels. Culture solution experiment no. 1.

<table>
<thead>
<tr>
<th>Aerating gas</th>
<th>Water lost from the culture jar (Average of 2 reps.)</th>
<th>1-5 day period</th>
<th>5-7 day period</th>
<th>Total 7 day period</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>gms</td>
<td>gms</td>
<td>gms</td>
<td></td>
</tr>
<tr>
<td>100% N₂</td>
<td>238</td>
<td>144</td>
<td>432</td>
<td></td>
</tr>
<tr>
<td>20% O₂</td>
<td>307</td>
<td>161</td>
<td>468</td>
<td></td>
</tr>
<tr>
<td>20% O₂</td>
<td>238</td>
<td>161</td>
<td>449</td>
<td></td>
</tr>
<tr>
<td>5% CO₂</td>
<td>322</td>
<td>180</td>
<td>502</td>
<td></td>
</tr>
<tr>
<td>20% O₂</td>
<td>322</td>
<td>180</td>
<td>502</td>
<td></td>
</tr>
<tr>
<td>10% CO₂</td>
<td>271</td>
<td>144</td>
<td>415</td>
<td></td>
</tr>
<tr>
<td>20% O₂</td>
<td>251</td>
<td>116</td>
<td>367</td>
<td></td>
</tr>
<tr>
<td>20% O₂</td>
<td>251</td>
<td>116</td>
<td>367</td>
<td></td>
</tr>
<tr>
<td>50% CO₂</td>
<td>257</td>
<td>115</td>
<td>372</td>
<td></td>
</tr>
</tbody>
</table>

1In each aerating gas the remaining percentage not given is nitrogen gas.
Table 12. Percentage composition (expected and actual\(^1\)) of aerating gases used in culture solution experiment no. 1.

<table>
<thead>
<tr>
<th>Composition of gases</th>
<th>Expected</th>
<th>Actual</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>CO(_2)</td>
<td>O(_2)</td>
</tr>
<tr>
<td>%</td>
<td></td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>0</td>
<td>20</td>
<td>0</td>
</tr>
<tr>
<td>5</td>
<td>20</td>
<td>4.46((3))</td>
</tr>
<tr>
<td>10</td>
<td>20</td>
<td>9.67((3))</td>
</tr>
<tr>
<td>20</td>
<td>20</td>
<td>19.69((3))</td>
</tr>
<tr>
<td>50</td>
<td>20</td>
<td>48.16((3))</td>
</tr>
</tbody>
</table>

\(^1\)Samples were taken at the inlet to the jars

\(^2\)Figures in parenthesis indicate the number of analyses represented in the average given
nitrogen was about the same as from the 50% carbon dioxide aeration treatments. The 20% oxygen plus 20% carbon dioxide aeration treatment was intermediate between the two extremes in affecting potassium uptake.

Frequent sampling during the first few days of the first experiment did not prove of value. It was found that the highest rate of potassium absorption occurred during the day. The difference in the content of the potassium solution in the early evening and the following morning was little more than experimental error in most cases.

The fact that the potassium uptake curves in Figure 15 were almost parallel after the third day was considered sufficient reason for cutting the duration of subsequent experiments to five days. Therefore, in order that this first experiment may possibly be compared with later experiments the potassium uptake and water absorption data for a five day period are presented graphically in Figure 16. It is interesting to note that the nitrogen and the 50% carbon dioxide treatments differed little in potassium uptake from the unaerated treatment. The unaerated jars were not closed to prevent gaseous diffusion from the atmosphere. However, the plywood cover itself restricted the area for gaseous diffusion to one small hole, about 3/8 inch in diameter, plus whatever space existed between the plants and the plywood cover. It is apparent from these data that either the
oxygen supply was not sufficient in the unaerated jars or carbon dioxide accumulated in toxic amounts or both.

An analysis of variance of the potassium uptake under the six aeration treatments indicates significance at the 1% level. The break in the effect of carbon dioxide on potassium uptake when sufficient oxygen is present comes between 10 and 20% carbon dioxide. This in general parallels the results obtained in the soil aeration study although in the soil the differences were not so well defined.

The water losses (Table 11 and Figure 16) in most cases tended to parallel the potassium uptake, the most notable exception to this being the nitrogen aeration treatment. Some of this high loss may be due to the fact that dry nitrogen was used causing a greater loss of water due to evaporation. Differences in water absorption were significant at the 5% level.

Culture solution experiment no. 2. The influence of the level of carbon dioxide in the aerating gas without adequate oxygen upon water and potassium absorption by corn

**Experimental** The preceding experiment demonstrated the marked effect of both carbon dioxide and oxygen on the absorption of water and potassium by corn. The question then arises as to the effect of carbon dioxide when the oxygen is low. Consequently experiment number 2 was designed to determine
whether or not an excess of carbon dioxide over an oxygen deficiency would produce an additive effect on the absorption of water and potassium by corn.

The plants used for this experiment were started at the same time as those used in experiment number 1, and during the four weeks of growth they had not received artificial aeration. The gas mixing and dispensing unit was modified to give the following gas mixtures:

1. 100% \( \text{N}_2 \)
2. 20% \( \text{O}_2 \), 80% \( \text{N}_2 \)
3. 5% \( \text{CO}_2 \), 95% \( \text{N}_2 \)
4. 10% \( \text{CO}_2 \), 90% \( \text{N}_2 \)
5. 20% \( \text{CO}_2 \), 80% \( \text{N}_2 \)
6. 50% \( \text{CO}_2 \), 50% \( \text{N}_2 \)

The only change necessary in the apparatus to accomplish this was the connection of the nitrogen into the manifold previously used for oxygen. Of course it was necessary to disconnect one capillary from this manifold to allow oxygen to flow into the one mixing chamber (number 2).

The plant roots were sealed into the jars and the aeration accomplished in the same manner as in the first experiment. A known weight of fresh Hoagland's complete nutrient solution was used in each jar and sampling and water additions were made once daily. The potassium analysis and the calculations
of potassium absorption, taking into consideration the weight of solution at sampling and the potassium loss due to previous samples, were made as before. Again no attempt was made to remove the oxygen impurity from the nitrogen. The aeration was continued for five days.

**Results and discussion**  The effect of carbon dioxide at a very low oxygen level on potassium uptake and water absorption is given in Table 13 and presented graphically in Figure 17. It is possible to compare the unaerated jars, and the nitrogen and the 20% oxygen aeration treatments with the same treatments in the first experiment. The greater uptake of potassium and the greater water loss in the second experiment with the 20% oxygen aeration can be partly explained by the differences in weather conditions. During the second experiment the days were largely sunny and the temperatures of the culture solution ranged from 20°C to 30°C, while at least three days were cloudy and the temperatures ranged from 18°C to 25°C during the first experiment. This indicates that environmental conditions were better for rapid growth and potassium uptake during the second experiment. This is evident by the fact that the plants aerated with 20% oxygen absorbed more potassium than the plants aerated with the same gas in experiment no. 1.

The same explanation based on the environment can be used
Table 13. Absorption of water and potassium during a 5 day period by corn plants in Hoagland's nutrient solution continuously aerated with gases of varying oxygen and carbon dioxide levels. Culture solution experiment no. 2.

<table>
<thead>
<tr>
<th>Aerating gas¹</th>
<th>Potassium (mg)</th>
<th>Water (gms)</th>
</tr>
</thead>
<tbody>
<tr>
<td>100% N₂</td>
<td>53.66</td>
<td>366</td>
</tr>
<tr>
<td>20% O₂</td>
<td>131.27</td>
<td>390</td>
</tr>
<tr>
<td>5% CO₂</td>
<td>33.58</td>
<td>301</td>
</tr>
<tr>
<td>10% CO₂</td>
<td>29.31</td>
<td>270</td>
</tr>
<tr>
<td>20% CO₂</td>
<td>20.75</td>
<td>240</td>
</tr>
<tr>
<td>50% CO₂</td>
<td>11.49</td>
<td>214</td>
</tr>
<tr>
<td>No aeration</td>
<td>39.15</td>
<td>256</td>
</tr>
</tbody>
</table>

¹In each aerating gas the remaining percentage not given is nitrogen gas.
Figure 17. Potassium and water absorption by corn plants growing in Hoagland's nutrient solution during five days of continuous aeration with various gases. Culture solution experiment no. 2.
to account for the lowered uptake of potassium and the
greater water loss in the nitrogen aerated and in the un-
aerated cultures during the second experiment. The higher
temperatures and more sunlight of course increased tran-
spiration. The higher temperature of the culture solutions
reduced their dissolved oxygen capacity, increased the need
of the plant for oxygen (55) and at the same time probably
increased the production of carbon dioxide by the roots.
Many roots were damaged (dark brown to black around the root
tips and usually extending back several inches) in both the
nitrogen aerated and the unaerated jars. Therefore, a re-
duction in the oxygen supply at a time when there was an in-
creased need for oxygen, plus the root damage probably caused
by several factors, could very well account for the reduction
in potassium uptake by these plants.

