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A STUDY OF THE RELATION OF PHOSPHORUS AND FUNGI TO "BLACKHEART" OF SUGAR BEETS

Submitted by

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for the Degree of Master of Science

Colorado Agricultural College

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COLORADO AGRICULTURAL COLLEGE

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I HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER MY SUPERVISION BY MAX MEIER ENTITLED "A STUDY OF THE RELATION OF PHOSPHORUS AND FUNGI TO "BLACKHEART" OF SUGAR BEETS" BE ACCEPTED AS FULFILLING THIS PART OF THE REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE

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This is to certify that Mr. Max Meier has translated for me assigned passages of technical German bearing upon his graduate Botanical work.

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Fort Collins, Colorado

May 1, 1931

THIS THESIS HAS BEEN APPROVED AND RECOMMENDED
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A STUDY OF THE RELATION OF PHOSPHORUS AND FUNGI TO "BLACKHEART" OF SUGAR BEETS

INTRODUCTION

The study of phosphorus in relation to nutritional functions has received increasing attention in the last decade not only in human and animal physiology, but also in the botanical field.

Recently the so-called Blackheart disease of beets has been attributed to phosphorus deficiency and has become a matter of investigation in various sections of the sugar beet-raising areas of the world.

However, there has arisen some confusion between the effect of phosphorus deficiency on beets and injury from so-called "Late Blight" generally attributed to water deficiency and soil reactions. Also little is known of the occurrence of organisms which appear to be associated with the diseases.

There is a general assumption that phosphorus stimulates root development;whether this holds true for beets has not been definitely shown.

Further, no complete bibliography has been assembled of phosphorus on plants generally and beets in particular.

It is the purpose of the following discussion to give a brief account of the fungi found on Blackheart beets, to show the root development of beets at different stages of growth with different phosphate applications and to present a rather complete review and bibliography of literature on the role of phosphorus in plants.

HISTORICAL REVIEW

The history of the study of phosphorus in plant life may be divided into three periods:

1. The beginning of research - up to 1874
2. The early plant physiologists 1874-1902
3. The new century - since 1902

1. Previous to the discoveries of Lavoisier, Priestley, Cavendish and others in the chemical sciences very little had been done in the study of the mineral nutrition of plants. With the newer knowledge gained by these men Ingen-Housz, Senebier, DeSaussure (21, 110) showed the relation of the interchange of gases in plants to nutrition and respiration.

Although the favorable effect of organic waste products and manures upon plants was generally known, it was not until 1743 that L. Margraf, (21) who discovered the sugar in the sugar beet, first obtained Phosphorus out of plants (Mustard, Lepidium and wheat).

Ruckert, (21, 110) in 1789, far ahead of many of his contemporaries in his views concerning the role of mineral nutrition had already known phosphorus as an important element in plant life. Boussingault (108) in 1834 was the first one perhaps to conduct field experiments and to determine quantitatively the manures applied and the crops harvested.

In 1795 the Earl of Dandonald (108) considered alkaline phosphate a nutritive salt. He placed his chief emphasis however upon the humus as a plant food. DeSaussure in his classic "Recherches chimiques sur la vegetation" 1804, definitely stated that no normal nutrition of plants was possible without the introduction of nitrates and mineral matters (110, 47).

A new and more intensive study of mineral nutrition was begun by Liebig (108, 110, 21) in 1840 when he disregarded the humus and vital force theory. Instead of those prevalent views he stressed the influence of minerals upon plant growth. His research and discussions started great opposition and at the same time renewed investigationson that subject. In his book "Chemistry in its application to agriculture and physiology" (1840), the first specific function of phosphorus was given, namely that it was necessary for seed formation. The law of minimum previously formulated was applied to plant nutrition by Liebig. Thus almost a hundred years ago the importance of nutritional balance of the elements was emphasized.

During the same period of increased interest shown in agricultural chemistry, the famous Rothamsted experiments, started by Lawes and Gilbert(108) began to lead to the same conclusions, that mineral nutrition was of vital importance. This, however, was overemphasized by some workers at the expense of photosynthetic activities. A few years later observations made by Lawes brought out another important point: that phosphates enhance root development, especially of lateral and fibrous roots. Besides the field experiments two methods of studying plant nutrition were employed. The first, the media for plants consisted of insoluble artificial soil (pulverized rock crystal and carbon obtained from candy sugar), the idea was probably based on Wiegman's and Polstoff's (21) platinum filings and sand media (1842). This method was used by Salm-Horstmann,1856, (21) who declared phosphorus to be essential to plant growth. From that time the sand-peat method replaced the somewhat delicate older one. The other method of finding out whether an element was needed for growth or not was worked out by Knop, Nobbe and Sachs who used the water culture method (109, 110). DeSaussure (110) used this method to some extent for water plant studies but the addition of nutrient solutions and the use of land plants for experiments is ascribed to the above mentioned investigators.

2. Sachs (111) in 1874 published his "Textbook of Botany" in which he confirmed the previous view taken that phosphorus is indispensable. He furthermore added that if it is not present growth stops or abnormal growth would

take place. He stated clearly, however, that no definite relations had been determined as to special physiological functions, but he indicated the possible role phosphates may play in cell formation.

Eight years later Sachs (109) made some further advances in this view concerning the influence of phosphorus upon plants. He found that it was a constituent of protoplasm, that minerals were brought to the leaves in extremely diluted solutions and had to be in suitable, available combinations. Furthermore he mentioned that molds grow very rapidly in weak nutrient solutions of phosphoric acid but no relations to assimilation and metabolism had been investigated. During this period further light upon the role of minerals was shed by the chemical ash analyses which Wolff, Konig and others carried out (47).

Another well known plant physiologist, Pfeffer, (99) was able to give some new information concerning the occurrence of phosphorus. It was found in the form of organic compounds, in proteids, nucleins, lecithin, and in globoids deposited in seeds. Reacting phosphates, it was understood, were liberated again by proteid-decomposition and by metabolism in general. Phosphorus was detected in living cells in a dissolved form as organic compounds but after death of the cells reprecipitated in combination with calcium or magnesium. In regard to the question whether phosphorus would be preferred by some plants in organic form, Pfeffer answered that certain fungi were able to obtain their requirement of phosphorus from proteid compounds. Oats was found to be able to partially satisfy its needs of phosphorus by absorbing lecithin. The solvent action of carbonic acid was already known at that time. Miyoshi (99) observed a strong attraction of phosphates upon fungi of the Saprolegniaceae. Chemotropism of root radicles of Lupinus toward phosphates had been studied by the same author. Macallum (21) was able to demonstrate in 1898 by microchemical methods the presence of phosphorus as an integral constituent of the nucleus and nucleolus.

The next important contribution to the knowledge of that study of mineral nutrition was made by Loew (72) in 1899. Loew believed, as Pfeffer, Sachs and others had shown, that phosphorus was necessary for lecithin formation and nucleo-proteids. He said, "Embryos develop only by cell division, if phosphorus is stored up in seeds." Phosphorus was determined as calcium- and magnesium-phosphate in globoids and as potassium phosphate in the seed. Phospate moreover was found more or less abundant in the ash of cereals, some as high as 75 per cent. Loew indirectly considered the function of phosphorus as an aid in respiration, because lecithin was necessary and used in this life process. He said, "Lecithin represents the form into which the fat must be changed to become combustible in the protoplasm since the substance serving for respiration must be present in the protoplasm in a dissolved condition." Furthermore he maintained that phosphorus was absolutely required in chlorophyll formation. This statement he sought to prove by such prominent investigators as Stocklasa, Macchiata, Frecul, Gautier and Hoppe, that crystallized chlorophyllan contains 1.39 per cent phosphoric acid. Loew himself made experiments with Spirogyra to determine the phosphorus requirement of chlorophyll. In nutrient solutions without phosphorus the chlorophyll turned yellow and an accumulation of fats and albumins took place. In the control solution, chlorophyll retained its normal color, the amount of fat and albumin stored up was much smaller than in the untreated one, the number of cells had more than doubled while in the phosphorus deficient solution no growth occurred. After eight weeks extreme amounts of potassium phosphate were added and in a short time a normal functioning of cell division began. An interesting contrast has been cited by Sorauer (123) who mentioned experiments made by Nobbe, which would indicate that chlorophyll could be formed without phosphorus. Another contradictive experiment was carried out by Eichen (123) who grew an oak seedling for three years in a phosphorus-free solution. The foliage remained dark green, while in other plants the color changed to a dark orange to red. No interpretation, however, has been found to this experiment.

On the basis of the knowledge gained from previous investigators and from his own studies Jost (64) in 1902 published his "Plant Physiology". But little new information was added in that short period. Jost thought that phosphates may be stored up by plants in compounds which did not show any reaction to tests with the usual methods.

3. During the last 30 years a great number of experiments have been carried out in the field of plant nutrition and other factors influencing it. The first two years comparatively few contributions were published on the phosphorus relation. Stoklasa (129) in 1911 published his research done on the "Biochemical cycle of the phosphate-ion in the soil" in which he described the important role played by microorganisms, in giving off immense quantities of carbon dioxide, their extensive microbiological activities by enzymes in building up in some phases and decomposing of organic compounds in others. He also emphasized the large amounts of phosphates needed for bacteria in the soil. Stoklasa furthermore pointed out that bacteria have a similar list of elements which are essential for their growth. The fact brought out, that microorganisms need such inorganic compounds to begin with, in order to increase the productiveness of the soil, greatly stimulated

new research in the same direction. The different experiments conducted during this last period will be considered under the various titles and subdivisions.

The Occurrence of Phosphorus in the Soil

Phosphorus is found in the soil in organic and inorganic forms fully oxidized as phosphate. The organic compounds are formed from the decomposition of plant and animal tissues and from all the lower organisms present in the soil. Inorganic phosphorus compounds occur in various forms, originally as apatite. By the addition of various phosphate fertilizers different inorganic compounds may result, such as calcium-, iron- and aluminum-phosphates as well as in other combinations.

The Occurrence of Phosphorus in Plants

In plants, phosphorus has been found in the cells of any part of the seed, root, stem or leaves (21, 101, 80). The protoplasm was found to contain very complex organic compounds in the form of proteins, phosphatides, lecithin, lipoids and in various other combinations. The difficulty is pointed out that phosphate seems to be in combination with many substances which are rapidly used up in the metabolic processes and which are so unstable that they are extracted with great difficulty in their original form. The quantity of phosphorus in plants varies greatly.

Three methods usually have been employed to study the phosphorus requirement and the amounts in plants. The first method is the ash analysis of plants, the second, the solution culture (99, 109). The third method, the sand-peat method of Hellriegel (54) has been used successfully since 1880 in studying the phosphate requirements of sugar beets.

The Role of Phosphorus in Plants

a. The cell and its activities -

The study of the cell, as the unit of plant structure, brought to light the requirement of essential mineral elements. That phosphorus is necessary for normal plant life has been already mentioned. Not so very many new discoveries have been made since the time of the earlier plant physiologists. Barton (3) in his book on "Recent Advances in Plant Physiology" made the statement that the functions of phosphorus in cells were difficult to ascertain. A short review, however, will be given of the experiments conducted in relation to cells, their content and activities.

Brelik (9) thought that a close physiological relation existed between phosphorus and chlorophyll. He believed that this element was of equal value to magnesium or potassium. In contrast to this view Mameli (77) observed that the lack of magnesium had an etiolating effect upon chloroplasts, whereas in the case of phosphorus the plastids remained normal in those respects. Schertz (116) working with cotton and potato leaves, noticed a daily variation of the chlorophyll components and a narrowing of the absorption band when phosphorus was deficient or lacking. The absence of phosphorus, compared to that of nitrogen or potassium, resulted in the least amount of chlorophyll formed. In a Russian article,(65) the author observed that with an increasing quantity of phosphorus the amount of chlorophyll decreased, especially at shortened day-light periods, while the maximum coincides either with solutions keeping a minimum amount of phosphorus or in free phosphorus solutions.

The influence of phosphoric acid upon the anthocyanin in culms of barley was studied by Suzuki (132). He thought that the production of anthocyanin was due to a nutritional derangement, mostly a deficiency of readily available phosphoric acid or nitrogen or a lack of both. Doak and Miller (27) studied anthocyanin production in sorghum by various applications of phosphorus and nitrogen. The results indicated a rather complex picture. Anthocyanin was produced in a maximum quantity in three varieties when N was at the lowest level regardless of the amounts of phosphorus present. With an excess of N the maximum production appeared only when phosphorus was deficient. Excess of phosphorus in combination with moderate surplus N gave a minimum production of anthocyanin. Some varieties produced no such pigment at all under any given conditions, others only medium amounts when phosphorus was deficient whether N was deficient or in excess. Harvey (51) gives this explanation for the production of anthocyanin after phosphorus deficiency or starvation in apple trees and in barley, that anthocyanin production may be associated with alumnium absorption.

After a longer period of phosphorus depletion Eckerson (33) found protoplasm became refractive. Phosphatides began to dissociate and to break down, sugars increased, while the carbohydrates decreased. Chloroplasts gradually disintegrated in the upper leaves until finally the protoplasm further decomposed. After a certain stage of disintegration it was usually very difficult for the cell to recover and it frequently failed to do so. McCool (82) studying various mineral elements influencing cell sap concentration observed that phosphorus alone decreased the cell sap concentration while in combination with potassium the concentration increased.

