EFFECT OF ROOT GROWTH AND RATE OF PHOSPHORUS ABSORPTION BY ROOTS ON THE UTILIZATION OF APPLIED PHOSPHORUS BY FLAX, WHEAT, RAPE AND BUCKWHEAT

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ABSTRACT

A comparative study has been made of the root properties of four crops, flax, wheat, rape, and buckwheat, which are known to vary in their utilization of applied phosphorus. Results of this investigation showed that crop utilization of phosphorus from 'pellet-type' applications of phosphorus compounds could be accounted for by; (a) root development within the reaction zone of applied phosphorus, and (b) the rate of phosphorus absorption by the root, i.e. mg P absorbed/mg root/unit time.

Root development within the reaction zone was a function of the crop, the soil phosphorus availability and the solubility of the reaction products formed within the reaction zone. When soil phosphorus availability was low, roots of the four crops grew preferentially within the applied phosphorus reaction zone. The extent of preferential root growth of the crops increased in the order; flax, wheat, buckwheat, and rape. When soil phosphorus availability was increased, preferential root growth within the reaction zone was absent for flax, rape and buckwheat and was diminished for wheat. Roots of the four crops grew preferentially within reaction zones containing dicalcium phosphate dihydrate and octacalcium phosphate. However, roots of none of the crops grew preferentially within reaction zones containing hydroxyapatite.

The maximum velocity of phosphorus absorption by excised roots of the four crops increased in the order; flax, wheat, rape, and buckwheat. This was also the crop order for increasing apparent rate of phosphorus

absorption by the root from the reaction zone of applied phosphorus, i.e. the amount of applied phosphorus absorbed by the crop per unit mass of roots recovered from the reaction zone. Variability in the concentration of the metabolically produced phosphate ion carriers per unit mass of root was chiefly responsible for variability in the inherent rate of phosphorus absorption by roots of the four crops.

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CHAPTER I

INTRODUCTION

Because of the widespread use of phosphatic fertilizers, the efficiency of utilization of applied phosphorus by various crops is, at present, a problem of vast economic importance. Crops vary greatly in their growth responses to phosphorus applications, on the same soil and under the same growth conditions. Field studies in Manitoba indicated that growth responses to applied phosphorus of several crops, grown on phosphorus deficient calcareous soils, ranked in the order; rape $>$ cereals $>$ flax. Kalra (86) showed for a number of crops that growth response was inversely related to the ratio of soil phosphorus to applied phosphorus contained in the plant.

Kalra and Soper (87) reported that the variability among three crops (rape, oats and flax) in their ratios of soil phosphorus to applied phosphorus taken up, was largely due to the variability among them in their phosphorus utilizations from the application. Their results suggested that factors, other than those which control the utilization of soil phosphorus, control the utilization of applied phosphorus by the four crops studied. They found that soybeans, which absorbed a large quantity of soil phosphorus relative to flax, oats, and rape, absorbed only a small proportion of applied phosphorus. In contrast, they found that rape absorbed a large proportion of similarly applied phosphorus but its absorption of soil phosphorus was small relative to the other three crops.

Soper and Kalra (145) later demonstrated some characteristic phosphorus feeding habits of four crops (flax, oats, rape and buckwheat) by altering the mode of application of phosphorus to a calcareous soil. They showed that the availability of the applied phosphorus to flax and oats could be enhanced by spreading the application through an increasing fractional soil volume within the pots. In contrast, they showed that spreading the phosphorus application in a similar manner had either no effect or slightly decreased the availability of applied phosphorus to rape and buckwheat. These investigators suggested that these characteristic phosphorus feeding habits of various crops might be explained by the behavior of their roots within the phosphorus application. The present study was an investigation of the root behavior of a variety of crops differing in their phosphorus feeding habits, within concentrated applications of phosphorus, similar to the reaction zones formed between soil and applied phosphorus dissolving out of phosphatic fertilizer pellets.