The second experiment was designed to determine whether
or not an excess of carbon dioxide would produce an additive
effect over an oxygen deficiency. From the graphs in Figure
17 this would appear to be the case. An analysis of variance
of potassium absorption under five aeration treatments having
no oxygen reveals significance at the 5% level. From the gas
analyses given in Table 14 it is obvious that the aerating
gases were not absolutely free of oxygen. The particular
cylinder of nitrogen used in these first two experiments
seemed to be contaminated with oxygen to a greater degree
Table 14. Percentage composition (expected and actual\(^1\)) of aerating gases used in culture solution experiment no. 2.

<table>
<thead>
<tr>
<th>Composition of gases</th>
<th>Expected</th>
<th>Actual</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>CO(_2)</td>
<td>O(_2)</td>
</tr>
<tr>
<td>% : %</td>
<td></td>
<td></td>
</tr>
<tr>
<td>0 : 0</td>
<td>0(1)(^2) : 0.45(1)</td>
<td></td>
</tr>
<tr>
<td>0 : 20</td>
<td>0(1) : 20.69(1)</td>
<td></td>
</tr>
<tr>
<td>5 : 0</td>
<td>4.80(1) : 0.21(1)</td>
<td></td>
</tr>
<tr>
<td>10 : 0</td>
<td>10.47(1) : 0.33(1)</td>
<td></td>
</tr>
<tr>
<td>20 : 0</td>
<td>20.30(1) : 0.10(1)</td>
<td></td>
</tr>
<tr>
<td>50 : 0</td>
<td>48.50(1) : 0(1)</td>
<td></td>
</tr>
</tbody>
</table>

\(^1\)Samples were taken at the inlet to the jars.  
\(^2\)Figures in parenthesis indicate the number of analyses represented in the average given.
than usual. The diluting effect therefore of the added carbon dioxide would cut down the supply of oxygen progressively as the carbon dioxide percent was increased. This could be one factor in the steady reduction of potassium and water absorption.

It is, however, unlikely that the diluting effect of only 4.8% carbon dioxide would reduce the oxygen impurity enough to account for the relatively large difference in potassium uptake between this aeration treatment and the nitrogen treatment. Then in comparison to the previous nutrient culture experiment the data strongly suggest that the effect of carbon dioxide upon potassium uptake and water absorption is dependent upon the amount of oxygen present. When 20% oxygen was present in the aerating gas between 10 and 20% carbon dioxide was necessary to effect a reduction in potassium uptake. It is apparent in the second experiment, that smaller amounts of carbon dioxide can effectively reduce the potassium uptake when oxygen is present only as an impurity in the nitrogen gas. Stating the results in another way: small amounts of oxygen can be effective in increasing the potassium absorption of plants if carbon dioxide is not also present even in relatively small amounts. It could be concluded therefore, that the low potassium uptake of the plants in the unaerated jars was due to a low oxygen supply which was rendered partly ineffective by carbon dioxide accumulations.
It is of interest to note also in connection with the carbon dioxide treatments at a low oxygen concentration that the roots were severely damaged in all cases whereas when oxygen was present only the 20% and 50% carbon dioxide treatments showed slight damage to the roots.

Culture solution experiment no. 3. The influence of reciprocal amounts of carbon dioxide and oxygen in the aerating gas upon the growth of corn

Experimental Culture solution experiments numbers 1 and 2 have shown that the effect of carbon dioxide in the aerating gas upon potassium uptake and water absorption depends upon the amount of oxygen present. Since under aerobic conditions the increase in the carbon dioxide concentration more or less parallels the decrease in oxygen concentration, it seemed desirable to test the effects of carbon dioxide and oxygen varied reciprocally in the range of concentration of 0 to 20%. This is the range normally found in the soil atmosphere in the field. The next three experiments have to do with this phase of the problem, the present experiment being designed to test the aeration effects on growth only.

For this series of experiments six gases of the following composition were obtained by placing the necessary capillaries in the apparatus described earlier.
1. $100\% \text{ N}_2$
2. $20\% \text{ O}_2, 80\% \text{ N}_2$
3. $15\% \text{ O}_2, 5\% \text{ CO}_2, 80\% \text{ N}_2$
4. $10\% \text{ O}_2, 10\% \text{ CO}_2, 80\% \text{ N}_2$
5. $5\% \text{ O}_2, 15\% \text{ CO}_2, 80\% \text{ N}_2$
6. $20\% \text{ CO}_2, 80\% \text{ N}_2$

The nitrogen was freed of oxygen by passage through two towers of alkaline pyrogallol. Frequent analyses of the gases were made at the inlet to the pots.

In general the nutrient culture technique described earlier was used. The aerating gases were applied continuously for a period of three weeks to 15 day old corn plants (2 per jar). Iron was supplied during the first few days in the same manner as described earlier, and at the first change of solutions (10 days) the plants were placed in .01% ferric tartrate solution overnight. Hoagland's complete nutrient solution was then used for the remainder of the experimental period.

Water was added as necessary through a small u-type glass tube, fastened into the plywood cover. With this arrangement opening of the jars was avoided except when the solutions were changed. The tubes served as manometers indicating the level of the liquid in the culture jar so that water could be added to the desired level without danger of overflow. The plants were harvested at the end of three
weeks, dried in an oven at 60°C and the dry weights of the tops and roots were recorded. No chemical analyses were made on this material.

Results and discussion The growth data of the reciprocal oxygen and carbon dioxide aeration treatments are contained in Table 15. The gas analysis data are given in Table 16. Some idea of the appearance of the plants of this experiment can be gained from Figures 18 and 19. Figure 19 and the data in Table 15 indicate that under the conditions of this experiment there was an additive effect of carbon dioxide over an oxygen deficiency. About two to three inches of the root tips in one of the 20% carbon dioxide aerated jars were decaying. Too, the addition of even 5% carbon dioxide plus the reduction of oxygen to 15% in the aerating gases reduced the top and root yield below the value obtained with 20% oxygen without carbon dioxide. In view of the work of Cannon (55) such a decrease with 15% oxygen would hardly be expected. It should also be noted that 5% carbon dioxide in the presence of 20% oxygen was not greatly different from 20% oxygen in the potassium and water absorption experiment described previously. However these latter combinations of aeration treatments were not tested for their effect on growth.

A statistical analysis of the total dry weight data of
Table 15. Yield of corn grown in Hoagland’s nutrient solution continuously aerated with gases in which oxygen and carbon dioxide were varied reciprocally. Average of 2 replications.

<table>
<thead>
<tr>
<th>Aerating gas</th>
<th>Green weight</th>
<th>Dry weight</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>tops</td>
<td>tops</td>
</tr>
<tr>
<td></td>
<td>gms</td>
<td>gms</td>
</tr>
<tr>
<td>100% N₂</td>
<td>32.5</td>
<td>4.06</td>
</tr>
<tr>
<td>20% O₂</td>
<td>72.5</td>
<td>7.00</td>
</tr>
<tr>
<td>15% O₂</td>
<td>61.8</td>
<td>5.69</td>
</tr>
<tr>
<td>5% CO₂</td>
<td>64.0³</td>
<td>5.75</td>
</tr>
<tr>
<td>10% CO₂</td>
<td>56.8</td>
<td>5.90</td>
</tr>
<tr>
<td>5% O₂</td>
<td>16.8</td>
<td>2.57</td>
</tr>
<tr>
<td>No aeration</td>
<td>42.8</td>
<td>4.22</td>
</tr>
</tbody>
</table>

¹Plants had been growing in Hoagland's nutrient solution for two weeks when the aeration was begun. The aeration treatment continued for three weeks.

²In each aerating gas the remaining percentage not given is nitrogen gas.