The importance of the presence of phosphorus has already been emphasized by Loew (72) on Spirogyra. A similar experiment was carried out by Reed (102) who obtained the same results with the same algae, e. g. cell division was suppressed if the plant was grown without phosphorus for three weeks. If this element was added after that period, mitosis occurred but with difficulties. Reed believed that such cells first lose the soluble phosphorus compounds and later show injuries in the living parts of the cells.

The study of the influence upon mitosis was furthermore investigated by Sommer and Sorokin (122). They found that the external form of cells of root tips of peas in the absence of phosphorus appeared almost normal if boron was present. But the internal plasma arrangement seemed to have changed. The nuclei lost their typical more or less spherical shaped form and assumed an extremely irregular outline. "Amoeboid, elongated, spindle shaped and constricted nuclei were often found in the meristematic reiong." Smaller nuclei were observed under the same conditions compared to normal cells. The position of the nuclei was changed somewhat. Instead of being more or less in the center, they were found in a flattened position against the transverse cell wall. Moreover, normal mitotic figures proved to be absent. Those injuries described were similar to those found in pea-roots in the absence of boron which by these authors is claimed to have an even more serious effect than phosphorus.

b. Phosphorus in relation to bacteria, fungi and algae.

The pioneer work of Pasteur, Koch, Winogradsky and a great number of other scientists opened a new field of research in bacteriology.

The mineral requirement of those lower organisms is similar to that of the higher plants, but not as many elements have been discovered to be essential as in the case of the Spermatophytes. Also great differences exist between the various groups in the quantity necessary for normal growth. The ash analysis gives an approximate idea about the importance of phosphorus in the metabolic processes. It was found that the ash of bacteria, yeasts and fungi may show great variations in the quantity of this element deposited in these organisms. Sackett (112) found that bacteria may contain more than 50 per cent of phosphate in the ash. A. Mayer (148) , made the following determinations of ash analyses: Bacteria 10 to 55 percent, fungi 44.8 to 59.4 per cent, algae 51 to 59 per cent. These quantities of phosphates of those organisms are to a great extent determined by the phosphate content of their substrata. The importance of sufficient mineral supply to the algae, fungi and bacteria becomes more outstanding if one realizes the number of those microbepopulation in a gram of soil. Mayer shows the following soil flora:

1. Bacteria	50	- 1200 millions
2. Fungi	30.000 -	900.00
3. Algae	28.000 -	60.000

A number of investigations have been carried out to determine the influence of phosphorus upon bacteria. Buchanan (14) summarized the effect of phosphate thus: "Phosphates, in suitable concentration stimulate cell growth, fermentive and other metabolic activities."

The carbon dioxide production and its importance has been pointed out by many research workers. Waksman (148) mentions three ways in which micro-organisms are able to transform insoluble tricalcium-phosphate into soluble form:

1. By direct metabolism (enzyme action)
2. By the carbon dioxide production
3. By the formation of inorganic acids in the metabolism of the autotrophic nitrifying and sulphur oxidizing bacteria

The assimilation of phosphorus from the soil fungi has been shown by Brown (13). Dox (31) reports an experiment in which Aspergillus niger secured its phosphorus need from organic and inorganic compounds. (Pytin, nucleic acid, lecithin, casein, etc.)

In regard to the question whether molds have any important role to play in soil fertility has been doubted by Jones and Murdoch (63). CO_2 production has a dissolving ability but to what degree the inorganic compounds are made soluble no references gave any answer.

c. The Influence of Phosphorus on Enzymes.

Pasteur in his famous research on fermentation was probably the first to realize the importance of enzymes. As has been investigated, the enzymes also need elements; (147) six have been so far claimed to be essential, one of this phosphorus.

The function of the enzymes seems to be to transform organic and inorganic substances for the production of energy and to build up within the cell vital products and metabolic activities. The enzymes may also function as dissolving and digesting agents in order to prepare and facilitate the entrance of nutrients into the cell. Furthermore they are designated as catalysts and activators in various hydrolytic and synthetic processes in the cells. There are a great number of enzymes in each higher plant; bacteria and fungi have less. Phosphatase (147) hydrolyses organic phosphate compounds, e. g. esters of phosphoric acid and organic alcohols or their derivatives. Other enzymes act synthetically upon a mixture of sugar and phosphates to form complex organic compounds. Phosphates have been found to be of importance in diastase activity. Englis and Gerber (34) observed an increase in diastase activity when acid phosphate in small amounts was added. Above a certain quantity, however, this activity decreased noticably below that of the control experiment.

Thus without the help of those enzymes the phosphorus ion could never complete its cycle in nature.

d. The Influence of Phosphorus upon Fermentation

The various types of fermentation are closely related with enzyme action of microorganisms. Phosphates, as has been found out up to date, largely modify the fermentation process. Alkaline phosphate may increase the rate of yeast fermentation to 20 times the normal (3,20). Harden and Young and Henley (3) observed that phosphates enter into organic union with hexose to form hexodiphosphate. They consider this as the first stage in the process of fermentation.

e. The Influence of Phosphorus on Plant Respiration

Maximov (80) called attention to the fact that there exists a close relation between alcoholic fermentation and anaerobic respiration. Anaerobic respiration is designated as a vital process in certain microorganisms to obtain energy. The work of Lyons (73) dealt with the study of the role of phosphate in anaerobic and aerobic respiration. In his first paper he confirmed Witzemann's (73) view that phosphorus acts as a catalyst for the oxidation of glucose in the presence or absence of hydrogen peroxide. The conclusion drawn from his discussion is that phosphates may accelerate aerobic respiration.

Neutral phosphate solutions considerably increase the rate of carbon dioxide production in Elodea. This increase lasted from one to six hours, then gradually decreased. A second rising curve of carbon dioxide production, Lyons found to take place following the death of the plant cell, oxidation appeared to go on for several hours under the influence of phosphate. In another paper Lyons (74) studied the influence of phosphate on potato oxidase. In anaerobic respiration the carbon dioxide production increased as in aerobic respiration where phosphate acts as a catalyst toward oxidase. Iron-catalysis influenced by phosphate as the promoter catalyst is confirmed by Lyons who based his view partially on his judgment of Willstatter's investigation on the presence of iron in respiratory enzymes. Moreover Lyons emphasized the importance of the carbon dioxide production from anaerobic respiration which is little less than that of aerobic respiration, if phosphate is present.

The experiments of Gregory (48) show that the rate of respiration varies greatly when phosphate is deficient. In the first four weeks it increased, from the fifth to the ninth it decreased and did rise again the next three weeks.

In a Russian article (65), the author found that the energy of respiration changed but little when different quantities of phosphate were added. A slight increase was observed at a change from a higher to a lower concentration of phosphate in the solution. An excess of phosphorus sometimes caused a weakening of the energy of respiration.

f. The Influence of Phosphorus upon Transpiration

Apparently little conclusive data have been collected to demonstrate that soil fertility is a factor affecting transpiration. As a fact it is seldom mentioned directly in textbooks of physiology. However, the experiments conducted by Burgerstein (16) and others, point out that transpiration is less intense in a fertile soil than in a depleted soil. No specific fertilizers were used in these studies. McCool (82) stated that in his experiments the transpiration stream in sugar beet leaves was less in the case where a complete fertilizer was used compared to that where either an incomplete fertilizer or phosphate alone was applied. Another experiment to the same effect has been conducted by Newton (87) on barley. He confirmed definitely the statement that an increased concentration of the culture solution in contrast to a weak nutrient solution decreased the rate of transpiration. The amount of water transpired in the case of the more concentrated solution varied from 30 to 60 per cent of the amount given off in the weak solutions. Raber (101) states in a general way that acids may accelerate, alkalies, retard transpiration and pointed out that specific salts may exercise such inhibitory and accelerating effects.

The Influence of Phosphorus upon Photosynthesis and Translocation

"Very little is known regarding the role of mineral nutrients in photosynthesis." Spoehr (124). However Treboux (124) found that very dilute solutions of 0.0001N acid phosphate may have a stimulating effect. Whether the mineral concentration in Evard's (35) experiments have been the same as that which Treboux used, was not determined. This might leave a possible explanation for the contradictory statements. Another experiment in favor of the view held by Treboux was shown by a Russian investigator (65) who observed that with increasing amounts of phosphorus the photosynthetic activity augmented in the same proportion. A special rise was not noticed at the transition from free phosphorus to a solution with minimum amount of it and also at insignificant changes of P ion concentrations.

The deficiency of nutrient salts has been studied by Briggs (11). He noticed that a lack of or deficiency in any of these elements, K, Mg, P and Fe decreased photosynthetic activity. His explanation is that the "reactive surface of the chloroplasts is reduced." Andre (128) believed that there is a definite ratio between organic magnesium, and phosphate to residual magnesium and phosphate in the leaves and that photosynthetic activity depends upon this ratio.

g. The Influence of Phosphorus upon Assimilation and Metabolism

Investigations concerning the influence of phosphorus on assimilation have been conducted mainly by analytical methods. It is thought that lipoids, which contain organic phosphorus compounds, play an important part in the synthetic process of the cell (80) but no clear facts have been brought out so far. Loew (72) believed that phosphorus was necessary in the assimilation of fats , because there is no cell division without phosphorus and that the absence of phospholipoids may have been the cause.

It is the view of Kraus (68) that large quantities of PO_4 may exist or accumulate as reserves within the plant. They may be metabolized when a deficit of phosphorus is created in the nutrient medium.

Nitrates in tomatoes grown without phosphates were not reduced according to Eckerson (33). When the inorganic phosphorus was used up, the tissues became more acid. An accumulation of nitrates resulted. Later the chloroplasts and phosphatides disintegrated and the amount of sugar increased. If phosphate was added in the earlier stages, the plant was able to recover, but if added at a late stage only a small percentage was brought back to normal growth. Gregory and Richard (48) who studied the effect of phosphorus deficiency upon assimilation in barley found that barley grown in phosphate deficient sand cultures caused a slightly subnormal assimilation under low or high light intensity.

Phytin was assimilated by oats and red clover according to Heck and Whiting (53). This organic compound proved to be an important source of phosphorus to oat plants, it was even more readily assimilated than phosphorus from inorganic forms. Red clover gave a similar result. Two to three times as much phosphorus was found in clover under those conditions.

The conversion of sugar into starch and cellulose was found to go on in the absence of phosphorus but apparently not from insoluble carbohydrates into soluble and available sugars as food (135).

Silicates proved to be of influence in an increased assimilation of phosphate, as has been shown by several workers (3). There even seems to be a direct relation between the amount of phosphoric acid taken up by the plant and the amount of water soluble silicate in the soil.

h. The Influence of Phosphorus upon the Plant as Affected by Light, Temperature and Water

Ecological factors influencing the relation of phosphates to the plant have been but recently emphasized. The law of minimum as applied by Liebig (8) in regard to plant nutrition has been modified by Mitscherlich and Lundegarth (8) as follows: The relative effect of a factor is so much greater , the more the factor is in the minimum compared to the other factors. The relative effect decreases permanently with increasing intensity of the factor and approaches in the maximum region the effect of the value zero. They formulated it in such a way that all the factors influencing vegetation may be included under that law. With this consideration in mind, light, temperature and water have been included in the list of factors affecting the phosphate relation to plant growth.

In some very recent experiments Magistris (76) studied the effect of light and temperature upon the recession of water soluble phosphatides. During or previously to dialysis an increase in permeability took place which was expressed in an increased exudation of organic phosphoric compounds. The causes for those changes in permeability of the border layers of the cell were sought in the effect of light, e. g. that light may have caused a decomposition of the unstable molecules. An increase in temperature was followed by a greater excretion of water soluble phosphatides. This process was found to be reversable according to temperature.

Alkali-ions and magnesium-ion increased the exudation of phosphatides, while the alkali earth metals restrained this exchange. In solutions of acids and bases exomosis of phosphatides was always greater than in pure water, the concentration of those solutions naturally modified the rate of exomosis.

The absorption of phosphorus was increased with an increasing concentration and with an increased period of light (65).

Gracanin and Nemec (46) stated in their discussion of the influence of diffused light upon phosphorus absorption from the soil that direct light was less effective than diffused light. During intense radiation, a lower resorption of phosphate took place than with diffuse light. The explanation given by those investigators was that direct light caused greater transpiration and evaporation which decreased the availability of phosphate in the soil. A decrease in temperature resulted in a decrease of phosphorus.

An increase in water requirement by phosphorus deficiency was reported by Dickson(25) and Sorauer (123).

i. The Influence of Phosphorus upon Seeds and Fruits

As previously mentioned phosphorus is attributed an important function in seed formation (108). Phosphorus is stored in the seed in compounds of proteins, fats, phosphatides and carbohydrates. Most of the experiments cited dealt with the negative side of the problem, e. g. the absence or deficiency of phosphorus in relation to seeds.

An extreme deficiency of phosphorus in the soil suppressed seed formation in a large percentage of grasses according to Henrici (55). As soon as fertilized, innumerable kinds of grasses under observation, developed seeds,provided sufficient water was present. Phosphorus deficiency was considered as the primary cause, shortage of water as a secondary factor in the lack of forming grass seeds. The great loss of water by transpiration was considered by Henrici as a result of the extremely low concentration of the phosphorus in the soil solution. Several other investigators reported the failure to form seeds in the absence of available phosphorus.