CHAPTER II

LITERATURE REVIEW

A. PHOSPHORUS IN THE PLANT

Phosphorus may be found structurally incorporated into, or associated with, components of most subcellular fractions of biological tissue. The phosphorus in plants exists in both organic and inorganic forms. Phytin, phospholipids, nucleoproteins, nucleic acids, phosphorylated sugars, adenine nucleotides, flavin nucleotides, and pyridine nucleotides are but a few of the phosphorus containing organic compounds found in biological tissue, (3). The essentiality of phosphorus for life is apparent when one considers some of the functions of these phosphorus compounds in living processes. Phytin, the storage form of phosphorus in some seeds, supplies the phosphorus required in the metabolism of the seedling after germination. Phospholipids are the major components of living cell membranes. Nucleoproteins are intimately concerned with cellular organization, function, and reproduction, being constituents of the chromosomes and genes. Nucleic acids are the functional units of protein synthesis, i.e. they are responsible for the enzyme complement of the cell. Phosphorylated sugars are intermediates in anabolism and catabolism of carbohydrates. Adenine nucleotides store and transfer energy in metabolic reactions of living cells. Flavin nucleotides and pyridine nucleotides undergo oxidation-reduction reactions in the mitochondria and are therefore essential for energy production within the cell.

Inorganic phosphorus is largely concentrated in the vacuolar sap as orthophosphate ions. Inorganic phosphorus concentration of the expressed or exuded sap of some plants can be hundreds of times that of the soil solution in which they are grown (153). Phosphorus concentration in the sap varies with crop type, plant part, stage of growth soil type and with the fertilization program.

Seeds contain large amounts of organic phosphorus, whereas, in vegetative tissues, inorganic phosphorus usually makes up the bulk of the composition (92). In young plants, a considerable amount of phosphorus is soluble in water. Analysis of immature cabbage (plants) showed that 75 per cent to 80 per cent of their phosphorus was water soluble (128). As plant tissue differentiated and matured there was a decrease of the proportion of its phosphorus which was water soluble (92).

B. PHOSPHORUS REQUIREMENTS OF THE PLANT

Studies in nutrient solution culture indicated that species differed markedly in the minimum phosphorus concentration at which they make satisfactory growth (5, 126, 141, 144, 150, 153). Since none of these studies were continuous flow systems it is doubtful that phosphorus concentration was maintained at the specified levels. These studies did establish, however, that plants are able to absorb phosphorus from extremely dilute solutions at rates sufficient to support their maximum growth. Hoagland and Martin (69) found that 0.70ppm. of phosphorus was sufficient for favourable growth of barley. Parker and Pierre (127) found that corn produced its maximum yield on 0.10ppm. of phosphorus if that concentration was maintained throughout the growing period. Tidmore (153) obtained optimum yields of corn, sorghum, and tomatoes on 0.50ppm. of phosphorus. Asher and Loneragan (4) found that the phosphorus concentration at which each of eight species produced maximum yield varied over the range 1-24μM.

Phosphorus does not remain fixed in the cell or tissue in which it was originally deposited but is quite mobile within the plant (3). Arnon (3) formulated a general rule governing its distribution within the plant according to the physiological need. He stated that the requirement for phosphorus is highest in the youngest cells or those characterized by a high rate of metabolic activity. When the external supply of phosphorus becomes limiting, there occurs a redistribution of the phosphorus already contained in the plant; phosphorus is withdrawn from the older less metabolically active cells and moves into the younger, metabolically more active cells. Plants such as cereals, which are characterized by a determinate type of growth do not require a continuous supply of phosphorus during their life cycle. The phosphorus absorbed in the early stages of growth and deposited in the vegetative tissue is redirected to the seed, at the stage of its active formation.

It is well known that plants which have grown under conditions of phosphorus deficiency are characterized by a high root/shoot ratio relative to those plants grown under conditions of phosphorus sufficiency (75).

Growth of above and below ground portions determines the phosphorus distribution between those two portions of wheat plants (159). Alberda (1) and Helder (65) both stressed the importance of plant growth in regulating nutrient absorption. These workers suggested that phosphorus distribution within the plant is controlled by growth of individual plant parts. Short term absorption reduces the effect of growth to a minimum. Russell and Martin found a greater proportion of the phosphorus, absorbed during a short period, was retained in roots when plants absorbed from low rather than from high phosphorus concentrations (139). Thus, the suggestion by Loneragan and Asher (101) that phosphorus distribution between tops and roots is not a result of changes in the growth of above and below ground portions but is rather the cause of these changes seems plausible.

Asher and Loneragan (4) found that the rate of plant phosphorus absorption was limited by a maximal capacity of successive plant parts for its accumulation. They concluded that phosphorus is absorbed from a particular concentration at a rate which depends not only on the phosphorus concentration but also on the size of the 'sink' for phosphorus absorption. Since 'sink' size is directly related to plant growth the effect of external phosphorus concentration on rate of phosphorus absorption cannot be separated from its effect on growth.