³Represents only one replication.
Table 16. Percentage composition (expected and actual\(^1\)) of aerating gases used in culture solution experiments nos. 3, 4 and 5.

<table>
<thead>
<tr>
<th>Expected</th>
<th>Actual</th>
<th>Actual</th>
<th>Actual</th>
</tr>
</thead>
<tbody>
<tr>
<td>CO(_2)</td>
<td>(%)</td>
<td>CO(_2)</td>
<td>(%)</td>
</tr>
<tr>
<td>O(_2)</td>
<td>(%)</td>
<td>(%)(^2)</td>
<td>(%)(^2)</td>
</tr>
<tr>
<td>0</td>
<td>0</td>
<td>0(4)</td>
<td>0(4)</td>
</tr>
<tr>
<td>0</td>
<td>20</td>
<td>0(4)</td>
<td>0(4)</td>
</tr>
<tr>
<td>5</td>
<td>15</td>
<td>4.72(5)</td>
<td>4.72(5)</td>
</tr>
<tr>
<td>10</td>
<td>10</td>
<td>9.66(5)</td>
<td>9.66(5)</td>
</tr>
<tr>
<td>15</td>
<td>5</td>
<td>16.12(5)</td>
<td>16.12(5)</td>
</tr>
<tr>
<td>20</td>
<td>0</td>
<td>20.53(5)</td>
<td>20.53(5)</td>
</tr>
</tbody>
</table>

\(^1\) Samples were taken at the inlet to the jars.
\(^2\) Figures in parenthesis indicate the number of analyses represented in the average given.
Figure 18. Growth responses of corn in nutrient cultures to three weeks of continuous aeration with the following gases: 1) 100% N₂; 2) 20% O₂, 80% N₂; 3) 15% O₂, 5% CO₂, 80% N₂; 4) 10% O₂, 10% CO₂, 80% N₂; 5) 5% O₂, 15% CO₂, 80% N₂; 6) 20% CO₂, 80% N₂; 7) no aeration.

Figure 19. Comparison of the duplicate sets of plants under two aeration treatments: 1, those receiving 100% N₂ aeration and 2, those receiving 20% CO₂, 80% N₂ aeration, for a period of three weeks.
this growth experiment revealed treatment differences significant beyond the 5% level. It is interesting to note that the yields where the carbon dioxide was increased by steps up to 15% were still higher than when no aeration was applied. The yields in the unaerated cultures were about equal to those of the 100% nitrogen aeration treatment. This indicates, in view of the findings in experiment number 2, that the 15% carbon dioxide did not completely nullify the beneficial effects of aeration with 5% oxygen.

It is possible that the supply of oxygen with the 5% oxygen aeration was greater than where the oxygen diffused into the jars, but whether or not this 5% oxygen was as effective in producing growth as it would have been if no carbon dioxide were present must await further experimentation.

An additive effect of carbon dioxide over an oxygen deficiency should be easier to detect over the relatively longer period of this experiment. In potassium uptake studies growth is also a factor, so that even though the effect of various aeration treatments on potassium uptake may not appear too striking, the accumulation of the effects over an extended period in the life of the plant is to be considered. Too, it is very likely that the aeration needs of the plants during various stages of growth differ considerably.
Culture solution experiment no. 4. The influence of reciprocal amounts of carbon dioxide and oxygen in the aerating gas upon water and potassium absorption by corn

Experimental In connection with the growth data of culture solution experiment number 3, another experiment using the same aerating gases was carried out in which potassium uptake and water absorption were studied. The plants were leftovers from solution culture experiments number 1 and 2. They had not been used in the experiments and neither had they received artificial aeration during the entire six week period. Consequently their root systems were short and somewhat damaged, and therefore represented rather undesirable experimental material.

Aeration was applied as in previous experiments for a five day period. During this time the jars were opened only once (at two days) for the addition of water. Samples of the nutrient solution for potassium analysis were obtained at the close of the experiment.

Results and discussion The effect of the reciprocal amounts of oxygen and carbon dioxide upon potassium and water absorption is given in Table 17. The uptake of potassium and the loss of water was greater than in experiments number 1 and 2. This can be seen from a comparison of the 100% nitrogen and 20% oxygen aeration treatments in
Table 17. Absorption of potassium and water during a five day period by corn plants in Hoagland's nutrient solution continuously aerated with gases in which oxygen and carbon dioxide were varied reciprocally. (Culture solution experiment no. 4) Average per jar of three plants (two replications).

<table>
<thead>
<tr>
<th>Aerating gas(^1)</th>
<th>(K) absorption</th>
<th>Water loss</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>mg</td>
<td>gms</td>
</tr>
<tr>
<td>100% (N_2)</td>
<td>89.61</td>
<td>497</td>
</tr>
<tr>
<td>20% (O_2)</td>
<td>140.61</td>
<td>454</td>
</tr>
<tr>
<td>15% (O_2), 5% (CO_2)</td>
<td>138.70</td>
<td>457</td>
</tr>
<tr>
<td>10% (O_2), 10% (CO_2)</td>
<td>147.83</td>
<td>506</td>
</tr>
<tr>
<td>5% (O_2), 15% (CO_2)</td>
<td>95.84</td>
<td>379</td>
</tr>
<tr>
<td>20% (CO_2)</td>
<td>86.23</td>
<td>337</td>
</tr>
<tr>
<td>No aeration</td>
<td>-----</td>
<td>---</td>
</tr>
</tbody>
</table>

\(^1\)In each aerating gas the remaining percentage not given is nitrogen gas.
all three experiments. This would be expected since the plants were older and the root systems more extensive. Too, the tops exposed a greater surface area to the atmosphere, thus in part accounting for more transpiration.

The fact that the level of the solution was allowed to drop considerably during the experiment may also account for the relatively high uptake of potassium with 100% nitrogen aeration and 20% carbon dioxide aeration. This permitted a large air space to exist around a portion of the root system and probably allowed the roots access to more oxygen than was the case where the solution level was kept high throughout the five day period. It is easy to understand that oxygen from the atmosphere could diffuse into the air space much more rapidly than into the nutrient solution.

It is well to remember that the oxygen impurity was removed from the nitrogen in this experiment yet the potassium uptake with 20% carbon dioxide aeration was four times the uptake with the same aeration in experiment number 2. This is hard to understand except in the light of the different ages of the plants and the different treatment with regard to the maintenance of the nutrient solution in contact with the whole root system.

In comparing the 100% nitrogen aeration with the 20% carbon dioxide aeration when the traces of oxygen were removed, it can be seen that differences in potassium uptake
were not large, especially as was found in experiment number 2. There was however, a reduction in water absorption due to the presence of 20% carbon dioxide in addition to an oxygen deficiency. The fact that there was little difference in the potassium uptake indicates that any beneficial effect due to oxygen in the air space around the roots was about equal in both cases. It also lends support to the contention in culture solution experiment number 2 that carbon dioxide was responsible for reducing the beneficial effect of low amounts of oxygen. Here no oxygen was present in the solution in either case so no marked differences would be expected.

Potassium absorption was materially reduced by aeration with a gas containing 5% oxygen and 15% carbon dioxide. The effectiveness of 5% oxygen over no oxygen in increasing potassium absorption would be expected to have been better than was the case. This however must be based on an actual experiment with 5% oxygen alone. No reduction in potassium uptake or water absorption was evident until the oxygen in the aerating gas was lowered to 5% and the carbon dioxide increased to 15%.

A number of reasons, most of which are already apparent, made it desirable to repeat this experiment with new plant material and under more carefully controlled conditions.
Culture solution experiment no. 5. The influence of reciprocal amounts of carbon dioxide and oxygen in the aerating gas upon water and potassium absorption by corn

This experiment was essentially a repeat of experiment number 4 where determinations were made of the potassium and water absorption by corn from nutrient solutions as affected by aerating gases containing oxygen and carbon dioxide in reciprocal amounts. It was conducted because the plants used in experiment 4 were not particularly desirable experimental plants.

**Experimental** A new group of corn plants (2 per quart jar) were prepared for this experiment by growing them for five weeks in Hoagland's nutrient solution which was aerated with compressed air for short intervals each day.

During the five day absorption test, in which the plants were sealed into quart jars of fresh Hoagland's solution as described earlier, the solution level in the quart jars was maintained very close to the plywood cover. This was accomplished by frequent additions of distilled water through glass tubes as described for culture solution experiment number 3. It was thus possible to keep the air space between the cover and the solution surface to a minimum and to avoid opening the jars until the end of the experiment when samples of the solution were obtained for potassium analysis. An effort was made to measure the water added to each jar, but the results
were not very accurate.