Bartz (123) believed that the falling off of plums at the time of stone formation was due to the deficiency of phosphorus. Soybeans failed to produce viable seed in the absence of phosphate according to experiments conducted by Ginsburg (43).

A deficiency of phosphorus in grains lowered the total dry weight (24). The ratio of grain to straw increased if phosphorus was insufficiently supplied. Likewise an increase in weight of individual kernel was noticed. It is understood, of course, that a relative shortage of phosphorus decreases the yield of any crop. The total phosphorus content of grain, was reported by Dickson (25) in another test, dropped to 46 per cent, that of straw to 10 per cent of the normal amount, only one-tenth of the normal amount of phosphorus was supplied.

The effect of phosphorus starvation on the composition of the tomato plant has been worked out by MacGillivray (75). The results obtained corroborate with the observations made by other research workers and may be summarized thus (75):

1. The percentage of phosphorus decreased in all parts of the plant.
2. A re-utilization of phosphorus is possible.
3. The regions of growth contain the highest percentage of phosphorus.
4. An insufficiency of phosphorus caused a decrease in the size of the fruit.
5. The dry weight of the plant trebled in two months; about half of the total phosphorus in the fruit

slowly recovered after two months of lack of phosphorus.
6. The absence of phosphorus effected a greater drop of blossoms.
7. The chlorophyll content in leaves decreased by a shortage of phosphorus.
8. More sugar accumulated and less starch was formed when phosphorus was wanting. The reverse was found to be true in the case of nitrogen.
9. The plant may absorb more phorphorus than needed for its growth and maturation.

Sorauer (123) reported a case where an excess of phosphorus was said to have brought about a greater percentage of sterile spikelets.

Recently, Morgan (185) advocated the tobacco plant as an indicator in studying nutritional deficiencies of soils on account of the sensitiveness and easily detectable symptoms of the plant.

j. The Influence of Phosphorus upon Seed Germination

The utilization of the stored food material of the seed includes an energetic process of bringing those reserve substances into proper combinations. The phosphate located in seeds is liberated from organic compounds into inorganic form during its translocation toward the growing points where it again enters into organic combinations. This was reported on *Phaseolus multiflorum* by Klein (90) and sustained by vonOhlen (90) in his experiments on soybeans. Moreover he stated that inorganic phosphorus was found in roots, except the root tips where only organic phosphorus could be detected. No organic phosphorus was discovered in the exhausted cotyledons but the inorganic salts were still present.

Turnips, vetch, rye, sunflower and grass seeds were studied by Gracanin (45) to determine the influence of phosphorus upon the release of energy. He reported that phosphoric acid had a stimulating effect upon the germinative energy of seeds and that it "awakened the germinative capacity" of seeds which otherwise would not have germinated. The effect of phosphorus as a stimulant accelerated the germination process and was more effective than HCl, H_2SO_4 or HNO_3. Even old oat and barley seeds showed a more favorable germinating effect in a solution of .1 to 1 per cent PO_4 concentration than in plain water. Buckwheat seed, however, gave negative results. The difficulty of obtaining accurate results from such phosphorus determinations is illustrated by experiments made by Pazler (95) who believes that sprouting seeds may even absorb phosphorus from glass sand.

An excess of phosphorus affected seed germination of corn and sugar beets unfavorably. Rost (106) found that an excess of superphosphate showed no deleterious effects on germinating corn seeds in the first year but the second year serious damage was done to the seedlings.

Placing the phosphate too near sugar beet seeds in dry soil retarded or even reduced germination (89).

k. The Influence of Phosphorus upon Development of Roots

Comparatively few exact data are accumulated on the subject of phosphorus in relation to root growth.

Perhaps the first man to observe root development influenced by phosphate was Sir John Lawes (108) when he wrote in 1847 on the apparent influence of superphosphate upon turnip roots. Solacolu (121) showed that Lupines had shorter roots, especially lateral roots, if placed in a nutrient solution deprived of phosphorus.

Soil structure has a profound influence upon root development. If a layer of clay is present in a more or less sandy soil, it may contain more nutrients. Lateral roots may thus invade that region to absorb them, in spite of sufficient water in another section with less clay.(61)

Lees (71) working with wheat found that the plants where the plot was treated with superphosphate showed an average of three inches increase over the untreated. A second reading later on showed a difference of 7 to 8 inches and the final check up demonstrated a length of 5 to 11 inches over those without phosphate. There existed great variations, however, in different varieties and in different plants.

Fruit trees wanting phosphate were reported by Wallace (149) to have small coarse roots with a little lateral, absorptive root system. The color of the root appearte brownish.

The experiments conducted by Turner (143, 144) on barley, wheat, cotton and corn illustrate a different relation and are somewhat in contrast to previous statements made. He found that the ratio between roots and tops decreased in the treated plots. An increase in the phosphate concentration did not stimulate root growth, neither in depth nor in lateral development, both indicated a retarding effect under given conditions. Cellular activities were not augmented. The investigator explained this decrease in the ratio of top to roots that "compounds or simple substances were formed in connection with photosynthetic activities in the tops, which are translocated to the roots and manifest themselves there by stimulation or storage effects."

Nygard (89) in studying phosphate deficiency of soils reported a very slight difference (0.07%) in the relation between top and root growth on sugar beets.

1. The Influence of Phosphorus upon Different Periods of Growth

Pember (96) studied the effect of phosphate upon growth when applied for only certain periods. When phosphate was added during the first eight weeks and none afterwards, barley, oats and wheat plants developed the best. Reducing the amount of phosphate to half a quantity, depressed growth and reduced phosphorus absorption. In a later experiment, Pember (97) found that applying small amounts of phosphate, during different periods of growth, effected the plant equally well as given during the early part. This was not the case in Brenchley's experiment as later mentioned. The plants grown in solutions with limiting amounts of phosphorus absorbed this element most vigorously during the second half of a seventeen-week period of growth (9 to 13 weeks).

The results obtained by Brenchley (10) do not entirely agree with those of Pember. Plants deprived of phosphorus after four weeks were said to show no decrease in any functional activity, while Brenchley found six weeks the minimum time. Six week's growth in a complete solution insured normal development of barley plants, although phosphate was omitted afterwards. Shorter initial periods of phosphate supply seriously depressed growth, the number of tillers, ears and grain was less, dry weight decreased. Phosphate withheld the first four weeks prohibited the heading of the plant, but tillers were not affected. Brenchley thought that the discrepancies in Pember's experiment were due to the fact that he used well water which had traces of phosphate and the tillers removed from the plants permitted the main shoot to develop. The experiments conducted by Gericke (41) on wheat bring out again the importance of having a sufficient quantity of phosphate at hand in the earliest period of the life of the plant. According to Gericke the first four weeks were adequate enough to supply the phosphate need for the plant if afterwards it was removed.

Thomas (138) working on _Pyrus malus_ found that contrary to Lagatu's report, an omission of either nitrogen, phosphorus or K from a nutrient treatment always resulted in a decreased absorption of the particular element. Wallace (149) reported a decrease in absorption of phosphorus if it was deficient in the soil. It is pointed out by Thomas (138) and Wallace (149) that the differences in their experiments might have been due to the other factors which were difficult to control.

A rapid development of barley, according to Russell (108), due to phosphate application, saved the crop from the larvae of the gout fly which attacks the plant during the periods before heading. If those plants matured a little earlier, the damage done by those larvae appeared to be much less.

m. <u>The Influence of Phosphorus upon Stems, Stalks and Culms</u>

Solacolu (121) noticed that the influence of phosphorus shortage in nutrient solutions affected the anatomical structure of Lupinus very little.

An insufficient quantity of the same element showed variations in the anatomy of the culms of barley. However the cells were larger, with thinner walls. The tissue appeared to be more spongy and brittle while under normal conditions the tissues were more firm with smaller cells and thicker walls. These experiments were in agreement with those made by Guffroy, Lienau, Kissel and others as reported by Doerrell (28). It needs to be kept in mind that a phosphorus deficiency gives a relative nitrogen excess and in that particular soil, tests showed a high content of potassium.

Hoagland (56) in discussing artificial culture solutions pointed out the many factors influencing phosphate concentration and absorption (soil reaction, buffer power, colloidal content of the soil, etc.).

An excess of phosphoric acid in the solution gave small and frequently compressed cell forms in potato stems as indicated by the experiments of Huxdorff (58). The collenchyma material on stems and petiole with an excess of phosphorus caused the cells to be somewhat irregularly arranged. On the tubers a one-sided phosphate fertilization increased the cortical cell layer.

Anatomical observations made by Volk and Tiemann (113, 114, 115) on various herbaceous and woody dicotyledon stems showed, by a lack or insufficient quantity of phosphorus, a smaller development of phloem and xylem. Phosphorus excess plants, due to the rapid development early in the season ultimately caused a nitrogen deficiency which showed similar signs of derangement in the plant structure as phosphorus.

n. The Influence of Phosphorus upon Leaves.

A great amount of work has been done in the study of the effect of phosphorus upon leaves. In most of the experiments conducted a shortage of phosphorus was studied. Wallace (149) observed that phosphorus-starvation on fruit trees was followed by a delay and restriction in the opening of the leaf buds and owing to the death of lateral buds the flowers were seriously affected. A smaller amount of leaves was produced, terminal leaves may only develop. On the leaves themselves appeared bronzed and purple tints accompanied with brownish spots. The first season no such effects were found but the next summer, the lack of phosphorus became obvious. The leaves dropped in June and no further sign of growth was noticed that year. The fruits of such trees were found to have poor keeping quality.

The parenchyma layer, of leaves of Lupinus deprived of phosphorus showed a smaller amount of that tissue.

Eichen (123) reported an interesting experiment with oak plants. They were grown for three years in solutions without phosphorus. The leaves remained dark green, while in other species they changed to dark orange or red. Pine needles turned to a dull violet in the absence of phosphorus according to Moller (123). The same results were reported by Busgen (17) . Vater (17) suggested that this discoloration may possibly be due to anthocyanin formation in an alkaline reaction. An insufficient amount of phosphorus made brown to purplish spots appear on the leaves of beans and peas. An excess of this element seemed to have no typical injurious effect as observed by Jacob (59). Tobacco leaves turned first yellow, later brown, according to Dreyspring and Krugel (32), if phosphorus was wanting. The leaves remained greenish brown. In general such plants lacking phosphorus soon dried up.

Kruger and Wimmer (69) reported their results on the phosphorus deficiency on potatoes, red clover, oats and tobacco which fairly well agree in the essentials with the previous authors mentioned. Volk and Tiemann (113, 114) found the following results due to a shortage of phosphorus

The leaves were smaller per leaf area. The margins may show deeper incisions. The thickening of leaves was less, due to a shortening of the palisade cells. Similar results were obtained in tests with Monocotyledons.

In another paper, Schaffnit and Volk (114, 115), did draw the following conclusions, based on studies of phosphorus deficiency in 32 different tribes, that this lack or shortage of phosphorus had similar effects, both in monocots and dicots, upon the changes in leaf color, appearance of necrotic area and the typical changes of the "habitation representation" (Habitationsbild) which gives an applicable criterion concerning the nutritional condition of the plant. Phosphorus deficiency is expressed in delicate, small plant forms. The delicate structure of plants short on phosphorus is anatomically correlated with a different development of the supporting tissue.

The wood elements of the dicotyledons and the sclerenchymatous elements of the monocots were suppressed.

Anthocyanin formation was believed to have taken place due to a shortage of phosphorus which normally would not have taken place, according to the investigators.

Volk and Tiemann(113) found in their work carried out on peach seedlings that an excess of phosphorus in the leaves made the leaves fall during the months of September and October. A deficiency of phosphorus seemed to have had the opposite effect. The leaves were still green on December 15. The surprising thing was, however, to be noticed next spring, when the buds of those seedlings with a deficiency of phosphorus opened first. The importance of proper nutrition in respect to frost injury is emphasized by the same investigators.

The influence of phosphorus deficiency upon the effect of fungi infection on leaves will be taken up under the heading of plant diseases.

o. <u>The Influence of Phosphorus upon Flower Formation</u>

In several instances experiments have been carried out to determine whether flower formation is in any way influenced by phosphate relations. Schaffnit (113) found Chrysanthemum flowers were much smaller, the number of flowers was only one-eighth of the check plants, if an extreme shortage of phosphorus was allowed to take place. It was also reported that phosphorus deficiency may cause an increased formation of pistillate flowers over staminate flowers. Staminate flowers showed no branching and at the base of the tassels pistillate fruit structures developed at the same time. This phenomenon was found now and then in normal plants, but in phosphorus deficient plants it was much more frequent.

p. The Influence of Phosphorus upon Earliness and Maturity

The observation made by Russell (108) on barley attacked by the gout fly has been mentioned, and that by Schaffnit (113) on peach seedlings. Little exact data has been found in literature which clearly stated the influence of phosphate upon earliness compared to other treatments. The statement thus frequently made that phosphate hastens maturity of fruits and seeds therefore needs further research.

Noll (88) working with cereals, cabbage and cotton found that phosphate fertilizers induced an earlier ripening of the crops grown on soils deficient in phosphorus . A confirmation of those results obtained by Noll was given by Dickson (24, 25) in his experiments, in so far that a deficiency of phosphorus , potassium or nitrogen showed a shortened period of development while by a shortage of Ca or Mg the period was lengthened. The results of Teakle's (134) experiment in soil cultures do not support the view that phosphate hastens maturity.

q. The Influence of Phosphorus as Affected by the Soil Media, pH Value, Sterilization, etc.