C. ABSORPTION OF PHOSPHORUS

Details of the incorporation of inorganic phosphorus into biological tissue are as yet unknown. Less than one minute after entry a significant proportion of absorbed labelled phosphorus is found incorporated into organic compounds (103). Jackson and Hagen (81) could not identify the initial precursor because the turnover rates for the individual products of phosphorus absorption are too rapid. They held the view that phosphorus absorption is coupled to oxidative phosphorylation. However, they could not find any labelled adenosine triphosphate, which is the primary product of oxidative phosphorylation. The absence of labelled adenosine triphosphate, they explained, was the result of an adenosine triphosphate turnover as fast as, or faster than, the rate-limiting absorption step.

It has been demonstrated repeatedly that oxidation of citric acid cycle intermediates by carefully prepared mitochondria is accompanied by formation of ATP from adenosine diphosphate, (ADP) and inorganic phosphorus, i.e. oxidative phosphorylation. There are three possible sites in the electron transport chain where oxidative phosphorylation can occur. It is agreed that an energy-rich compound is formed at each of the sites. This compound then reacts with inorganic phosphorus to form energy-rich phosphate esters which, in turn, may react with ADP to form ATP. Little else is known about this process.

Knowledge of the pathway of inorganic phosphorus across the plasmalemma or mitochondrial membranes is even more scant than that of oxidative phoshorylation. The phosphorus absorption process involves orthophosphate ions in a system of soil, water, and plant roots. The ion $H_2PO_4^-$, was long regarded as the form in which phosphorus was taken into the plant. Under acid conditions, this is the dominant phosphate ion in soil systems. Even in alkaline soils, in local areas around plant roots, and in decomposing organic matter, the pH may be below 7. Hagen and Hopkins (61) described a kinetic analysis of measurement of phosphorus absorption by excised roots. The study (61) indicated that both $H_2PO_4^-$ and $HPO_4^=$ are absorbed under aerobic conditions. They pointed out that the concentration of $HPO_4^=$ in an acid system in low and might, therefore, be considered of little importance in phosphorus absorption. However, the high affinity between it and its respective carrier or site of absorption on the root makes it, in fact, as important in phosphorus absorption as $H_2PO_4^-$.

Some workers have suggested an anion carrier mechanism similar to that postulated for cations to account for the absorption of anions by plant roots (104). Lundegardh (104) proposed cytochrome to be the carrier for anions. He postulated that an oxidation-reduction potential gradient exists across a functional membrane, such that cytochrome molecules become oxidized at the outer surface and reduced at the inner. Anions such as phosphate are taken up when cytochrome becomes oxidized at the outer surface and released when it becomes reduced at the inner surface. According to his hypothesis, the transport of anions inward across a membrane would be accompanied by movement of an equivalent number of electrons and hydrogen ions outwards. A maximum of four anions are transported by such a mechanism per oxygen molecule consumed in respiration since four electrons are utilized in the reduction of a molecule of oxygen to water, and one anion is absorbed per electron transferred.

If ion absorption is directly linked to aerobic respiration, as suggested by Lundegardh, (104), then no active movement of ions should be detectable as a result of anaerobic metabolism. The capacity of roots to absorb ions in anoxic media apparently depends on whether they are attached or excised. Considerable absorption, observed with whole plants, was possibly due to the maintenance of aerobic respiration by transport of oxygen via the shoot to the root (155). Removal of the shoot resulted in relatively low ion absorption in anoxic media. Larkum and Loughman (88) demonstrated anaerobic phosphorus absorption from a phosphorus concentration of a $1 \times 10^{-6}M$ by intact plants. At higher phosphorus concentrations, $1 \times 10^{-4}M$, absorption was strongly inhibited and a large quantity of previously absorbed phosphorus was released to the external solution and, probably to the shoot.

Sutcliffe (149) suggested that nutrient absorption need not necessarily involve the active transport of both cations and anions. The electrical gradient created by the accumulation of either cations or anions might, he suggested, be sufficient to attract ions of the opposite charge.

Elgabaly and Wiklander (46) considered that any investigation into the mechanisms involved in anion uptake must recognize the negatively charged root surfaces and, consequently, the electrostatic repulsion that anions are expected to meet on approaching root surfaces. Work must be done to overcome the repulsion exerted by the negative surfaces. Elgabaly and Wiklander suggested this could be accomplished by an expenditure of energy, presumably metabolic, or through a reduction in the negative potential resulting from the charge on the root surface. They studied the absorption of chloride from chloride-resin systems, their filtrates, and calcium chloride solutions and found a greater absorption of chloride from the chloride-resin than from their equilibrium filtrates. They attributed this to a reduction in the negative potential of the root due to a mutual interaction between the double layers of the negative root surface and the positively charged chloride-resin. Franklin (51) observed the opposite effect with negatively charged colloidal particles (clay); i.e. greater absorption of anions ($SO_4^{=}$, I^-) from the equilibrium dialysate phase than from the suspension phase of a colloidal system. Since the "suspension" effect has been shown, on two occasions to influence anion absorption, it cannot be overlooked when considering phosphorus absorption from colloidal systems.