At the completion of the absorption experiment the aerators were placed in quart jars of distilled water and sealed as was normal when the plants were present. Aeration was continued for 42 hours after which pH and dissolved oxygen determinations were made. Corn plants six weeks old which had not previously been used in the experiment were placed in one jar of each aeration treatment and after a few hours (2 to 4) pH and dissolved oxygen determinations were again made on the distilled water. The sampling technique of Allison and Shive (3), and the Winkler method as described by Treadwell and Hall (170) were used to determine the dissolved oxygen. Approximately 140 milliliters of solution was taken for the dissolved oxygen analysis, however, the exact weight of solution was obtained by weighing the bottle after the addition of hydrochloric acid had liberated the iodine.

Results and discussion Potassium uptake and water absorption data from this experiment were presented in Table 18 and Figure 20. The effects of the aerating gases on potassium uptake are highly significant, while the effects on water absorption are rather variable. The method of adding water to the jars did not allow for an accurate measurement of the amounts.
Table 18. Absorption of potassium and water during a five day period by corn plants in Hoagland's nutrient solution continuously aerated with gases in which oxygen and carbon dioxide were varied reciprocally. (Culture solution experiment no. 5.) Average per jar of two plants (two replications).

<table>
<thead>
<tr>
<th>Aerating gas</th>
<th>K absorption</th>
<th>Water loss</th>
</tr>
</thead>
<tbody>
<tr>
<td>100% N₂</td>
<td>20.21 mg</td>
<td>261 gms</td>
</tr>
<tr>
<td>20% O₂</td>
<td>140.45 mg</td>
<td>366 gms</td>
</tr>
<tr>
<td>15% O₂</td>
<td>126.44 mg</td>
<td>309 gms</td>
</tr>
<tr>
<td>5% CO₂</td>
<td>130.89 mg</td>
<td>330 gms</td>
</tr>
<tr>
<td>10% CO₂</td>
<td>130.89 mg</td>
<td>330 gms</td>
</tr>
<tr>
<td>5% O₂</td>
<td>61.91 mg</td>
<td>340 gms</td>
</tr>
<tr>
<td>15% CO₂</td>
<td>17.55 mg</td>
<td>304 gms</td>
</tr>
<tr>
<td>No aeration</td>
<td>105.27 mg</td>
<td>384 gms</td>
</tr>
</tbody>
</table>

1 In each aerating gas the remaining percentage not given is nitrogen gas.
Figure 20. Potassium absorption by corn plants growing in Hoagland’s nutrient solution during five days of continuous aeration with gases in which oxygen and carbon dioxide were varied reciprocally. Culture solution experiment no. 5.
In comparison with the potassium uptake data of culture solution experiment number 4, the data of this experiment reveal more prominent treatment differences. The data are parallel, however, and emphasize the importance of the air space above the culture solution. In all culture solution experiments except number 4, water was added at least once each day to maintain the level of the solution very close to the cover of the culture jar. The best control, however, was obtained with culture solution experiments number 3 and 5 where the water was added through u-type glass tubes without opening the tops of the culture jars.

Five percent carbon dioxide in the aerating gas plus a reduction of the oxygen to 15% reduced the potassium uptake slightly below the uptake when the plants were aerated with 20% oxygen and no carbon dioxide. Since a further reduction of oxygen to 10% did not cause an additional lower uptake, it may be concluded that the lowering of the oxygen to 15% was not in itself the cause of the lower potassium uptake, but that the addition of 5% carbon dioxide to the aerating gas was the main contributing factor. It should be recalled, however, that 5% carbon dioxide with 20% oxygen had no effect on potassium uptake in culture solution experiment number 1. It is not possible to separate the effects of the presence of carbon dioxide and a reduced supply of oxygen in this experiment (number 5).
The effect of these aeration treatments on potassium uptake are interesting when compared with their effects on growth (culture solution experiments number 3, Table 15). In the growth experiment the additive effect of 20% carbon dioxide in addition to an oxygen deficiency is more prominent than in the short period potassium uptake experiments number 4 and 5. The growth of the plants was also reduced by the 5% carbon dioxide-15% oxygen aeration treatment, but was not further reduced where the 10% carbon dioxide-10% oxygen and 15% carbon dioxide-5% oxygen aeration treatments were used. This indicates that under these conditions the uptake of potassium was more sensitive to the 15% carbon dioxide and 5% oxygen than was growth. Certainly an oxygen deficiency alone affected the potassium uptake relatively more than it affected growth.

These results will be discussed further in connection with the discussion of the dissolved oxygen values found under these aeration treatments.

The aeration results obtained thus far especially with nutrient cultures indicate the need for a knowledge of the oxygen and carbon dioxide levels in the solution around the roots. Because of the difficulty of measuring the dissolved oxygen in the nutrient culture where there is some organic matter and possibly nitrites, distilled water has been used in studies of this nature.

The results of dissolved oxygen and pH measurements made
at the end of the above experiment using distilled water are given in Table 19. The pH values were used as a rough criterion of the amount of carbon dioxide dissolved in the solution. When the tests were made the temperatures of the solutions varied between 32° and 35° C.

The dissolved oxygen in the jars without plants is shown to be in fairly good equilibrium with the aerating gases (Table 16). The calculated value for dissolved oxygen in equilibrium with the atmosphere at 35° C is 6.63 ppm. These values indicate that the carbon dioxide had no effect on the amount of dissolved oxygen in the solution. The two dissolved oxygen values with 100% nitrogen and 20% oxygen aeration may indicate that the presence of carbon dioxide in the aerating gas made the sweeping of oxygen from the solution more effective over the period of the aeration. No oxygen impurity could be detected in the nitrogen gas. These are but single determinations, however, and the possibility for errors is great. Arrington and Shive (9) also found that dissolved carbon dioxide in relatively small amounts had no effect on the dissolved oxygen content of culture solutions.

The pH values being rather variable were not used for any quantitative calculations of the carbon dioxide level in the solutions. Due to the fact that the distilled water may have had some buffering capacity it would have been
Table 19. Dissolved oxygen and pH determinations made on distilled water, with and without corn plants, after aeration with gases containing varying amounts of oxygen and carbon dioxide.

<table>
<thead>
<tr>
<th>Aerating gas</th>
<th>Dissolved oxygen</th>
<th>pH</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Without plants</td>
<td>With plants</td>
</tr>
<tr>
<td></td>
<td>ppm</td>
<td>ppm</td>
</tr>
<tr>
<td>100% N₂</td>
<td>0.45</td>
<td>0.04</td>
</tr>
<tr>
<td>20% O₂</td>
<td>5.96</td>
<td>1.03</td>
</tr>
<tr>
<td>15% O₂</td>
<td>4.45</td>
<td>0.49</td>
</tr>
<tr>
<td>5% CO₂</td>
<td>3.31</td>
<td>0.18</td>
</tr>
<tr>
<td>10% O₂</td>
<td>3.11</td>
<td>0.18</td>
</tr>
<tr>
<td>10% CO₂</td>
<td>3.11</td>
<td>0.18</td>
</tr>
<tr>
<td>5% O₂</td>
<td>1.61</td>
<td>0.09</td>
</tr>
<tr>
<td>15% CO₂</td>
<td>1.61</td>
<td>0.09</td>
</tr>
<tr>
<td>20% CO₂</td>
<td>0.13</td>
<td>----</td>
</tr>
<tr>
<td>No aeration</td>
<td>6.58</td>
<td>0.23</td>
</tr>
</tbody>
</table>

1 In each aeration treatment nitrogen gas takes up the remaining percentage not given.
necessary to calibrate the pH values with actual quantitative determinations of the carbon dioxide in solution. The pH values obtained are somewhat higher than the theoretical values which would be expected if the dissolved carbon dioxide were in equilibrium with the aerating gases.

During the potassium uptake study the pH values of the culture solutions were also determined. Pure Hoagland's solution had a pH of about 6.5 and the presence of the plants without aeration tended to lower this value slightly. With 100% nitrogen aeration the pH was around 7.1, and for all other aeration treatments the pH ranged between 6.0 and 6.9 except with 20% carbon dioxide where the pH was lowest (5.8 to 6.0). This indicates that the pH of the culture solutions probably had no important effects on the experimental results obtained.