Since the plant uses the soil as substrata it is of great importance to understand the factors which influence phosphate absorption and plant nutrition. The role of microorganisms has already been discussed.

Phosphates need to be in an available, soluble form in order to be of any value to plants.

Sterilization of a soil may first have an unfavorable influence upon the availability of minerals, microbiological activities but within a short period an increased activity of soil microflora takes place which may stimulate plant growth (62, 66, 98).

Soil reaction is one of the most important factors in the relation to plant nutrition. Davidson (22) found that wheat seedlings absorbed more phosphorus from soils have an initial H-ion concentration of 5 or less. A similar experiment carried out by Tidmore (140) confirms the statement made by Davidson (22) that acid soils are giving off more phosphoric acid to the plant. Indication of the physiological availability depends upon the pH value of the medium. An excess of phosphorus absorbed from the solution was found in the tops of the seedlings. The roots of plants absorbing phosphorus from neutral solutions contained more than those from the acid solution.

In contrast to the above stated experiments, is the one by Domontovitch (30). According to him, the pH of the nutrient solution had little influence upon the rapidity of absorption of PO_4 .

Burd (15) showed that the phosphate concentration may be increased to a certain pH, then it declined or even may precipitate if the reaction becomes too acid. The buffer power of the soil has a great influence upon the soil reaction. The full significance of phosphorus in the ionic equilibrium of the soil solution has not been fully understood, states McKibbin (83). The fact brought out by Teakle (133) again demonstrates that the solubility of various phosphates at various reactions under different treatments is not always the same. Thus what may be of benefit in a calcareous soil under different moisture relations may be of disadvantage in an acid or neutral soil.

Parker (92) found that liming increased the phosphorus content of the soil solution and soil extract from a soil receiving acid phosphate or basig slag. This holds true only under given conditions.

The availability of acid phosphates was shown by Stoklasa (129) to decrease rapidly. It was observed that within 30 to 50 days according to the kind of phosphate (mono- di- or tricalcium-phosphate or in the form of orthophosphoric acid) applied, it became water-insoluble.

Truog (142) thinks that plants containing a relatively high calcium oxide content have a relatively high feeding power. He explains this by the law of mass action and chemical equilibrium. Based upon the experiment of Czapek and other, Truog (142) believes that CO_2 and water are the only important agents to bring mineral material into available form. Chemotropism as an active agent toward the root hairs has been advanced as a theory concerning the factors influencing phosphorus absorption.

Parker (92 and Schreiner (117) and others showed in their experiments that a considerable amount of phosphate in the soil is found in organic form which undergoes a different chemical process of decomposition than the inorganic compounds. Thus the absorptive power of organic phosphate is much lower than inorganic. Pierre and Parker (100) worked on similar questions and in general agreed with the above mentioned authors.

r. The Influence of Phosphorus upon Animal Nutrition

The analysis of various agricultural plants, plus other factors observed, led to the supposition that a lack of phosphorus and Ca in the plant was closely related with diseases of cattle known as "brittle bone", chewing bone, (osteomalacia), Pica in America and Europe, or lanziekte in South Africa. Prominent investigators in this field of research were Theiler (136), Ritter (104), Scott (118) and a great number of others (104, 118).

The experiments carried out so far by these scientists generally agree that an extreme shortage of phosphorus and other factors causes serious disturbances and abnormalities in animal nutrition.

s. The Influence of Phosphorus on Plant Diseases: Their Susceptibility and Resistance

Proper nutrition of plants was thought to have an influence upon their susceptibility or resistance to fungus attack. Up to the present time there is no clear conception as to the efficiency of fertilizers in protecting or favoring parasitic diseases. There exists a great variation in different plants and fungi in their requirement of nutrients, water, pH value and temperature. The genetic factors have been here omitted and only the above mentioned factors are considered in this discussion.

The stage of development plays an important role in the life of the plant when infected with fungi. The study of chemical resistance in cells just recently received increased attention. It is to be expected that many new important facts will be brought out in studying this phase of plant resistance.

Maze (81) thought that a natural immunity in a cell may be established in a few days by an active elaboration of the organic-mineral substances due to an intense insolation and a raised temperature. Those rather new experiments need further investigation.

Verticillium wilt of potatoes was found by Martin (78) to be more destructive on underfed plants than to those treated with a properly balanced nutrition. He suggested, to maintain cell sap acidity, an application of phosphates instead too much nitrogen fertilizers.

Neal (86) working on cotton wilt in relation to nutritional problems was unable to find a definite, uniform relation between nutrition and the development of cotton wilt. The pots receiving an excess of potassium and phosphate showed varied vascular discoloration in the plants. Lateral root discoloration was found in plants where phosphorus was omitted. In the latter case the number of plants infected with wilt was 20 per cent less than in the phosphorus surplus. Discrepancies in the checks and on other field plots prohibited giving a conclusive statement.

The proper application and use of fertilizers was found by Haenseler (50) to delay and reduce injurious effects of pea root rot. Superphosphate in this instance proved to be not as effective as nitrate sulfate and chloride-fertilizers.

Benes (6) observed that phosphoric acid had completely checked mildew on potatoes whereas no treatment or an application of sulfur showed no effects.

Bernastky (7) described a chlorosis of grapes, which he thinks was the result of an application of alkaline phosphate while acid phosphate had a curative effect.

An increase in tip burn and mildew of cabbage is reported by Chupp (18). He found, that if nitrogen and potassium were deficient or lacking an application of super-phosphate increased tip burn. The experiments reported were not completed at the time of that report and no further results were obtained in literature on this subject.

The effect of one-tenth of the normal amount of phosphate in an acid solution reduced the infection of Gibberella saubinetti on corn by 37.8 per cent against 10.5 per cent in the alkaline solution, according to Hoffer and Trost (57) who also found that the injuries from Gibberella differed in a normal solution.

Miles (84) studied the influence of phosphate upon the susceptibility of blighted potatoes to disease. In all but one case, the per cent infection increased with an increase in the amount of superphosphate added as against that where no phosphate was added, but the total per cent of plants attacked by other diseases was much higher. An application of gypsum on some plots without phosphate added, had a deleterious effect upon the health of the

the plant.

The writer's conclusion drawn from those tests were that with gradual increase of compound manurial fertilizers the degree of immunity, on the part of the plant, was inclined to be higher than without fertilizers.

The quantities of an excess of ammonium sulfate supplied had a beneficial effect upon the health of the potato plant provided potassium was adequately supplied. This experiment is in contradiction to the views held by Stakeman (125), Spinks (84) and others that an excess of $(NH_4)_2SO_4$ favored a greater susceptibility in plants to disease.

Stakeman and Aamodt (125) studying the effect of fertilizers in relation to stem rust of wheat concluded that if needed, phosphate should be added and an excess of nitrogen was indirectly conducive to stem rust.

The influence of the stage of the development upon susceptibility to stem rust was worked out by Gassner (38). He did not find a definite influence of phosphate deficiency or excess upon resistance or susceptibility of cereals to rust. In two varieties of club wheat little or no Puccinia graminis occurred on a plot fertilized with phosphate at the time of seeding. Gassner emphasized that it was more important that the plants had reached a certain stage of development than the amount of phosphate applied to a soil. Doak (26) studying wheat rust in relation to mineral nutrition, noticed that an excess of phosphorus decreased the per cent of infected points by Uredinia, it decreased chlorosis in both the susceptible and more or less susceptible varieties. In another group of varieties, phosphorus surplus did not prevent the formation of primary uredinia, but it retarded or prevented the development of secondary uredinia.

An unbalanced fertilizer application, e. g. without phosphate, according to Janssen (60) caused potatoes to be more susceptible to Phytophtora infestans.

An excess of phosphate brought about an increase of 40 to 72 per cent in more diseased plants than when applied normally.

Cormany (19) found that curly top of sugar beets was influenced by fertilizers. The symptoms of this disease developed slower in fertilized plots than in the untreated plots, which also greatly influenced the yield.

Schaffnit and Volk (114, 115) made detailed studies of the influence of various nutritional treatments upon the susceptibility of ten different species from ten different fungi. They found that the manner of nutrition has a great influence upon the degree of susceptibility of plants to fungi. Mostly herbaceous plants were used. Phosphorus nutrition as a whole in most cases had no definite preventive power. Phosphorus deficiency, however, played an important role in the susceptibility of plants to disease. In all cases a phosphorus shortage decreased the severity of infection of the fungi. In other experiments no fructification of the fungi occurred on infected plants. The lesions on leaves caused by fungual infection usually were much smaller than the other treated plots.

The phosphorus surplus plants were in many instances less susceptible if the infection took place after the completion of the main development of the plant, in cereals shortly before heading. Infections at earlier stages did not show any differences between normally developed plants and those fed with unbalanced solutions.

The ions phosphate and potassium showed higher resistance to fungiwhich is explained by Schaffnit (114) due to the relative nitrogen deficiency which was almost as resistant as phosphorus shortage.

With an increasing application of amounts of the deficient nutrients, in this case, phosphorus and nitrogen, the percentage of infection became greater. The resistance of such plants, deficient in one element or in another is attributed partially to the chemical composition of the cells, the food supply for fungi and the mechanical protection of the tissues as influenced by various treatments. A later study made on woody dicotyledons in general agreed with the results obtained on the herbaceous plants.

t. The Influence of Phosphate upon Sugar Beets

The mineral requirement of sugar beets is studied by greenhouse and field experiments. The sand-peat method, developed by Hellriegel (54) is to be preferred over the water culture because it approaches more nearly the normal conditions of the soil, although the shortcomings are many. Phosphate requirements of beets differ with soil, climate and quality of beets and crop rotation. The amount required for a good crop per acre has been established by various workers from 50 to 70 kg of phosphoric acid.

Jean and Weaver (61), Andrews (1) and others found that moisture has a great influence upon root development. The depth beet roots penetrated was dependent upon the amount of available moisture, the soil structure and soil fertility. Roots irrigated compared to dry land conditions were from one to several feet longer than without irrigation. But gradually the latter seemed to penetrate a little deeper so that in the final end the depth was less marked than the increase in diameter of the root.

Wilfarth, Romer and Wimmer (153) in 1904 determined that about 1 gr. of P_2O_5 per beet was considered to be about the normal and sufficient amount for a normal crop under the given conditions. The amount of phosphate absorbed was found to be in close relation with the amount of phosphorus supplied to the plant. An insufficient quantity of phosphate resulted in a decrease in the number of leaves which noramlly averaged around fifty as well as an enormous decrease in yield.

The influence of pH value upon the fibrous rootlets and extremely fine root structures was said to be visibly deteriated if the layers of soils were acid (49).'

Nygard (89) working on phosphorus deficiency observed that no "blackheart" was detected in fields treated with phosphate. The yield increase was five-fold. Similar results in the Larimer County gave even higher figures. (Six to eight times as much in treated fields reported by farmers.) Similar results of the sugar company's investigations are reported.

The sugar content of beets was very little affected when phosphorus deficient soil was the medium of the beets grown. Nygard (89) gives 0.16 per cent decrease. Similar reports as to the slight changes induced by phosphate deficient soils upon the sugar content of beets have been read in German publications. According to

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'(Abstract of a German publication which appeared just before finishing this paper so that the original article could not be obtained.)

Schaffnit (115) a phosphorus deficiency of the soil caused a delay in maturity.

Water requirements of beets vary considerable. The figures given by over 10 workers vary from 268 to 497 kg of water per kg dry substance produced (105). Those differences may be partially explained by differences in climate, soil fertility and individual differences in the beets.

Diseases in relation to phosphate supply have frequently been studied. Stormer (131) in 1909 attributed false mildews and Pythium root rot to some extent to low phosphorus and Ca contents. The study of the so-called "blight" in America, "heart and dry root" in Europe, has been going on in Germany for more than 30 years and still no definite uniform results have been obtained.

There seemed to be a number of factors influencing this disease, any one of those factors may be more dominant in one section of the country than in another. Because it was thought that the influence of fertilizers perhaps may bring a solution to the problem, Gaumann (39) experimented on three varieties with 15 different fertilizer combinations. Only one combination consistently decreased the percentage of diseased beets, namely Thomas slag, sodium nitrate and potassium carbonate. An alkali reaction above 7.8 pH favored the disease. Nitrogen deficiency was more harmful than normal quantities. The presence of *Phoma betae* either at the initial stage or later on gave no definite conclusion to its importance in producing the disease. Richard and Tompkins (103) considered three main factors influencing blight: the effect on tillage, the soil fertility and moisture relations.

METHODS OF INVESTIGATION

INTRODUCTION

In Colorado and adjacent states a new disease, commonly called "blackheart", had been seriously affecting the yields of sugar beets for several years. Later it became known that where a sufficient amount of available phosphate was in the soil the symptoms of blackheart did not develop. Upon the investigations conducted by agriculturists of some sugar companies it was disclosed that soils deficient in available phosphate showed the highest percentage of blackheart. The close relations between the symptoms of "blackheart" and of "late blight" of beets and the uncertainty which exists as to the actual causal agents of these disease, make it very difficult to ascribe the underlying causes to one disease or another. The succeeding experiment and discussion covers the following phases:

1. What kind of microorganisms are connected with blackheart?
2. Is there a consistency of one or several organisms present?
3. Does the statement: "phosphate increases lateral root development" hold true in the case of sugar beets when grown on soil deficient in phosphorus?