Kinetic studies lead to the postulation of a number of rather precise relationships with respect to the mechanism of phosphorus uptake by excised barley roots, (64, 91, 93). Most significant has been the interpretation that two apparent sites or mechanisms of phosphorus absorption are involved. The dual mechanism data have been interpreted to imply separate sites for the absorption of the two phosphate ionic species, $H_2PO_4^-$ and HPO_4^{--} (61, 62). Other workers besides Hagen and Hopkins have noted that phosphorus uptake by plant roots involves two reactions (23, 64). Carter and Lathwell (23) consider that the reaction which dominates at low external phosphorus concentration is linked to nicotinamide adenine dinucleotide in the electron transport chain and possibly involves combination of ADP with inorganic phosphorus at the membrane surface. The second mechanism, operating at high external phosphorus concentration, they suggest involves movement of glucose-1-phosphate into a membrane and release of inorganic phosphorus on hydrolysis at the inner surface. Since Q_{10} values indicated that both mechanisms involved chemical reactions, Carter and Lathwell concluded that both reactions are active processes (23). Hagen _et al._ (62) concluded that the rate limiting steps in phosphorus absorption at each site is coupled to one of the sites of oxidative phosphorylation associated with isolated mitochondria. A later study indicated the mitochondrion as being the site of this rate limiting step (82). Russell and Bishop (138) argued that phosphorus absorption is not directly linked to respiration. They interpreted the dual mechanism of phosphorus absorption as being due to a metabolic retention within the root or to a transfer of ions across the root to the stele.

Helder (66) suggested that phosphorus is initially absorbed from solutions labelled with radiophosphorus, by roots of intact plants, by way of an exchange reaction. Rapid exchange between root and solution phosphorus, which continues for two hours, he found to be followed by a slower exchange reaction. He hypothesized that phosphorus from the medium which enters the exchangeable pool of phosphorus in the roots can be subsequently either back-exchanged for phosphorus in the medium, fixed within the roots, or transferred to the shoot. Assuming this, he calculated that about 75 per cent of the total influx of phosphorus is back exchanged into the medium. Exchangeable phosphorus amounted to approximately 6 per cent of the total phosphorus of barley roots.

Phosphorus diffuses out of roots in both organic and inorganic forms (105). Lundegardh and Stenlid (105) found that both nucleotides and inorganic phosphorus diffused out of growing roots, but not from mature ones. Hevesy (68) made similar observations using radiophosphorus and concluded that one phosphorus atom is lost for every six entering the roots of plants supplied with a phosphorus concentration of 4×10^{-4}M. It is probable, therefore, that outward diffusion of phosphorus either in organic or inorganic forms must be regarded as normal occurences in actively growing roots (139). Helder (66) found that approximately 20 per cent of the total phosphorus of barley plants could be released. He determined that its origin could have been either root or shoot tissue. His results suggested that phosphorus release is closely related to phosphorus absorption since its presence depends on a continued phosphorus supply in the medium. Hai and Laudebout (63), on the other hand, showed that phosphorus release from fifty day old rice plants was affected by flow rate in a continuous flow nutrient culture system. These workers concluded that phosphorus release from roots is more by way of a passive process rather than the active process suggested by Helder (66).

Phosphorus entering the root mixed with only a small proportion of the root's total phosphorus content before moving to shoots of barley plants (34, 36). Changes in the shoot environment e.g. light, modified the turnover rate of the root phosphorus pool that lay in the path of phosphorus translocation. In contrast with these findings, Russell and Bishop (138) observed that the balance between shoot and root phosphorus was influenced mainly by root environment. e.g. external phosphorus concentration. They suggested that the small proportion of absorbed phosphorus translocated to shoots of plants supplied with low phosphorus concentrations is due to a metabolic retention of phosphorus in the roots. A large proportion of phosphorus absorbed from dilute concentrations was released when the roots were transferred to phosphorus free medium (139). A smaller proportion of the phosphorus absorbed from higher concentration was released to phosphorus free medium.