The dissolved oxygen in the distilled water was considerably reduced by the plants even though they had been in the water only a relatively short time. This indicates that 20 liters of gas per 24 hours did not maintain the dissolved oxygen level in the presence of the plants. This points to the real problem in such aeration studies. It is not only the percentage of oxygen in the aerating gas that is important, but also the rate at which the aerating gas is supplied to the plants. Cannon (55), Hutchins (97) and Hutchins and Livingston (98) have stressed this point in soil aeration
studies, and two investigators, Taylor (169) and Raney (141), have recently advanced the rate of oxygen supply concept as being a better criterion of soil aeration than the gaseous composition per se. The above considerations do not invalidate these results however, since the rate of supply of oxygen was fairly constant.

Unfortunately these experiments do not answer a vital question which might be raised at this point. Do the plants use all of the oxygen from the gas bubbling into the solution, or were the bubbles too large for all of the oxygen to diffuse from them into the solution before they passed into the atmosphere? This question might profitably be studied with minor modifications of the aeration apparatus used. Porous carbon tubes would probably be better as aerators than the capillary tubes used. If the plants could then be sealed air tight into the containers so that the air passing through the solution could be trapped for analysis then the consumption of oxygen and discharge of carbon dioxide could be determined. Some of the techniques of Woodford and Gregory (163) and Gilbert and Shive (74, 75) very likely could be useful for such an experiment. The data of Table 16 indicate that an aerating gas containing 5% oxygen could probably be made to give the growth and absorption responses of the 20% oxygen aeration treatment if the rate of aeration or the bubble size was regulated so as to maintain the
dissolved oxygen at around 1 ppm. If 15% carbon dioxide was also included with 5% oxygen the higher aeration rate necessary to maintain the dissolved oxygen at 1 ppm might increase the toxicity of the carbon dioxide. Also the rate of diffusion of oxygen into the solutions from a rapid air stream low in oxygen may not be sufficiently rapid to maintain the dissolved oxygen at 1 ppm. These and other theoretical considerations will require further experimentation.

Under the conditions of these experiments there is apparently a point around 0.2 ppm of dissolved oxygen below which the rate of oxygen supply to the root surface becomes limiting enough to significantly reduce growth and potassium absorption.

The Influence of Tillage Practices on the Composition of the Soil Atmosphere Under Corn.

Experimental

In view of the differential response of corn to tillage as found by Bower, et al (20), it was considered desirable to investigate the soil air composition as affected by different tillage practices. Fortunately some of the same tillage plots used by these investigators were made available for this study. These plots were located in a Webster soil area on the Iowa State College Agricultural Engineering Experimental Farm, and during 1949 they were in their second year of corn in a four year rotation of corn, corn, oats and
red clover-timothy. Tillage treatments consisted of diskng, listing, plowing and subsurface cultivation superimposed upon unfertilized, fertilized, and cover crop (rye and vetch) plots.

Soil air samples were taken periodically during June, July and August from one replication of the fertilized and unfertilized plots. The largest number of samples were taken from the unfertilized plowed and listed plots, because the effect of tillage on the corn was most obvious here. Due to a very dry late summer and to the fact that no differences were being obtained between treatments this study was not extensive.

Sampling and analysis of the soil gases was conducted by the employment of the same technique and apparatus as used in the greenhouse. All samples were taken in the row as close to the corn plants as possible. The sampling process consisted of scraping off the slight ridge of soil thrown up around the plants by cultivation, and immediately pouring a small layer of paraffin-vaseline mixture over an area of about 40 square inches. The soil air sample was then withdrawn through a 4 inch hypodermic needle as described earlier.

Results and discussion

The field air analyses (Table 20) on all plots failed to reveal extremes in carbon dioxide and oxygen composition
Table 20. Composition of the soil atmosphere (4 inch depth) under corn on Webster silt loam soil receiving various types of tillage.

<table>
<thead>
<tr>
<th>Treatments</th>
<th>No. of analyses</th>
<th>Gas composition</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>CO₂ : O₂</td>
</tr>
<tr>
<td></td>
<td></td>
<td>% : %</td>
</tr>
<tr>
<td>Unfertilized</td>
<td></td>
<td></td>
</tr>
<tr>
<td>: plowed</td>
<td>8</td>
<td>0.81 : 20.00</td>
</tr>
<tr>
<td>: disked</td>
<td>2</td>
<td>0.88 : 20.44</td>
</tr>
<tr>
<td>: listed</td>
<td>7</td>
<td>0.89 : 20.09</td>
</tr>
<tr>
<td>Fertilized</td>
<td></td>
<td></td>
</tr>
<tr>
<td>: plowed</td>
<td>2</td>
<td>1.57 : 19.51</td>
</tr>
<tr>
<td>: tilled</td>
<td>5</td>
<td>1.63 : 19.38</td>
</tr>
<tr>
<td>: disked</td>
<td>2</td>
<td>1.58 : 19.54</td>
</tr>
<tr>
<td>: listed</td>
<td>3</td>
<td>0.87 : 20.22</td>
</tr>
</tbody>
</table>

166 pounds of 3-12-12 in the row
which are commonly considered to be detrimental to plant
growth and mineral absorption, even though the differences
due to tillage treatments were readily visible on the corn
throughout the growing season. These differences are shown
in Figure 21 where the corn on the plowed plot is tasseling
while that on the listed plot is stunted and shows nitrogen
and potassium deficiency symptoms. These growth differences
have been attributed to a lack of aeration, especially where
the soil was listed. Such assumptions were made without
knowledge of the air composition. There was a tendency
(as shown by a comparison of the fertilized and unfertilized
plots) for the carbon dioxide to be higher and the oxygen to
be lower where the corn was growing more vigorously. The
comparison in Table 20 between the fertilized and unfertilized
plots is not, however, an absolutely valid one due to the fact
that most of the measurements on the fertilized plots were
made when the soil was rather moist from a rain of two days
earlier. However, a few analyses with the soil considerably
drier still showed the carbon dioxide content to be above 1%.

The composition of the soil air was about the same at 4
and 12 inch depths. This was the case when an 8 inch hole
was dug from which an air sample was taken with the 4 inch
needle and also when a special 12 inch needle was used.

The effect of the fertilizers on the growth differences
between the various tillage practices was striking. Dif-
Figure 21. Response of corn to plowing (left) and listing (right) in Webster soil without fertilizer applications.
ferences due to tillage practically disappeared. In this connection the results of potassium fertilization in the greenhouse where pure carbon dioxide was passed through the soil in one gallon pots planted to corn is recalled. The growth of the tops was practically the same as under other aeration treatments. In that case a limited root system was almost adequately supplied with nutrients in the zone where the roots could grow. It is therefore possible that these field results are somewhat comparable to the greenhouse results. Even though the root system under certain tillage practices is limited in extent, as long as all the nutrients needed are supplied in sufficient amounts in the zone of root growth, it would be expected that tillage effects might disappear.

No studies were made of the extent of the root systems under the different tillage practices. It is interesting to consider, however, what factors might limit the root growth in the listed plots, for example. First, there is the possibility of the soil being a physical barrier to normal root penetration. It was noted, especially during the early part of the growing season, that the listed plots were much more resistant to the penetration of the hypodermic needle than the plowed plots. Second, the composition of the air around the root tips may become high in carbon dioxide or low in oxygen or both and effectively reduce the root growth. Hunter and
Rich (96) have indicated this possibility. It should be emphasized again that the composition of the soil air sample represents an average of conditions in a soil volume much larger than the volume of the air sample. Therefore, the condition of the air layer next to the root, or for that matter the moisture film on the root surface is not indicated by the gaseous composition values obtained.

Investigations concerning the rate of oxygen supply to root surfaces in the soil (141, 168) might indicate that the rate of supply of oxygen through the soil in the case of the listed plot was too slow to allow normal root growth. This is a distinct possibility and should be investigated further along with air composition at the root surface and soil compaction.
GENERAL DISCUSSION

The research here reported was principally concerned with the interrelationship of oxygen and carbon dioxide levels in the substrate upon growth, potassium uptake and water absorption by plants. The results of both soil and nutrient culture experiments indicate that oxygen deficiency and carbon dioxide toxicity especially under field conditions are not active separately in their effect on the physiology of the plants. That is to say that carbon dioxide does not become detrimental to the plant until concentrations on the order of 20% are attained when 20% oxygen is present in the aerating gas. This is based on the growth of corn and soybeans, and it is possible that other plants may respond differently, for example, Vlamis and Davis (175) found that 20 to 30% carbon dioxide was toxic to barley plants even if the oxygen was increased 70 to 80%. Cannon (39, 55) has also reported that rather high concentrations of carbon dioxide in the soil atmosphere were necessary to reduce root growth if sufficient oxygen were present.