The experiment was divided into two parts, first, "Fungi in relation to blackheart", and secondly, "Root development of sugar beets under various fertilizer treatments." In the time allotted it was possible to study only a few phases of this disease and the effects of phosphate on beet growth.

SYMPTOMS OF BLACKHEART

Blackheart, when seriously affecting sugar beets, influences primarily the leaves and roots. The petioles are seldom affected.

The first signs of this disease become apparent in the spring, if an extreme phosphorus shortage exists, in a reduced, slow growth, which may go on at that rate during the whole season and produce a beet of small size with smaller leaves and less in number. (Figure 1) If phosphorus deficiency affects the beets in a later stage of development, little increase in leaf area and diameter of the beets takes place. The leaves may turn to a dull dark greenish blue color. The healthy lusturous appearance of the leaves gradually changes into a dull, tarnished tinge. Along with these symptoms, localized or widespread, areas of brownish color may show on the leaves. They may originate on the margin or between the veins, and eventually some cover almost the whole leaf area leaving the green veins in a marked contrast to the drying leaf. (Figures 2, 3 and 4) There is a tendency of the leaves and petioles to lie flatly on the ground (Figure 5). The nature and

Fig. 1. Sugar beet field in Wellington (September, 1930). Effect of phosphorus deficiency upon beets. At the left, fertilized,with superphosphate, at the right, untreated.

Fig. 2. Effect of "blackheart" upon sugar beet leaf. Necrotic areas beginning from the margin.

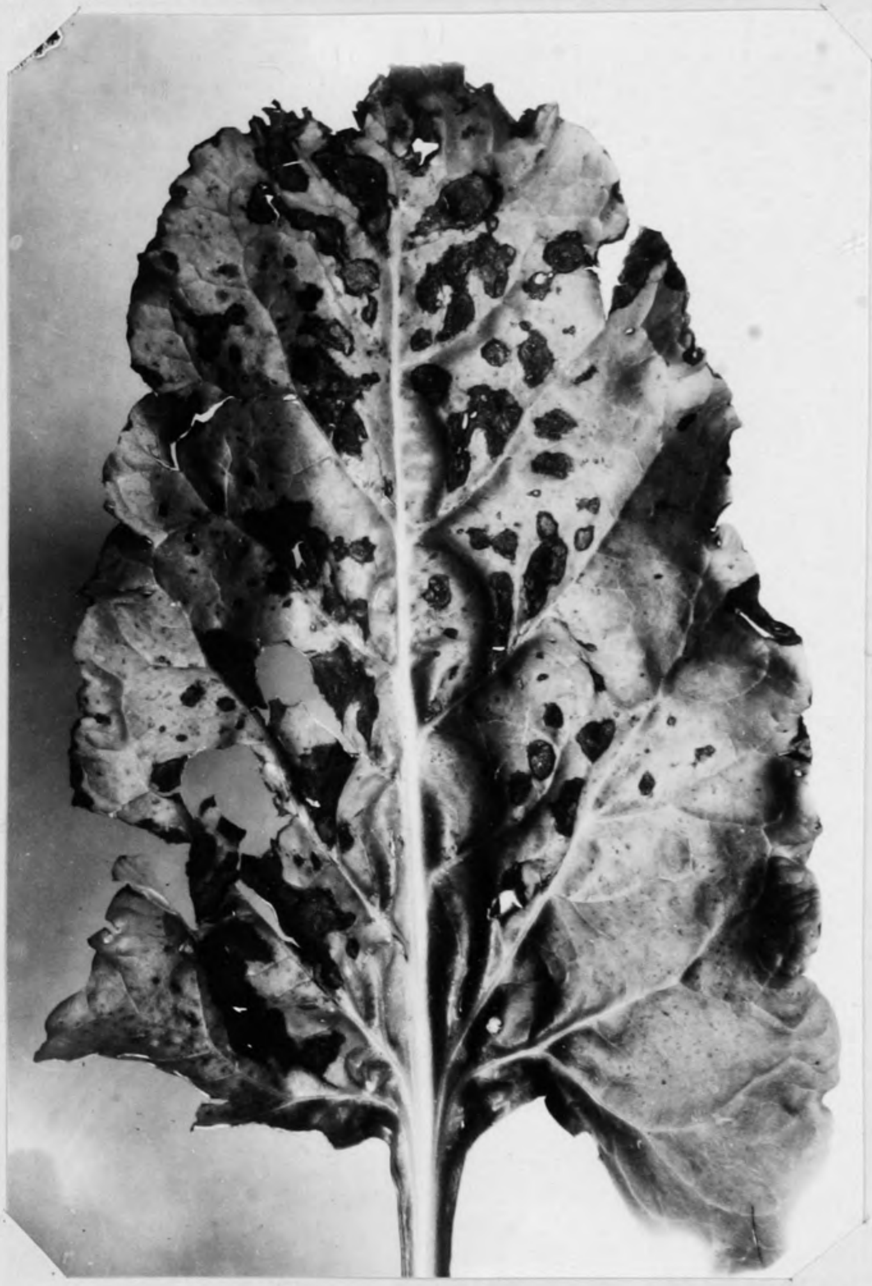

Fig. 3. Sugar beet leaf affected by "blackheart". Localized spots beginning in the middle of the leaf.

Fig. 4. Sugar beet leaf affected by "blackheart" showing more advanced stage.

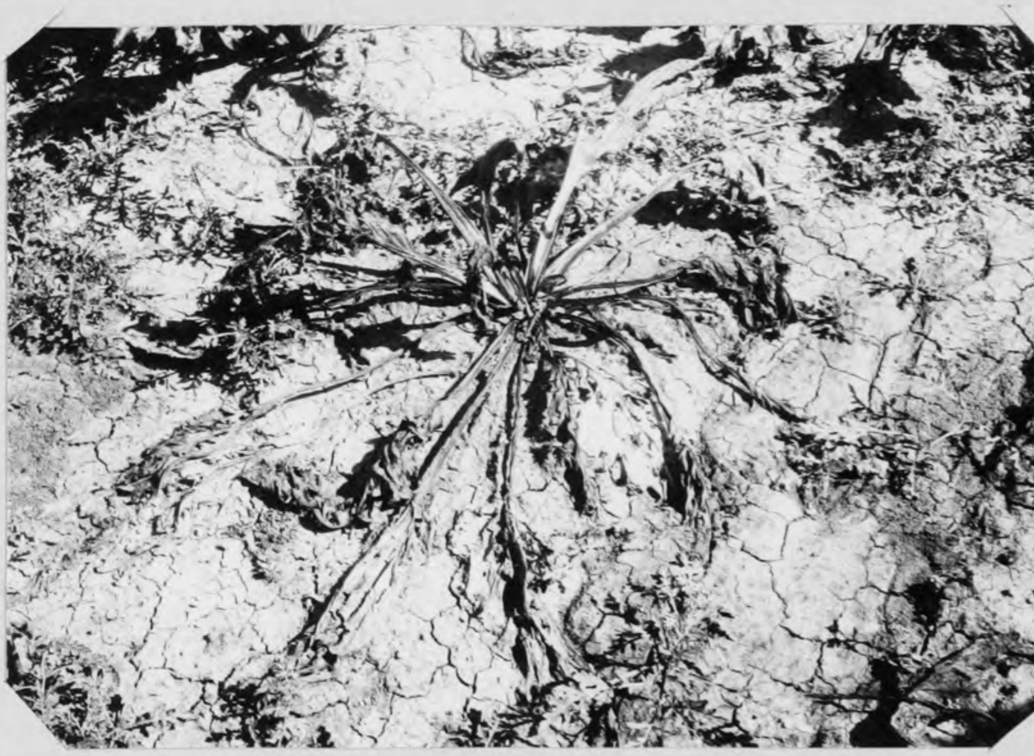

Fig. 5. The effect of "blackheart" upon the position of petiole in an advanced stage upon sugar beet.

extent of these leaf distortions are subject to great many variations due to the stage of the development of the beet, the mineral supply in the soil, the water relations and the activities of the microorganisms.

No pronounced effects have been observed on petioles except a less firm structure to uphold the leaf when lying flatly on the ground. Somewhat bent or twisted petioles are reported by Kruger and Wimmer (69). Roemer (105) states that petioles never have those spots characteristic of the leaves.

The roots are influenced, if a greater deficiency of phosphorus occurs in the soil at an earlier stage. The rate of development of the roots becomes retarded and a beet of only medium size is formed. Coarse roots with few lateral and fibrous roots are often associated with phosphorus deficiency. Dark lesions appear on the surface of the root, and the internal vascular system is discolored. Other beets again, may show no evidence of tissue destruction of the presence of fungi (Figs.6,7,and 8). There is some question as to whether these symptoms on leaves, petioles and roots here described are due entirely to phosphorus deficiency or to unfavorable water relation and other factors as suggested by Richard and Tompkins (103) who discuss in a recent paper heart- and dry-rot in Europe and their own investigations on "late blight of sugar beets".

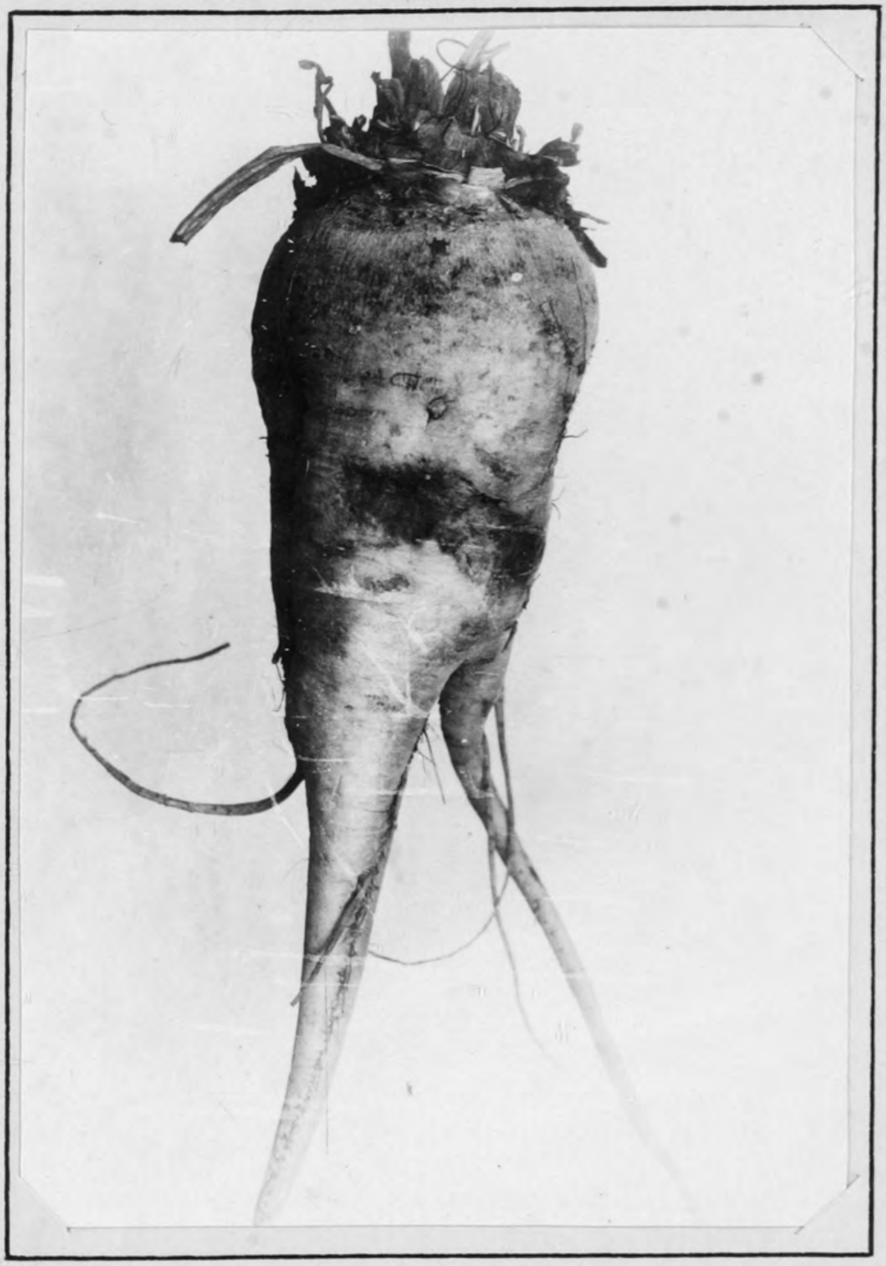

Fig. 6. Effect of "blackheart" and
subsequent fungous attack.
Localized spot.

Fig. 7. Effect of "blackheart" on root followed by fungi invasion.

Fig. 8. Advanced stage of effect of fungi after "blackheart" disease on the beet root.

ISOLATION OF FUNGI

During the months of September and October the whole beets were brought into the laboratory. Discolored tissues were surface treated with mercuric chloride and sterile water and plated as were also apparently normal inside tissues. Common potato dextrose agar was used as substrata. With leaves and petioles the same method was used as with tissues of the roots.