Loughman (102) attempted to distinguish between the process of absorption of phosphorus by roots of intact barley plants and that of subsequent translocation to the shoot. He concluded that translocation is directly dependent on the prior incorporation of absorbed phosphorus into a specific sequence of organic compounds. Although phosphorus absorption was relatively unaffected by a treatment which altered the normal sequence of organic compounds, further transport of the metabolized phosphorus to the shoot was inhibited.

D. FACTORS AFFECTING PHOSPHORUS ABSORPTION

The inverse relationship found between the pH of the medium and phosphorus absorption by excised barley roots was suggested by Hagen and Hopkins (61) to be the result of a competitive inhibition by the hydroxyl ion on the absorption of the phosphate ion species, $H_2PO_4^-$ and HPO_4^{--}. Medappa and Dats (108), however, found no direct effect of pH on phosphorus absorption by intact plants over the range 3 to 7. At pH 8, however, phosphorus absorption was drastically reduced.

Some cations have specific effects on phosphorus absorption. Low aluminium concentration ($1 x 10^{-4}$M.) enhanced phosphorus absorption by excised roots (131), and intact plants (132). High aluminium concentration ($1x10^{-3}$M.), on the other hand, depressed phosphorus absorption. Clarkson (26) showed that a large proportion of the phosphorus in aluminium treated roots was exchangeable and made no contribution to the phosphorus incorporated into phosphorylated intermediates in metabolism. He later (27) showed that aluminium was adsorbed to cell wall material which he isolated from roots. The free carboxyl groups of polygalacturonic acid chains in the middle lamella were suggested as probable sites of adsorption. The resistance of the adsorbed aluminium to exchange caused him to suspect precipitation as $Al(OH)_3$ on the root or cell surface. These surfaces were the probable phosphorus fixation sites analagous to those found on soil particles. Iron has been shown to have an effect similar to aluminium in tying up phosphorus in or on roots (13).

Rate of phosphorus absorption by intact plants of Trifolium subterraneum was significantly increased by raising the calcium concentration of nutrient solution from virtually nil to 25μM or 250μM(45). Increasing the magnesium concentration of nutrient solution from 10uM to 100uM substantially activated phosphorus absorption also. Hyde (76) showed that calcium had its most significant effect on phosphorus absorption by intact plants at low phosphorus concentration. He concluded, as did Nassery and Harley (114) that phosphorus absorption from low concentrations is impeded by a negative potential at the root surface which can be reduced by the addition of cations.

E. AVAILABILITY OF SOIL PHOSPHORUS

Although there is some evidence for contact feeding by roots of soil grown plants (94), most investigators believe that plants obtain their phosphorus from soil solution (57). Rate of phosphorus absorption from soil, however, is controlled not only by the phosphorus concentration of the soil solution (the intensity factor), but also by the buffer power of the soil for phosphorus (capacity factor) i.e. the quantity of solid phase phosphorus released when the solution concentration is lowered over a given range (10, 52, 77).

Soil phosphorus exists in a variety of organic and inorganic forms. The average concentration of inorganic phosphorus, in displaced soil solution of 20 soils, was 0.09ppm and of organic phosphorus 0.47ppm (130). It was found that plants absorbed all of the inorganic phosphorus from soil extracts, but none of the organic phosphorus (130). Only when a continuous flow system was employed did 0.1ppm of phosphorus maintain good plant growth in nutrient culture solutions (126). Many soils which contain solution concentrations of 0.1ppm of phosphorus or less are quite productive (126). Solution phosphorus of these soils must, therefore, be continually replenished from other phosphorus sources in order to supply the phosphorus required during cropping (77, 92). Assuming plants could utilize phosphorus from the entire soil mass, it was shown that the rate of dissolution of solid phase phosphorus was at least 250 fold that of the rate of phosphorus absorption by the plant (54). Because of its immobility in soil, however, phosphorus absorbed by the plant is probably extracted from a small cylindrical soil volume around each root (98). Assuming only a fraction of the soil mass supplies the plant with phosphorus, rate of dissolution of solid phase soil phosphorus would still not be rate limiting in plant phosphorus absorption (123).

There are two main concepts of the solid phase phosphorus supply to plants (52). These are, (a) Phosphorus which may be utilized by plants exists in the soil in several chemical or adsorbed forms which together constitute 'available phosphorus'. (b) A fraction of the soil phosphorus exists in a 'labile pool' which maintains a definite equilibrium potential in the soil solution.