When the oxygen percentage of the atmosphere in contact with the roots of plants is reduced below 20% then smaller percentages of carbon dioxide may be detrimental to plants.
This is indicated by the results of culture solution experiments number 2 and 5. Oxygen impurity in the nitrogen gas was effective in increasing the potassium absorption of corn above the unaerated plants. When slightly less than 5% carbon dioxide was included in the nitrogen gas the effectiveness of the oxygen impurity in increasing potassium absorption was markedly reduced. If the oxygen impurity is removed from the nitrogen gas the effects of this gas with and without carbon dioxide on the potassium uptake of corn are practically the same with a slight indication of an additive effect due to the presence of carbon dioxide. It should be emphasized that the potassium uptake studies were of short duration and since the uptake of potassium was small where oxygen was lacking the difference due to the presence or absence of carbon dioxide would be difficult to establish. In this connection the culture solution experiment number 3, where growth responses were studied over a period of three weeks, is more revealing of the detrimental effect of carbon dioxide when no oxygen or a very small amount is present. In that experiment the growth of the corn was considerably less when 20% carbon dioxide was included with an oxygen deficiency.

This introduces a point concerning these findings in their relationship to the problem of soil aeration in the field. The cumulative effect of long periods of poor aeration conditions on both growth and mineral nutrition of
plants must also be considered. The results of culture solution experiments number 3 and 5 indicate that detrimental effects of an excess of carbon dioxide and a deficiency of oxygen on potassium uptake may not be well defined in short time experiments, but that over a longer period of time the effects on growth become readily apparent. It can be seen, therefore, that poor soil aeration conditions which reduce growth and thus the extent of the root system will also reduce the mineral nutrition of the plant even if the effect of the aeration on mineral uptake is not so marked. This cumulative effect then, over a period of time will result in greatly reduced yields of crop plants. The results of the soil aeration experiment number 2 in which the growth of corn was very poor in unfertilized soil aerated with carbon dioxide serves to emphasize the importance of the above considerations.

The soil air composition in relation to the above results is of considerable interest. In these studies the composition of the soil atmosphere was found to deviate only slightly from the composition of the atmosphere above the soil. However, growth increases were obtained by passing a slow stream of air through the soil in the greenhouse and also growth differences were observed in the field when soil air composition differences were not apparent. Neither an oxygen deficiency nor a carbon dioxide toxicity can be used
to explain these results since findings in the soil and nutrient culture aeration experiments with controlled air compositions indicate that relatively lower oxygen and higher carbon dioxide levels are necessary to affect growth than were found in the greenhouse and field experiments. Other investigators (18, 55) have noted this problem. Boicourt and Allen (18) obtained increased growth of roses by the forced aeration of the soil in the rose beds. The difference in the soil air composition of the aerated and unaerated beds was not marked. Seeley (155) on the other hand found that the oxygen in the aerating gas used to aerate soil in 4 by 7 inch cans had to be lowered to 5% to obtain reduced growth of roses in the greenhouse. As far as the oxygen supply is concerned there is a possible explanation for these discrepancies in the studies of Cannon (55), Hutchins (97) and Hutchins and Livingston (98) and more recently the studies of Taylor (168, 169) and Raney (141). These investigators emphasize the fact that the soil air composition does not indicate the oxygen supplying power of the soil. It is therefore, very likely that the streaming of a gas through the soil increases the supply of oxygen to the root surface to an extent not measureable in an air sample withdrawn from the soil. Cannon (55) emphasized that a very small percentage of oxygen in the atmosphere is sufficient if the atmosphere is changed rapidly enough. Raney
(141) could correlate growth differences under certain tillage practices with the rate of oxygen diffusion in the soil much better than the soil air composition.

The question of carbon dioxide is also important in these considerations. While a stream of gas containing a low percentage of oxygen passing through a soil may increase the rate of oxygen supply, it also sweeps out the carbon dioxide from around the roots and prevents the existence of unfavorable carbon dioxide and oxygen gradients around the roots. If the rate of oxygen diffusion is more rapid in one soil than in another then the rate of carbon dioxide diffusion is also faster.

Important theoretical considerations may be discussed from the rates of diffusion of various gases into each other. The diffusion coefficients\footnote{International critical tables of numerical data, physics chemistry, and technology. N. Y., McGraw Hill. 1929. 5:62-63.} for various gas pairs are given below.

<table>
<thead>
<tr>
<th>Gas Pair</th>
<th>$D_0$ cm/second</th>
</tr>
</thead>
<tbody>
<tr>
<td>$O_2-N_2$</td>
<td>0.181</td>
</tr>
<tr>
<td>$O_2-CO_2$</td>
<td>0.139</td>
</tr>
<tr>
<td>$O_2$-air</td>
<td>0.178</td>
</tr>
<tr>
<td>$CO_2$-air</td>
<td>0.138</td>
</tr>
</tbody>
</table>

It can be seen that carbon dioxide diffuses slower into air than oxygen into air, and that oxygen diffuses slower...
into carbon dioxide than into air. In view of Cannon's (55) findings on the importance of diffusion of oxygen in helium and in nitrogen it is interesting to consider the effect of an accumulation of carbon dioxide immediately adjacent to a respiring body. Obviously the rate at which oxygen would pass through an accumulated layer of carbon dioxide would be considerably slower than if no carbon dioxide were present. Since no micro-analyses of the atmosphere adjacent to roots have been made it is difficult to visualize just what concentration of carbon dioxide may exist next to the root under conditions of poor aeration. However, an idea may be had from Leather's (114) results on the air composition next to plant roots at a 15 inch depth which are as follows.

<table>
<thead>
<tr>
<th></th>
<th>% O₂</th>
<th>% CO₂</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crotolaria</td>
<td>2.23-9.00</td>
<td>4.84-16.99</td>
</tr>
<tr>
<td>Indigofera</td>
<td>3.33-5.24</td>
<td>12.62-21.14</td>
</tr>
<tr>
<td>Corn</td>
<td>6.28-13.82</td>
<td>3.34-12.30</td>
</tr>
</tbody>
</table>

It is possible that carbon dioxide could accumulate around the root under conditions of restricted diffusion to a concentration which may become toxic to the root or which may reduce the rate of diffusion of oxygen to the respiring root and in either case be detrimental. In this connection the culture solution experiment number 2 is recalled. Here, less than 5% carbon dioxide in the aerating gas considerably reduced the effectiveness of the very small amount of oxygen
impurity in the aerating gas. The reduction in the effectiveness of 20% oxygen by the addition of 20% and 50% carbon dioxide in the aerating gas in culture solution experiment number 1 may be accounted for by a reduced diffusion rate of oxygen in addition to the toxic effects of carbon dioxide. It is well to point out, however, that Arrington and Shive (9) have shown that carbon dioxide had no effect on the solubility of oxygen in solution cultures. This was also found to be the case in culture solution experiment number 5. These findings would indicate that carbon dioxide might not affect the solubility of oxygen in the water film on the root surface. However, the rate of supply of oxygen to the water film and through it into the root may be affected by high concentrations of carbon dioxide.

The improved growth of crops noted in these experiments and also reported by others (18, 55, 100) when a stream of gas is passed through the soil may be due to an improved oxygen supply brought about by sweeping the carbon dioxide away from the root surface. From the above considerations it can be seen that carbon dioxide even though measured in relatively small concentrations in the soil air must still receive attention. The need is for a method of measuring the soil air in contact with the root surface. It is suggested that the micro-technique of several investigators (106, 160,
The possible effect on plant growth of soil compaction other than its effect on soil aeration has been mentioned by several investigators (151, 168, 172). The root system of plants besides being limited in extent by the aeration factors mentioned above may also be limited by physical resistance of the soil to root penetration. In this connection the results of the soil air composition studies in the field have already been discussed. Suffice to say however, that the effect of fertilization in overcoming detrimental effects where the soil was listed gives strong support to the theory that the root system was limited by the listing tillage practice possibly due to either or both restricted aeration and compaction of the soil.