GROWING THE BEETS IN THE GREENHOUSE

In order to give the roots a fair range of development, wooden boxes were made up. The size of these boxes was 36 x 24 x 18 inches. The bottom was punctured with 6 to 8 holes to permit sufficient drainage. The front side, e. g. the 24 inch width, was closed with three boards, each 12 inches wide, which were screwed on to the box in order to open up the box readily. Twelve of the boxes were filled with soil as follows:

3 "untreated soil"

3 "sterilized soil"

3 "75lbs. of 46 per cent superphosphate per acre"

3 "150lbs. of 46 per cent superphosphate per acre"

The soil was hauled in onDecember 22, 1930 from Mr. Muntz's farm located about two miles west of Wellington, Colorado. In order to gain a soil of more or less uniform phosphorus deficiency, the depth at which the sample was taken varied from 12 to 24 inches. Each box contained close to 450 pounds of soil. In the case of the untreated soil the box was filled about two to three inches with cinder and sand at the bottom and on top of it was placed the soil. The sterilized soil had been treated for 30 minutes with steam in the greenhouse; three fillings were made for each box and for each filling the steam applied. The two groups of boxes which were to contain some fertilizers were filled up to six inches from the top. About 100 pounds of soil were mixed with 1.8 gr. of superphosphate in the case of the "75 pound treatment" for each box and 3.8 gr. in the "150 pound treatment".

The soil was allowed to settle several days. The seed was a "selfed line", obtained from Dr. D. Stewart of the U. S. Dept. of Agr. Four rows were planted lengthwise through the soil in the boxes so that each of the four intended diggings would leave the rest of the beets, still growing, toward the rear of the boxes.

The water was uniformly applied to each box. The amount of water added was regulated according to the moisture content of the soil.

At the time of the first excavation of the roots it was necessary to remove only one board, because the roots were comparatively small. Later, another board was taken off and the rest of the soil dug out. The soil was carefully removed from the roots by use of a slender pick which loosened the soil little by little. Difficulties were encountered in breaking up some of the clods or heavy particles without injuring the finer roots, and in preventing the rest of the soil to loosing and to sliding down. Careful drawings were made of natural size of all roots dug and selected. From these were selected typical roots for photographic reproduction.

EXPERIMENTAL DATA

Fungi in relation to blackheart -

Platings were made from two hundred and fifty beet roots affected by "blackheart" and the percentage of fungus infection determined. The same was done with the fungi isolated on the leaves and stems. All bacteria were omitted from this study, only the proportion of them was included in the data. The following genera of fungi were determined from lesions and discolored regions of "blackheart" beets, petioles and leaves. Time did not permit of identification of all the species isolated.

(a) On leaves:
- Alternaria
- Fusarium
- Phoma

(b) On petioles:
- Altenaria
- Fusarium

(c) On roots:

Altenaria	Phoma	Penicillium
Fusarium	Rhizoctonia	Aspergillus

(c) On roots: (continued)
Rhizopus and Pythium.

Bacteria were found most dominant on the roots. They composed about one-fourth of all the organisms isolated. Phoma was represented with one-sixth, Fusarium one-eighth, Alternaria one-fifth, Rhizoctonia one-twelfth of the fungi isolated, with a few other fungi with less than two per cent. About 15 per cent of the platings made showed no fungus growth.

On the leaves and petioles Alternaria was the most common fungus. It amounted to two-thirds in leaves and two-fifths on the petioles. Next in frequency came Fusarium and Phoma.

This brief survey and the concensus of the literature does not suggest a consistant relationship between so-called "Black heart" and microorganisms. The kind of soil flora, soil conditions, climate, etc., may vary with the time of examination of the beets. A recent publication by Richard and Tompkin on "Late Blight" of sugar beets further shows the complexity of the factors involved in this problem of unbalanced nutrient solution. These investigators summarized and confirmed in general the results obtained so far in Europe on late blight that water relation, soil reaction, (pH value), soil fertility and possibly attacks of _Phoma betae_, etc., are among the main factors causing this disease. Because several factors above indicated are also found in "blackheart" and the symptoms of both diseases have many things in common, it seems probable that a phosphorus deficiency was the initial cause for the symptoms as ascribed to "blackheart" but that also other factors, such as water relations , high lime content, soil reaction and subsequent invasion by various fungi, etc., played an important part in bringing about "blackheart" and later on "late blight". The presence of such a great number of fungi and bacteria, which has nowhere been reported before, may be explained by the lateness of the season when the beets were examined. (Fifteenth of September to fifteenth of October.)

THE ANALYSIS OF THE SOIL

As the problem itself suggests, the relation of the plant to the soil made a soil analysis indispensable. Soil relations rank next in importance to the water relations considered from the standpoint of "blackheart" and "late blight". The following analysis of the soil was carried out.

a. Phosphorus determination
   (1) Total phosphorus
   (2) Winogradsky test
   (3) Colorimetric, method Dirke

b. Nitrogen determination
   (1) Total nitrogen amount
   (2) Nitrate nitrogen amount

c. Calcium carbonate determination

d. Hydrogen-ion determination

e. Mechanical analysis

Soil Analyses

1. (a) The total phosphorus content of the soil was found to be .123% P_2O_5

(b) The Colorimetric determination of available phosphorus was 1.24 p.p.m.

(c) The Winogradski test showed ready response to phosphate treatment.

2. (a) The total N content was 0.083%

Nitrate N 16 p.p.m.

3. Calcium carbonate 8.5%

4. The H-ion concentration of the soil was 8 to 8.5pH

5. The mechanical analysis showed:

Sand	36.16%	(1 - 0.05 mm.)
Silt	18.2 %	(0.005 - 0.0005 mm)
Clay	45.64%	(0.0005-.0002 mm)
Finer clay	40.4	(0.0002-0.000 mm)

This classifies this soil as a heavy clay soil.

The conclusion drawn from the soil analyses made is that the soil is distinctly alkaline. It has a high % of lime carbonate.

The available phosphorus is very deficient. The condition of this soil suggests these factors as predisposing to "Blackheart" and "Late Blight" of sugarbeets.

The moisture content of the soil in the boxes varied from 16 per cent to 20 per cent, according to determinations made during the different periods of the experiments.

The temperature in the greenhouse during the day varied between 24° C. to 32° C. During the night the temperature was 15° to 20° C. The actual loss of water per day from an atmometer during March was 17 cc. April 1 to 14, and 28 cc.

THE ROOT AND TOP DEVELOPMENT OF THE BEETS

Four days after planting in the greenhouse the seed had come up in a fairly uniform manner. About two weeks after planting "damping off" was observed on all the unsterilized soil. The fungi isolated from a few seedlings were Pythium deBaryanum, Fusaria species and Phoma betae. The plants in the untreated soil were the most seriously affected and showed the least resistance to recovery from the fungual attack. The other two groups showed a marked ability to recover and overcome the injury by a more rapid growth which resulted in a callus growth of the infected areas on the root. The beets in the sterilized soil did grow in a uniform manner.

The first beets were taken out four weeks after planting. The roots excavated showed a marked difference in their development of lateral roots. In figures 9 to 16 are shown the root development of the beets at different periods of growth under different soil conditions. It will be noted in Fig. 9, which represents the first 28 days of growth, that the length of roots did not differ very much but the formation of a root system for rapid water and mineral absorption developed much faster in the case of the treated soil. Little difference, if any, could be noticed between the two soils except that the roots of the 150 pound treatment had a few more lateral roots developed as clearly seen in Fig. 6, C and D. This brings out the fact which has been often pointed out, that phosphorus deficiency externally may not come to the attention of the investigator until later in the growing season because a reasonable amount of that mineral is present to start with. The root development of the beets in the sterilized soil was about the same as that of the untreated.(See Fig. 6B) Due to the effect of sterilization of the soils, the chemical reaction had to become readjusted and the lack of microbiological activities was, to a certain degree, another influential factor in bringing about somewhat different results than in the untreated soil.

The period of growth during the next 28 days brought no remarkable changes as indicated by Figures 10 and 11. The plants of the untreated soil were still suffering from "damping off" and recovered but slowly

A B C D

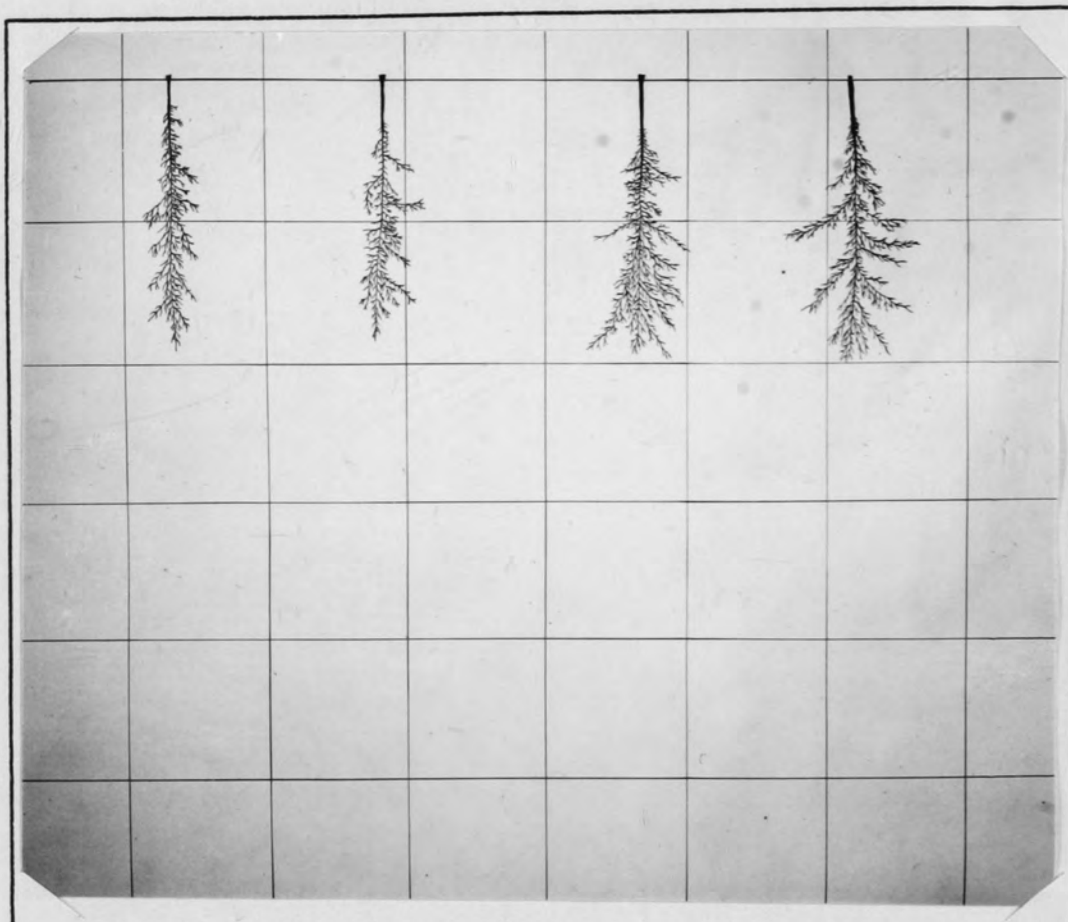

Fig. 9. Root system of sugar beets four weeks after planting.
A Untreated soil
B Sterilized soil
C Application of 75 lbs. superphosphate
D Application of 150 lbs. superphosphate

Fig. 10. Root system of sugar beets
Second period (5 to 8 weeks)
A - Sterilized soil
B - Untreated soil

A B

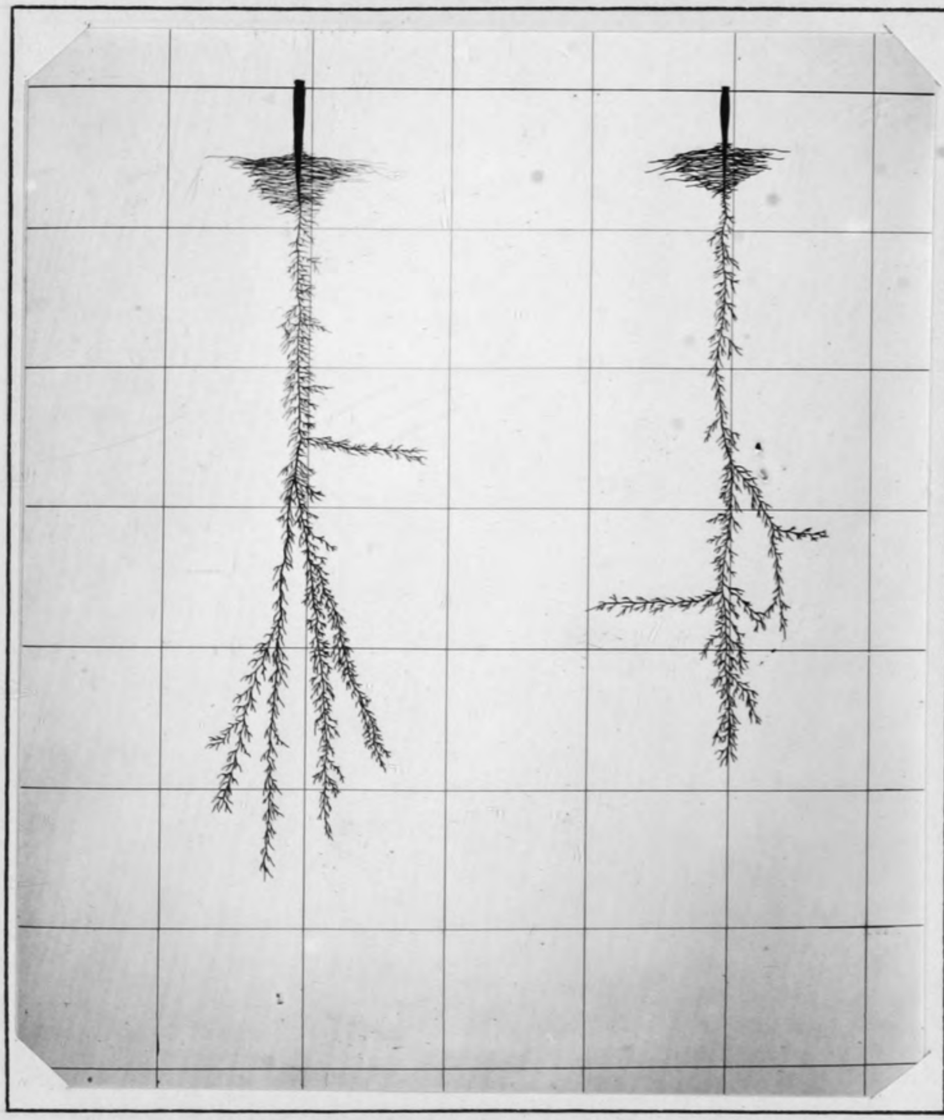

Fig. 11. Root system of sugar beets
Second excavation (4 to 8 weeks).
A - 75 lbs. phosphate added
B - 150 lbs. phosphate added