The chemical or adsorbed forms of phosphorus assumed to exist in soil have been described in terms of solution parameters e.g. chemical potential, solubility products, and surface adsorption equations. Phosphate potential or the chemical potential of mono-calcium phosphate, ($\frac{1}{2}pCa+pH_2PO_4$), was suggested by Schofield (142) as being the soil condition which controls phosphorus availability. In 1964, Wild (158) showed that phosphorus concentration and not the phosphate potential controlled phosphorus availability. He was not certain though whether it is the total inorganic phosphorus concentration or the $H_2PO_4^-$ ion concentration which is important in this regard.

Characterization of solid phase phosphorus in terms of its solubility product (25, 28), is based on the premise that its identification allows prediction of the phosphorus concentration in the soil solution. This approach is applied mainly to availability studies of fertilizer reaction products in soil (100).

Characterization of solid phase phosphorus by the use of adsorption equations, (160), does not necessarily identify the solid phase. It does, however, have the advantage of describing the system with a set of constants which, when known, can be used to predict the effect of placing a stress on the system e.g., plant extraction of phosphorus.

Schofield (142) suggested the existence of a labile pool of soil phosphorus from which he claimed plants absorb their phosphorus. This labile pool was determined by following the isotopic exchange between soil phosphorus and radiophosphorus (P^{32}) present in the solution in which the soil was suspended. The exchange of phosphorus between the two phases which is initially quite rapid is followed by a much slower exchange (107, 140, 157).

The labile pool of soil phosphorus has also been determined using the principle of isotopic dilution. The method originated by Larsen (89) requires measuring the ratio of soil phosphorus taken up by plants grown on soil with which P^{32} labelled phosphorus has been intimately mixed i.e. 'L' value. In using the 'L' value to assess the labile pool of soil phosphorus isotopic dilution between the soil and added phosphorus is assumed to occur prior to plant extraction.

A similar measurement of the labile pool was proposed by Fried and Dean (53) although the concept behind it was quite different, i.e. 'A' value. They regarded plant available phosphorus in a soil to which P^{32} labelled phosphorus had been intimately mixed, to exist as essentially two independent sources. They suggested that the ratio of soil to added phosphorus taken up by the plant from a system fertilized in this manner is a measure of the soil phosphorus availability relative to the availability of the added phosphorus. They assumed the applied phosphorus to be 100 per cent available during crop growth and that the plant does not distinguish between the soil and the added phosphorus.

Rennie and Spratt (135) considered that the ratio of soil to added phosphorus taken up by plants supplied with a banded application of phosphorus is more indicative of soil phosphorus availability than the 'A' value as determined by Fried and Dean (53).

Rennie and Spratt made the same basic assumptions as Fried and Dean as regards the availability of the added phosphorus. They utilized a banded application of phosphorus rather than mixed application to overcome the exchange between soil and added phosphorus in close association with one another, which was reported by Cooke (29).

The validity of the assumptions made in calculating 'A' values for use in assessing soil phosphorus availability are questionable. Plants utilize phosphorus from reaction products formed between the applied phosphorus and the soil rather than directly from applied water soluble compounds (100). This formation of reaction products between soil and added phosphorus decreases the rate of supply of added phosphorus to plants since the solubility products of the reaction products are in general lower than the solubility products of the added phosphates. It is, therefore, doubtful that 100 per cent of the added phosphorus is available during crop growth.

Recently Kalra and Soper (87) showed that crops which were good extractors of soil phosphorus were not necessarily good extractors of applied phosphorus. They showed that soybeans was a good extractor of soil phosphorus relative to other crops, e.g. rape. Extraction of added phosphorus by soybeans from a concentrated application was less than the extraction of added phosphorus by poorer extractors of soil phosphorus. That species differ in their phosphorus feeding habits from similar phosphorus fertilized systems might lead one to question the assumption that the plant does not distinguish between soil and added phosphorus.

The constancy of the 'L' value of a soil using a number of test crops suggested that plants could not significantly increase the size of the labile pool (118). Variability between species in their extraction of soil phosphorus was suggested, therefore, to be due to variability between them in their rates of phosphorus extraction from the low phosphorus concentration within the soil solution (118).

F. FACTORS AFFECTING SOIL PHOSPHORUS AVAILABILITY

(1) Soil Factors

Type of colloidal system (58), soil moisture (11, 38, 49), and an impedance factor (122) are but a few factors which influence phosphorus absorption of soil grown plants. The latter two factors influence the diffusion of phosphorus to the plant root (117). Mass flow of phosphorus is not regarded as being important in phosphorus transport to roots of soil grown plants (117, 143). Assuming either a constant rate of phosphorus uptake per unit area of root, or a constant phosphorus concentration at the root surface, phosphorus absorbed by a root model in ten days came from within 1mm of its surface (121).