The effect of carbon dioxide on the physiology of the plant has been established and the work here reported gives further evidence in support of the view that this effect of carbon dioxide depends upon the oxygen level.

The problem of growing plants in water-logged soils was considered briefly in that an attempt was made to supply oxygen for plant growth by the application of certain oxygen carrying chemicals to the soil before it was water-logged. The growth of corn was improved where ammonium persulphate applications were made, however, the results were variable and the best growth obtained was still far from normal.
Conway (63) indicates that the problem may not be entirely concerned with oxygen supply but rather reducing conditions under water-logging. The suggestion by Conway that oxygen is probably lower where there is mud and soil in water than where the water is clear should be experimentally investigated. The existence of a condition of this nature may in part account for the fact that some species of plants can be successfully grown in unaerated culture solutions but cannot be grown in water-logged soils.
SUMMARY

A series of experiments were conducted in both soils and nutrient culture to measure the effect of the levels of oxygen and carbon dioxide upon growth, potassium uptake and water absorption by corn and soybean plants. Apparatus for obtaining any desired gas mixture and for the controlled distribution of the gases through soils or solutions has been described. Also a simple technique for the sampling and analysis of the soil air especially from pots in the greenhouse was developed.

In the soil aeration experiments corn and soybeans were grown in 1 gallon glazed pots containing a mixture of equal parts of Carrington soil and sand. The nutrient culture work was conducted by growing corn plants in Hoagland's nutrient solution contained in quart Mason jars.

Data collected in this investigation are believed to corroborate and extend the findings of others in the field of plant substrate aeration. The practical and theoretical considerations of these findings were discussed in their relationship to the soil aeration problem and to possible future lines of investigation.

The results of these studies may be summarized as follows:
Soil Aeration

1. The extent of the root system of corn in greenhouse pots of soil was markedly reduced by a carbon dioxide concentration of 30% when about 10% oxygen was present. This reduction in the root system resulted in reduced top growth where no potassium fertilizer was added, but did not reduce the top growth when potassium was supplied.

2. Reduction of the oxygen in the soil atmosphere to about 16% by passing a continuous stream of nitrogen gas through the soil did not significantly affect the growth of corn. The tendency was for the dry weight to be higher than the unaerated check plants.

3. Potassium uptake and water absorption by corn and soybeans was unaffected by a reduction of the oxygen to 1.5 to 6.0% in the soil atmosphere. A stream of nitrogen gas was being passed through the soil so that the carbon dioxide concentration was also low.

4. With the oxygen concentration held at 20% in the aerating gas, 10% carbon dioxide had no effect on the potassium uptake and water absorption of corn and soybeans, while 20 and 50% carbon dioxide caused a reduction in these processes.

5. Field soil air composition measurements did not prove to be correlated with the growth responses of corn to certain tillage practices.
Culture Solution Aeration

1. A reduced oxygen supply in the culture solutions brought about by continuous aeration with purified nitrogen caused a marked reduction in potassium uptake and water absorption by corn plants.

2. When 20% carbon dioxide or above was used in an aerating gas containing 20% oxygen the reduction of potassium and water absorption was much more pronounced than in the soil aeration experiments.

3. Aeration with nitrogen gas which contained about 0.4% oxygen as an impurity increased the uptake of potassium over the unaerated treatment. The presence of 5% or more carbon dioxide considerably reduced the effectiveness of the low oxygen.

4. Fifteen percent carbon dioxide with 5% oxygen in the aerating gas reduced the uptake of potassium and absorption of water below the unaerated treatment. This along with the results above indicates that smaller concentrations of carbon dioxide may be necessary to obtain detrimental effects when the oxygen is also low.

5. The potassium uptake and water absorption of corn was not markedly affected by 10% carbon dioxide and 10% oxygen in the aerating gas, but the effect on the growth of corn during a three week period was more pronounced. The
cumulative effects on plant growth and mineral nutrition by long periods of poor aeration conditions are emphasized by these results.

6. Analyses of the dissolved oxygen in distilled water in contact with corn roots indicated that when the dissolved oxygen was around 0.2 ppm, then the rate of supply of oxygen to the root surface was not rapid enough for normal potassium uptake and water absorption.

7. When purified nitrogen gas was used the addition of 20% carbon dioxide to the nitrogen produced a marked additive effect on the growth of corn during a three week period. This additive effect was not as prominent on the potassium uptake over a five day period.
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   phosphate availability, soil permeability and carbon 
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Dr. W. V. Bartholomew, who suggested the capillary control apparatus and explained its basic principles.

The American Potash Institute whose financial support made this investigation possible.
APPENDIX

Analysis of Variance Tables

Appendix table 1. Analysis of variance of the dry weights of corn (tops) - oxygen-carrying fertilizer experiment. Data of Table 1.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Degrees of freedom</th>
<th>Sum of squares</th>
<th>Mean square</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Main plots:</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>K level</td>
<td>1</td>
<td>9.30</td>
<td>9.30</td>
</tr>
<tr>
<td>Blocks</td>
<td>2</td>
<td>10.45</td>
<td>5.22</td>
</tr>
<tr>
<td>Main plot error</td>
<td>2</td>
<td>6.74</td>
<td>3.37</td>
</tr>
<tr>
<td><strong>Subplots:</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Moisture level</td>
<td>2</td>
<td>165.34</td>
<td>82.67**</td>
</tr>
<tr>
<td>Moisture x K</td>
<td>2</td>
<td>12.00</td>
<td>6.00</td>
</tr>
<tr>
<td>Subplot error</td>
<td>8</td>
<td>17.03</td>
<td>2.13</td>
</tr>
<tr>
<td><strong>Sub-subplots:</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>O₂ fertilizer</td>
<td>2</td>
<td>3.18</td>
<td>1.59**</td>
</tr>
<tr>
<td>O₂ fertilizer x K</td>
<td>2</td>
<td>0.33</td>
<td>0.17</td>
</tr>
<tr>
<td>O₂ fertilizer x K</td>
<td>4</td>
<td>2.72</td>
<td>0.68*</td>
</tr>
<tr>
<td>x moisture</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>O₂ fertilizer x K</td>
<td>4</td>
<td>28.33</td>
<td>9.33**</td>
</tr>
<tr>
<td>x moisture</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Sub-subplot error</strong></td>
<td>24</td>
<td>3.34</td>
<td>0.139</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>53</td>
<td>258.74</td>
<td></td>
</tr>
</tbody>
</table>

*Significant between the 5% and 1% levels
**Significant beyond the 1% level
Appendix table 2. Analysis of variance of the dry weights of corn (tops and roots) - soil aeration experiment number 1. Data of Table 2.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Degrees of freedom</th>
<th>Sum of squares</th>
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</tr>
</thead>
<tbody>
<tr>
<td>Main plots:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aeration</td>
<td>2</td>
<td>249.18</td>
<td>124.59**</td>
</tr>
<tr>
<td>Blocks</td>
<td>3</td>
<td>5.77</td>
<td>1.92</td>
</tr>
<tr>
<td>Main plot error</td>
<td>6</td>
<td>22.59</td>
<td>3.77</td>
</tr>
<tr>
<td>Subplots:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>K level</td>
<td>2</td>
<td>64.00</td>
<td>32.00*</td>
</tr>
<tr>
<td>K level x aeration</td>
<td>4</td>
<td>16.78</td>
<td>4.20</td>
</tr>
<tr>
<td>Subplot error</td>
<td>18</td>
<td>143.49</td>
<td>7.92</td>
</tr>
<tr>
<td>Total</td>
<td>35</td>
<td>502.81</td>
<td></td>
</tr>
</tbody>
</table>

*Significant between the 5% and 1% levels
**Significant beyond the 1% level

Appendix table 3. Analysis of variance of the dry weights of corn (tops and roots) - soil aeration experiment number 2. Data of Table 4.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Degrees of freedom</th>
<th>Sum of squares</th>
<th>Mean square</th>
</tr>
</thead>
<tbody>
<tr>
<td>Main plots:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>K level</td>
<td>1</td>
<td>396.55</td>
<td>396.56**</td>
</tr>
<tr>
<td>Blocks</td>
<td>3</td>
<td>5.50</td>
<td>1.83</td>
</tr>
<tr>
<td>Main plot error</td>
<td>3</td>
<td>2.24</td>
<td>0.75</td>
</tr>
<tr>
<td>Subplots:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aeration</td>
<td>3</td>
<td>99.94</td>
<td>33.31**</td>
</tr>
<tr>
<td>Aeration x K level</td>
<td>3</td>
<td>3.73</td>
<td>1.24</td>
</tr>
<tr>
<td>Subplot error</td>
<td>18</td>
<td>20.30</td>
<td>1.13</td>
</tr>
<tr>
<td>Total</td>
<td>31</td>
<td>528.27</td>
<td></td>
</tr>
</tbody>
</table>