A B

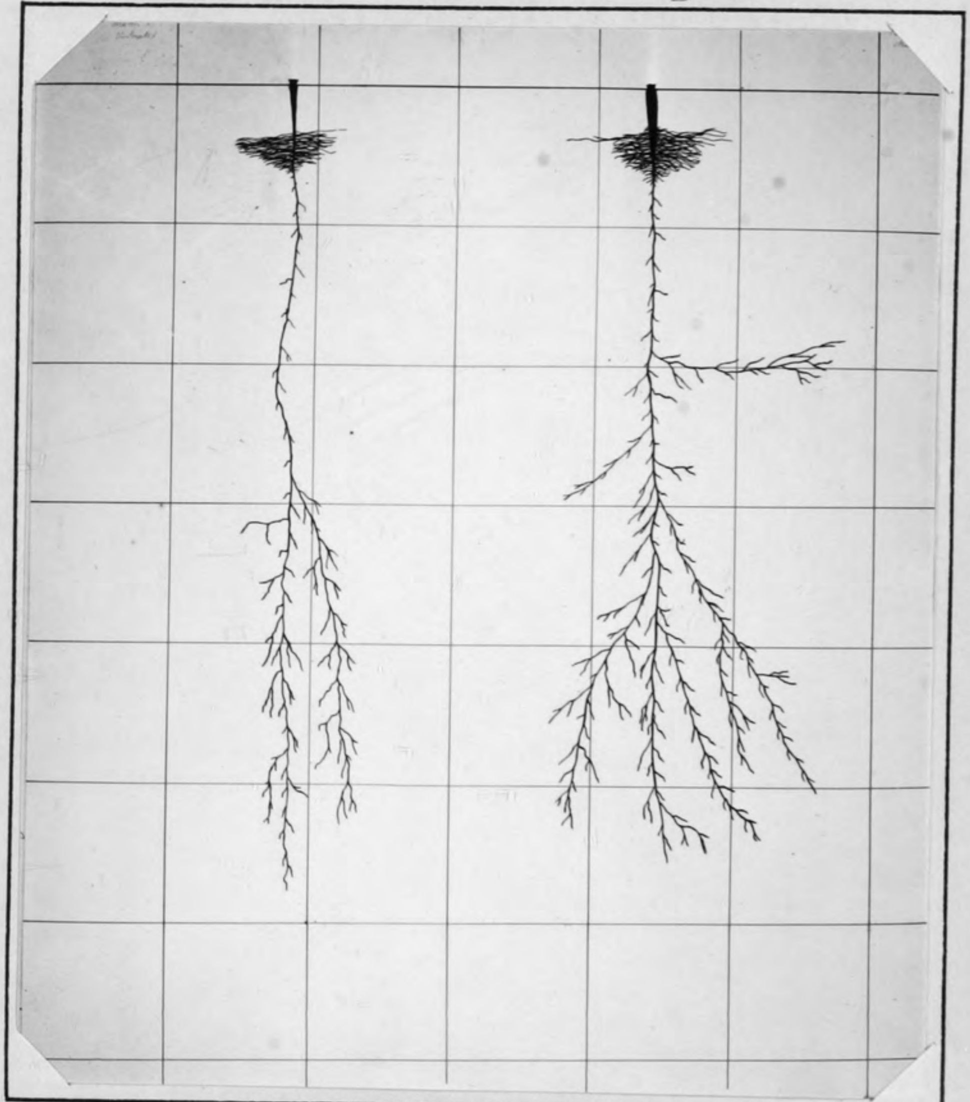

Fig. 12. Development of roots of beets
(9 to 12 weeks), third period.
A - Untreated soil
B - Sterilized soil

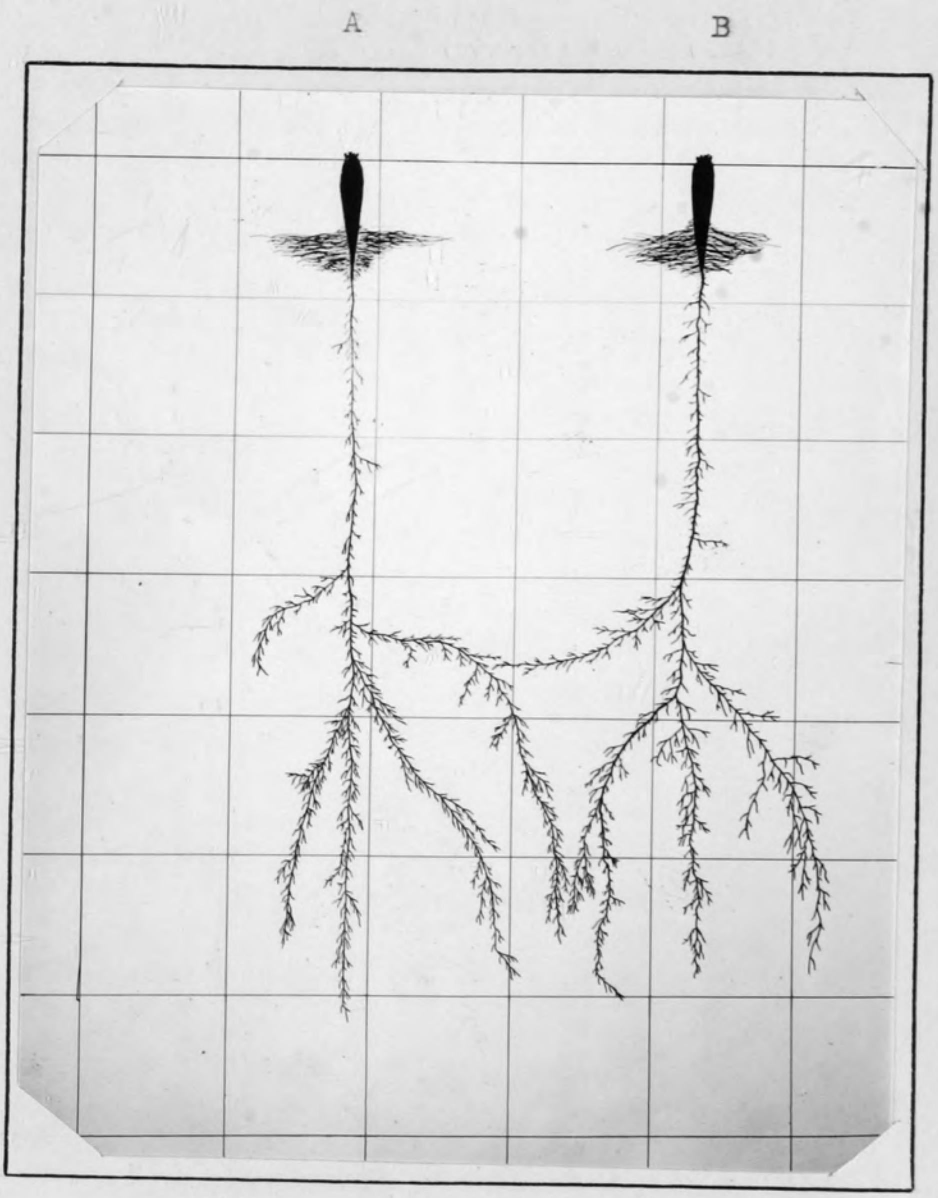

Fig. 13. Root development of beets in third period (9 to 12 weeks)
A - 75 lbs. superphosphate applied
B - 150 lbs. superphosphate applied

A B

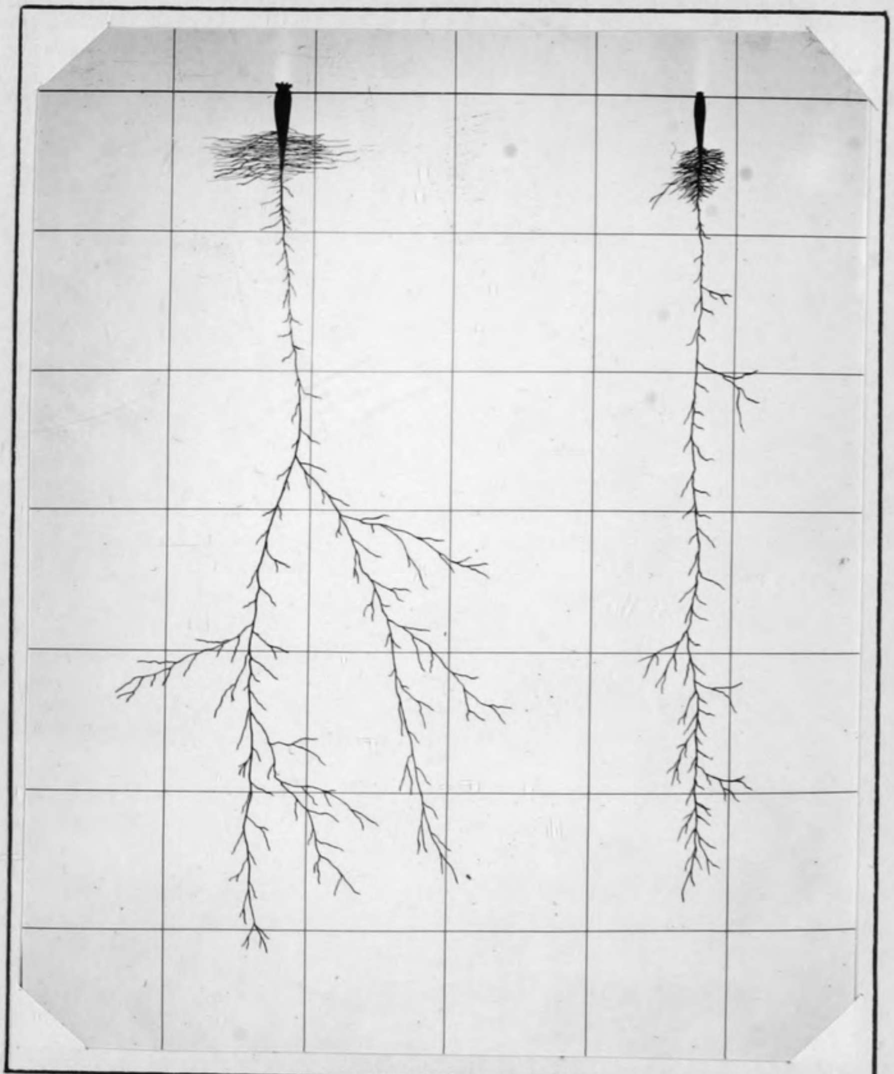

Fig. 14. Root development of beets.
Fourth period (13 to 15 weeks)

A - Beet from sterilized soil
B - Beet grown in untreated soil

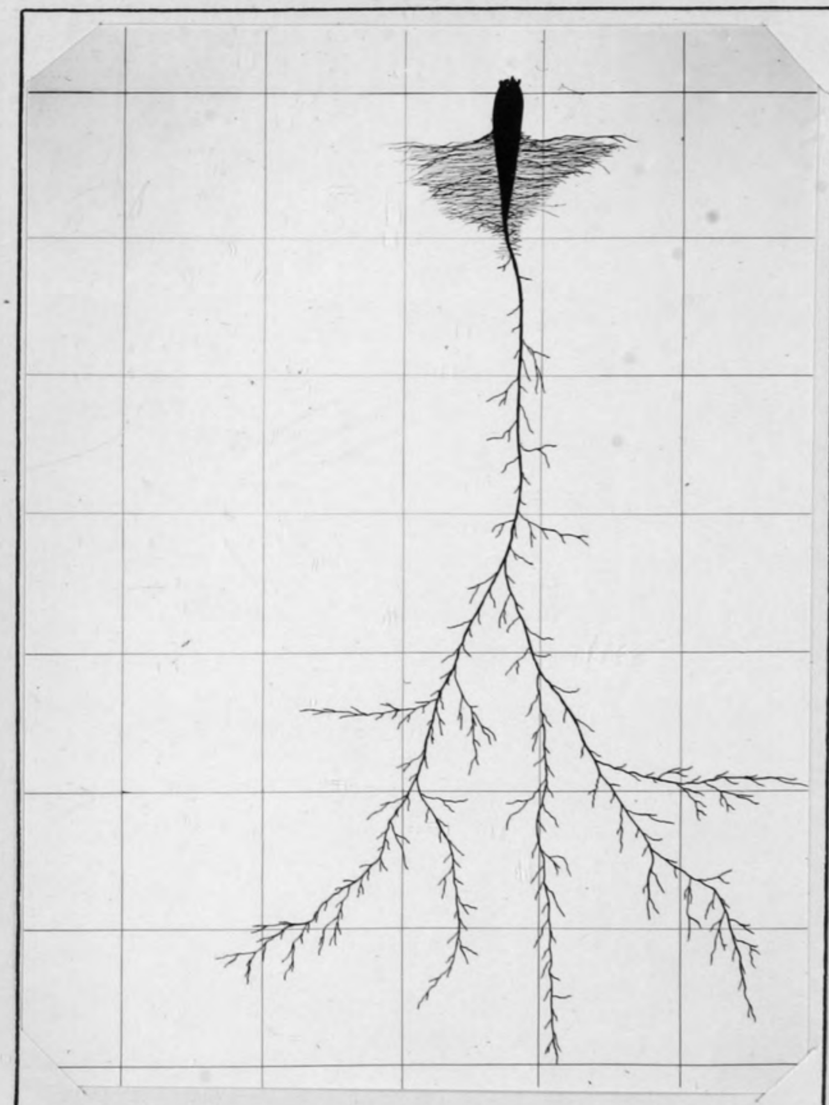

Fig. 15. Root system of sugar beet grown in the soil with 75 lbs. of phosphate treatment.