Consequently, diffusion has received more attention as the method of transport of phosphorus to roots of soil grown plants (9, 17, 95, 96, 97, 122, 129).

According to Bray (22) the value of soil nutrients to plants depends on their accessibility to roots which, in turn, is related to their mobilities in soil. He suggested that mobile nutrients are absorbed from the total soil volume containing roots whereas immobile nutrients are absorbed from a thin layer of soil around the root. It was pointed out by Nye (117) that the zone of nutrient disturbance around a single root for phosphorus is small relative to the zone of disturbance for either potassium or nitrate. He suggested that when the depletion zone is very small the cylinder of root hairs surrounding the root plays an important role in nutrient absorption (116). Lewis and Quirk (98) demonstrated that the depletion zone for phosphorus about wheat roots extended approximately 1mm from the root surface which coincided well with the length of root hairs. They suggested that root morphology influences the size of the depletion zone for phosphorus more than rate of phosphorus diffusion within the soil.

Plants absorbed more phosphorus per unit volume of soil when grown in small rather than large volumes of soil (7, 32, 90). Cornfield (32) correlated phosphorus uptake by oats, ryegrass, kale, and tomato plants with their rooting intensities (root mass per mass of soil) within the soil mass in which they were grown. When the soil volume in which they were grown was increased the rooting intensity of each crop was reduced.

(2) Plant Factors

In a review of literature Thomas (152) found that various plant species, when grown on media of similar phosphorus concentration, exhibit selective powers with respect to any specific ion or ions. Nye (117) considers the specific phosphorus requirement of a crop is expressed at its root surface. Little is known, however, about the rate of phosphorus absorption by roots of intact soil grown plants because of the lack of information regarding the phosphorus concentration at the root-soil interface. The phosphorus concentration at this interface depends not only on the rate of supply from the solid phase soil phosphorus but also on the rate of phosphorus absorption by the root.

Many workers have considered that the rate limiting step in phosphorus absorption is directly related to the internal metabolic system of the plant (23, 61, 81, 104, 118, 138). Other workers have alluded to a relationship between root surface area and rate of phosphorus absorption (85, 144). Changes in pH in the root surface (117), competition with rhizosphere organisms for phosphorus (8, 21), and root cation exchange capacity (41), are other plant factors which possibly influence the rate of phosphorus absorption by roots of intact soil grown plants.

The 'carrier' theory of anion absorption was used to describe phosphorus absorption by living plant roots (61). The theory assumes the presence of a metabolically produced carrier for phosphate ions which transports phosphorus into the root. The recent isolation of 'carriers' which function in transporting other ions across membranes supports this hypothesis (125). Pardee (125) argues that proteins should constitute these carriers since they are the only molecules with the observed degree of specificity to discriminate between possible substrates. He also argues that the carrier is probably part of the membrane structure, since approximately 60 per cent of the membrane constitutes proteins (40 per cent phospholipids) which, recent studies suggest, extend across the membrane thereby providing specific doors for ion absorption.

Two specific sites or carriers appeared operative in transporting phosphorus into excised barley roots (61). Kinetic analysis of phosphorus absorption by excised roots allows the calculation of, K_{ma} and K_{mb} i.e. the dissociation constants for the carrier-phosphate ion complex, k_{3a} and k_{3b} i.e. the reaction rates for the metabolic turnover of each carrier, and $\leq R_a$ and $\leq R_b$ i.e. the concentration of the carriers on the root. These constants serve to characterize the phosphorus absorption by roots of any crop.

Noggle and Fried 1960 (115) compared the biological constants which they calculated for millet, barley, and alfalfa roots. They found that the dissociation constant for each phosphate-carrier complex and the turnover rate for each 'carrier' were quite similar for three species. The major difference between species was in the concentration of 'carrier' on their roots. This finding was substantiated by two other groups of investigators (2, 114) who determined the biological constants of the phosphorus absorption process of a number of species. Noggle and Fried (115) concluded that the rate of phosphorus uptake by excised roots is controlled primarily by the concentration of 'carrier' on the root. Since the 'carrier' concentration is expressed as moles per gram of root, the total amount of 'carrier' per plant depends on the mass of roots produced.