**Significant beyond the 1% level
Appendix table 4. Analysis of variance of the potassium content (mg.+) of corn (tops) - soil aeration experiment number 3. Data of Table 6.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Degrees of freedom</th>
<th>Sum of squares</th>
<th>Mean square</th>
</tr>
</thead>
<tbody>
<tr>
<td>Blocks</td>
<td>3</td>
<td>271.65</td>
<td>90.55</td>
</tr>
<tr>
<td>Treatment</td>
<td>6</td>
<td>9,405.00</td>
<td>1,567.50*</td>
</tr>
<tr>
<td>Error</td>
<td>18</td>
<td>8,108.47</td>
<td>450.47</td>
</tr>
<tr>
<td>Total</td>
<td>27</td>
<td>17,785.12</td>
<td></td>
</tr>
</tbody>
</table>

Standard deviation = 21.23  Coefficient of variation = 8.79%

*Significant between the 5% and 1% levels.

Appendix table 5. Analysis of variance of the potassium content (mg.+) of corn (tops and roots) - soil aeration experiment number 3. Data of Table 6.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Degrees of freedom</th>
<th>Sum of squares</th>
<th>Mean square</th>
</tr>
</thead>
<tbody>
<tr>
<td>Blocks</td>
<td>3</td>
<td>555.62</td>
<td>185.27</td>
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<tr>
<td>Treatment</td>
<td>6</td>
<td>8,812.69</td>
<td>1,468.951</td>
</tr>
<tr>
<td>Error</td>
<td>18</td>
<td>10,677.00</td>
<td>593.17</td>
</tr>
<tr>
<td>Total</td>
<td>27</td>
<td>20,046.51</td>
<td></td>
</tr>
</tbody>
</table>

Standard deviation = 24.36  Coefficient of variation = 8.10%

1A comparison of the sum of all aeration treatments versus the unaerated, unfertilized treatment is significant beyond the 1% level.
Appendix table 6. Analysis of variance of the potassium content (mgs.) of soybeans (tops) - soil aeration experiment number 3. Data of Table 7.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Degrees of freedom</th>
<th>Sum of squares</th>
<th>Mean square</th>
</tr>
</thead>
<tbody>
<tr>
<td>Blocks</td>
<td>3</td>
<td>82.75</td>
<td>27.58</td>
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<tr>
<td>Treatment</td>
<td>6</td>
<td>1,849.54</td>
<td>308.26**</td>
</tr>
<tr>
<td>Error</td>
<td>18</td>
<td>1,262.72</td>
<td>70.15</td>
</tr>
<tr>
<td>Total</td>
<td>27</td>
<td>3,195.01</td>
<td></td>
</tr>
</tbody>
</table>

Standard deviation = 8.38  Coefficient of variation = 4.30%

**Significant beyond the 1% level

Appendix table 7. Analysis of variance of the potassium content (mgs.) of soybeans (tops and roots) - soil aeration experiment number 3. Data of Table 7.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Degrees of freedom</th>
<th>Sum of squares</th>
<th>Mean square</th>
</tr>
</thead>
<tbody>
<tr>
<td>Blocks</td>
<td>3</td>
<td>178.14</td>
<td>59.38</td>
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<tr>
<td>Treatment</td>
<td>6</td>
<td>2,550.57</td>
<td>425.09*</td>
</tr>
<tr>
<td>Error</td>
<td>18</td>
<td>2,026.71</td>
<td>112.59</td>
</tr>
<tr>
<td>Total</td>
<td>27</td>
<td>4,755.42</td>
<td></td>
</tr>
</tbody>
</table>

Standard deviation = 10.61  Coefficient of variation = 4.58%

*Significant between the 5% and 1% levels
Appendix table 8. Analysis of variance of the potassium absorption by corn - culture solution experiment number 1. Data for the first 5 days of Table 10.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Degrees of freedom</th>
<th>Sum of squares</th>
<th>Mean square</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment(^1)</td>
<td>5</td>
<td>6,643.12</td>
<td>1,328.62**</td>
</tr>
<tr>
<td>Error</td>
<td>6</td>
<td>518.23</td>
<td>36.38</td>
</tr>
<tr>
<td>Total</td>
<td>11</td>
<td>7,161.40</td>
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</table>

Standard deviation = 9.29
Coefficient of variation = 10.26%

\(^1\)The un aerated jars are not included in this analysis
\(^*\)Significant beyond the 1\% level

Appendix table 9. Analysis of variance of water absorption by corn - culture solution experiment number 1. Data for the first 5 days of Table 11.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Degrees of freedom</th>
<th>Sum of squares</th>
<th>Mean square</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment(^1)</td>
<td>5</td>
<td>6,389.50</td>
<td>1,277.90*</td>
</tr>
<tr>
<td>Error</td>
<td>6</td>
<td>963.50</td>
<td>160.58</td>
</tr>
<tr>
<td>Total</td>
<td>11</td>
<td>7,353.00</td>
<td></td>
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</table>

Standard deviation = 12.67
Coefficient of variation = 4.41%

\(^1\)The un aerated jars are not included in this analysis
\(^*\)Significant between the 5\% and 1\% levels
Appendix table 10. Analysis of variance of potassium absorption by corn - culture solution experiment number 2. Data of Table 13.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Degrees of freedom</th>
<th>Sum of squares</th>
<th>Mean square</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment (^1)</td>
<td>4</td>
<td>2,001.77</td>
<td>500.44*</td>
</tr>
<tr>
<td>Error</td>
<td>5</td>
<td>366.70</td>
<td>73.34</td>
</tr>
<tr>
<td>Total</td>
<td>9</td>
<td>2,368.47</td>
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</tbody>
</table>

Standard deviation = 8.56  Coefficient of variation = 28.77\%

\(^1\)The un aerated jars are not included in this analysis

\(^*\)Significant between the 5\% and 1\% levels

Appendix table 11. Analysis of variance of water absorption by corn - culture solution experiment number 2. Data of Table 13.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Degrees of freedom</th>
<th>Sum of squares</th>
<th>Mean square</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment (^1)</td>
<td>4</td>
<td>27,721.0</td>
<td>6,930.25</td>
</tr>
<tr>
<td>Error</td>
<td>5</td>
<td>11,215.5</td>
<td>2,243.10</td>
</tr>
<tr>
<td>Total</td>
<td>9</td>
<td>38,936.5</td>
<td></td>
</tr>
</tbody>
</table>

Standard deviation = 47.56  Coefficient of variation = 17.01\%

\(^1\)The un aerated jars are not included in this analysis
Appendix table 12. Analysis of variance of the dry weight of corn (tots and roots) - culture solution experiment number 3. Data of Table 15.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Degrees of freedom</th>
<th>Sum of squares</th>
<th>Mean square</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment¹</td>
<td>5</td>
<td>37.01</td>
<td>7.40*</td>
</tr>
<tr>
<td>Error</td>
<td>6</td>
<td>7.97</td>
<td>1.33</td>
</tr>
<tr>
<td>Total</td>
<td>11</td>
<td>44.98</td>
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</tr>
</tbody>
</table>

Standard deviation = 2.82  Coefficient of variation = 42.22%

¹The un aerated jars are not included in this analysis
*Significant between the 5% and 1% levels

Appendix table 15. Analysis of variance of potassium absorption by corn - culture solution experiment number 5. Data of Table 18.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Degrees of freedom</th>
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<th>Mean square</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment¹</td>
<td>5</td>
<td>32,303.09</td>
<td>6,460.62**</td>
</tr>
<tr>
<td>Error</td>
<td>6</td>
<td>89.19</td>
<td>14.87</td>
</tr>
<tr>
<td>Total</td>
<td>11</td>
<td>32,392.28</td>
<td></td>
</tr>
</tbody>
</table>

Standard deviation = 3.86  Coefficient of variation = 4.66%

¹The un aerated jars are not included in this analysis
**Significant beyond the 1% level