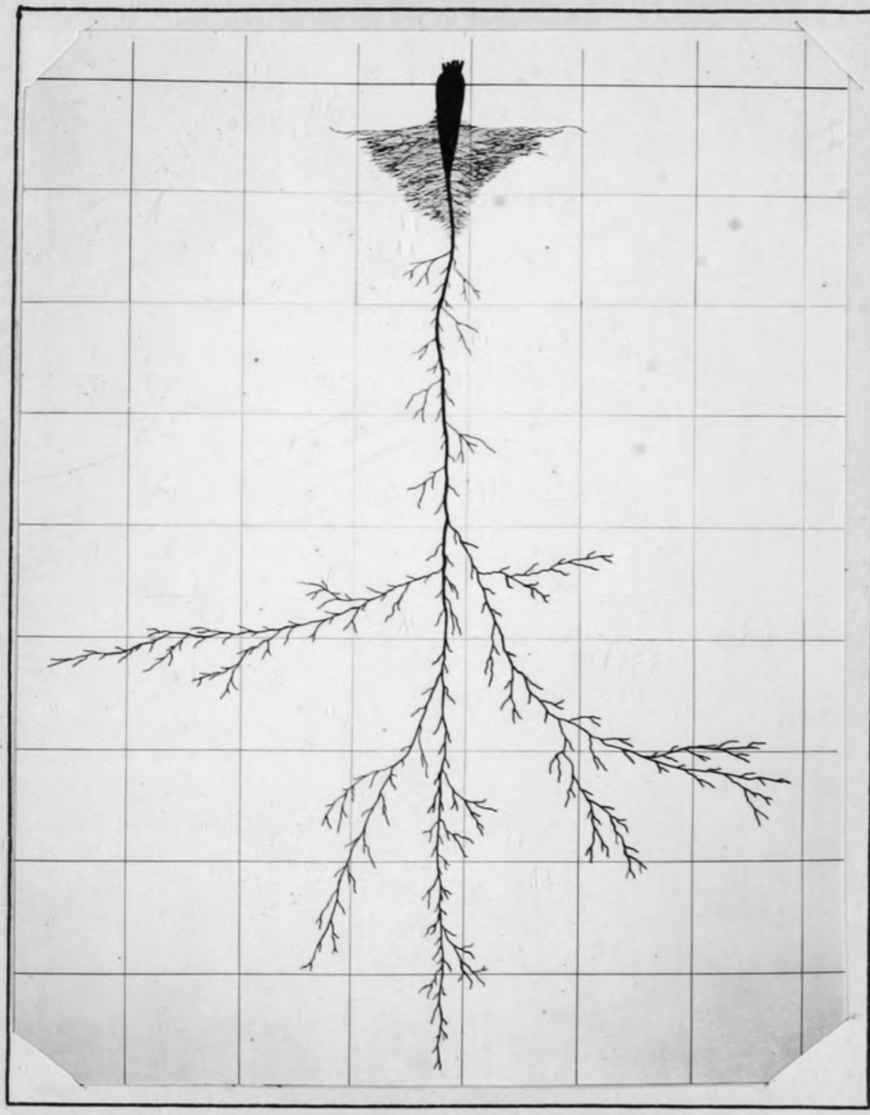

Fig. 16. Development of sugar beet root of soil supplied with 150 lbs. of superphosphate.

while those treated with phosphate showed a much better comeback. Some sand was placed on the soil of the boxes to diminish the effects of the fungi. The beets were able to grow comparatively rapidly and develop a considerable amount of leaves and leaf areas in this next four weeks. The second excavation of the roots showed an entirely different picture than the previous four weeks. A marked increase in the length of the roots was observed in all four plots. The most striking increase was found in the treated soil. (Figure 11 A and B and Table 1.) This rapid increase no doubt was due to the phosphate, because every soil received the same quantity of water. The beets in the sterilized plot during this period, increased in size and lateral root development much more than the untreated. (See Figure 10 B.)

The development of lateral roots in the boxes with phosphate compared to the untreated soil was not as pronounced because at this time the beets of the latter had gotten a better foothold in the soil and gradually the effects of the seedling disease were becoming less serious. (Figures 10 and 11) Increase in diameter of the roots in either one of the plots was very small as yet. (See Table 1.) Top development from this period on was of a slow, gradual nature in the case of the plants treated with phosphate and to a less degree in the sterilized plot. (Table 1.) The tops of the untreated plants increased but little from this time on.

The third period of growth showed about the same proportional increase as in the last four weeks. The root drawings (Figure 12 A) of the plants in the untreated soil indicate that they gradually developed somewhat more lateral growth and showed an increase in depth. The same was true of the plants in the sterilized soil, figure 12B. The beets in the treated soil had almost reached their greatest root development in the third period and began to increase rapidly in diameter and top growth. (Table 1 and figure 13.) Increase in diameter and top growth, in both the sterilized and untreated plots were still going on slowly. "Damping off" at this time had almost entirely disappeared. The characteristic lateral root development near the base of the main root was clearly noted in all four plots. (Figures 12 and 13.)

The fourth and last excavation showed the roots of the treated soil to have reached the bottom of the box. The actual depth of the soil at that time was about two and one-half feet. Some were already growing horizontally near the bottom. Branching did not increase much over the previous period. In most of the beets increase in diameter was at least twice as much as in four weeks before little difference could be observed between the two treated soils (Figures 14, 15, 16 and Table 1). As a whole the total increase in growth was slightly in favor of the 150 pound phosphate application. A very interesting observation was made on the development of the roots of the untreated soil. Only a few lateral roots were found to have grown from the extremely thin taproots which extended down about 60 cm. in spite of the fact that sufficient moisture was in the upper part of the soil, figure 16. The plants of the sterilized soil showed up better at this time than in the last period. The roots showed increased branching and depth as shown in figure 14 B.

Photographs taken at the end of the experiment give a suggestive illustration of the influence of phosphate upon leaf development, figures 17, 18, 19 and 20. It is obvious from figure 17 that a shortage of available phosphorus has serious effects, not only upon the root development, but also upon the leaf production. The leaves of the beets in the sterilized plot (Figure 18) show a much more favorable growth as compared to the untreated plot. This may have been partially due to the absence of the destructive fungi and partially due to the ascribed beneficial influence of soil sterilization. As is observed in figures 19 and 20, there is comparatively little difference in the number and size of leaves produced except that the leaves of the 150 pound treatment were uni-

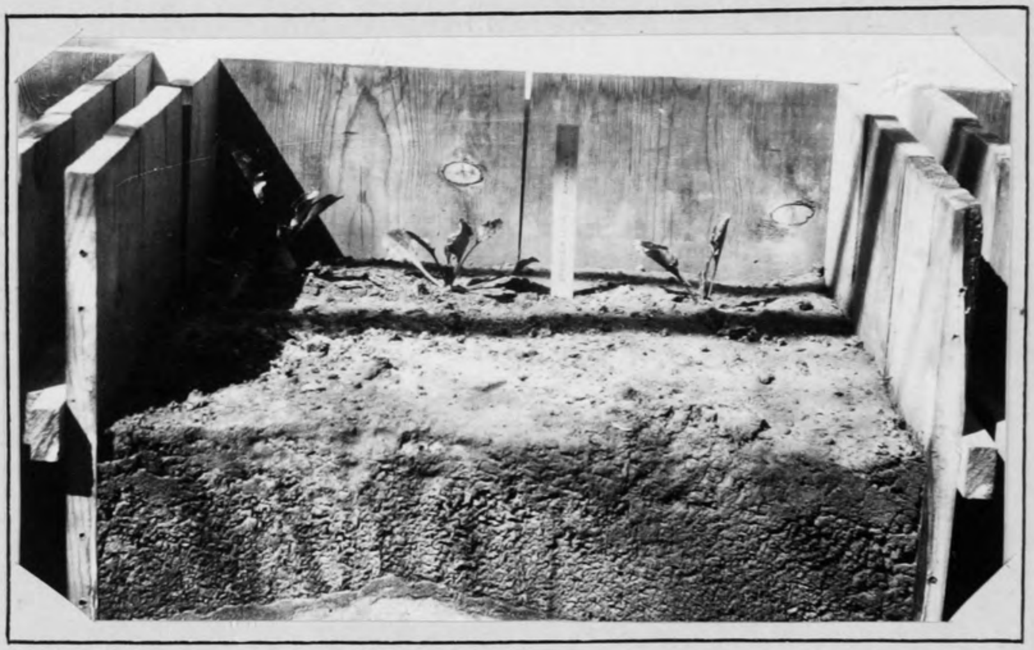

Fig. 17. Leaf development of sugar beets in the untreated soil.

Fig. 18. Leaf growth in sterilized soil.

Fig. 19. Effect of 75 lbs. superphosphate upon top growth.

Fig. 20. Effect of 150 lbs. super-
phosphate upon top growth.

formly large.

The following table gives the results of the effect of phosphate upon the development of the roots, diameter of roots and length of leaves.

It is observed that in the first four weeks the influence of phosphate was less pronounced upon the length of the roots than upon leaf development. The favorable effect of the fertilizer upon lateral root development is to be seen on the photographed drawings of the roots. Although during the next period lateral root development was still obvious, the increase in diameter of the root, and length of the leaves was much more striking in the case of the treated soil, over against the untreated. The increase in the development of the beets the next two periods again was most noticeable in the treated plots. No signs of blackheart were found on the beets in the untreated soil at the time of the last excavation of the sugar beet roots. This corroborates with the reports given by other workers, that the symptoms usually appear later in the season or only at extreme phosphorus deficiencies.

Table 1. Influence of Phosphate upon the Development of Sugar Beets

Soil Treatment	Length of roots				Diameter of roots				Length of leaves			
Periods of Growth	4. wk.	8. wk.	12. wk.	15. wk.	4. wk.	8. wk.	12. wk.	15. wk.	4. wk.	8. wk.	12. wk.	15 wk.
	cm	cm	cm	cm	mm	mm	mm	mm	cm	cm	cm	cm
Untreated Soil (Original)	12-18	20-35	25-50	30-60	1	1-2	1-3	1-4	6	6	7	7.5
Sterilized Soil	12-16	24-35	30-50	40-60	1	2-3	3-5	4-8	8	8	9	10
75lbs. Superphosphate per A.	14-18	30-46	42-60	52-70	1.2	3-4	7-12	15-25	11	12.5	14	15
150lbs. Superphosphate per A.	16-18	42-58	45-62	50-72	1.5	4-6	8-12	15-25	12	14	15	17

SUMMARY

1. In the above paper a careful survey has been made of the literature on the role of phosphorus in plants.

2. This literature review and bibliography is believed to be quite complete, comprising the chief articles on the role of phosphorus and particularly the effect of phosphorus deficiency in beets, not only in English but those papers written in German, French and a few Russian and Italian articles.

3. The thesis further considers the relation of fungi to "blackheart" and indicates that there is no consistant relationship.

4. The study of the development of sugar beets with various phosphate treatments includes drawings made periodically of the roots receiving different phosphate applications, the relation of top growth and a comparison between the different treatments as a whole.

a. The root development on the untreated soil showed little lateral and fibrous growth during all four periods. The leaves produced were small and few in number.

b. The sterilization of the untreated soil had a favorable effect upon the root development of the beets. They were larger, longer and more numerous, both the lateral roots and the leaves, than the plants grown in the untreated soil.

c. The growth of the beets in the soil supplied with 75 pounds superphosphate and 150 pounds respectively in general showed throughout the whole period a uniform development of the leaves, of the lateral root length, and diameter of the roots.

The 150 pound treatment slightly favored a somewhat greater and more even leaf production, diameter and lateral root development of the beets as compared to the 75 pound application of phosphate.

5. The effect of phosphorus upon the sugar beet, as compared to the soil deficient in this element, is expressed in an increased development of the leaves, both in size and number, a more extensive lateral and fibrous root system and greater diameter of the roots.

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