Many workers have alluded to the fact that the root surface area effective in nutrient absorption may be of major importance when considering plant nutrient availability, especially for phosphorus, (22, 85, 144). However, at present, one can but speculate as to what fraction of the total root surface is effective in nutrient absorption (33, 35), and where the barrier between external and absorbed ions exists within the root tissue. The anatomical features of plant root systems associated with nutrient absorption were discussed recently by Olsen and Kemper (120). They consider the epidermis as the rate limiting barrier to the diffusive flow of ions to the root. Within a single cell they consider the plasmalemma to be the rate limiting barrier. The roles of the anatomical features raise questions as to which boundary is important in measuring root surface area. Fried and Shapiro (57) concluded that diffusion of ions through the free space would not likely limit the rate of active uptake. If the concentration of ions within the free space are maintained equal to the adjacent external solution, possibly the area of the plasmalemma is more important than external root surface area in nutrient absorption.

It is widely believed that roots make nutrients more available, especially phosphorus, by rendering their environment more acid. It is believed that this occurs because of the excretion of CO_2 and H^+. Nye (117) suggested, however, that it was more likely that the root would raise rather than lower the pH of its immediate environment. Since it has been shown that on the average plants take up more anions than cations, assuming that all the nitrogen is taken up as nitrate (37), Nye (117) concluded that roots should excrete HCO_3^- and not H^+. In consequence, the proposed excretion of ions from actively growing roots for the maintenance of electrical neutrality should have increased rather than decreased the pH of the root environment. Nye (117) recognized, however, that there were 20 moles of CO_2 respired for every equivalent of HCO_3^- excreted and that this CO_2 affects the pH in the reverse direction i.e. decreases pH. Under aerobic soil conditions he assumed that HCO_3^- is confined to the solution where its mobility was only 10^{-4} times that of CO_2 i.e. CO_2 is able to diffuse rapidly away from the root through air filled pore spaces thus spreading its effect over a large soil volume. Consequently, although more CO_2 than HCO_3^- was excreted from the root the latter is probably more effective in altering the pH of the immediate root environment because its effect is confined to that soil close to the root surface.

There is no doubt that the rhizosphere contains more organisms (encouraged by the secretions or sloughs of roots) than the surrounding soil. Workers have recently shown that over short absorption periods and a low phosphorus concentration these organisms compete with roots for phosphorus (8, 21, 136). It is not known whether these organisms have the capacity to compete with the plant over longer periods, or alternatively, whether they have the ability to convert the phosphorus into organic forms that cannot be rapidly assimilated by the root.

The calcium bonding energy of plant roots was found to increase as the measured root cation exchange value increased, (42). The finding that substances such as ethylene diamine tetraacetic acid (EDTA) which react with calcium to form complexes (or compounds) of greater stability than the rock phosphate crystal were highly effective in dissolving rock phosphate, and that organic anions such as citrate and oxalate liberated appreciable amounts of phosphorus from rock phosphate, led Drake and Steckle (41) to postulate two mechanisms which plants employ in utilizing relatively unavailable soil and rock phosphate. These are: (a) bonding of calcium by the plant root colloid thus dissolving the rock phosphate crystal, and (b) complexation of aluminium and iron by organic anions thereby solubilizing soil aluminium and iron phosphates. Drake and Steckle (41) found better utilization of rock phosphate by plants possessing high cation exchange roots, thus high calcium bonding energies. They showed that when a species with high and low cation exchange roots (red clover and oats respectively) grew in association, 60 per cent more phosphorus was absorbed by the species with low cation exchange roots than when it was grown alone.

G. AVAILABILITY OF APPLIED PHOSPHORUS

Availability of fertilizer phosphorus, like that of soil phosphorus, is controlled by numerous soil and plant factors. A number of studies were carried out to evaluate the availability of various forms of phosphatic fertilizers (12, 19, 20, 39, 40) and in general their availabilities were shown to be related to their water solubilities. Most commercial phosphatic fertilizers are, in fact, water soluble. However, the soil-fertilizer reaction products, formed when water soluble phosphorus is applied and not the applied phosphorus are the forms of added phosphorus from which plants feed. Consequently, the availability of these reaction products has been the major approach to the study of the availability of various phosphatic fertilizers (71, 94, 100, 151). Factors which exert their influence on the availability of these reaction products, must, therefore, influence the availability of phosphatic fertilizers.

H. FACTORS AFFECTING APPLIED PHOSPHORUS AVAILABILITY

(1) Application

Inherent properties of the reaction products e.g. surface area, rate of dissolution, water solubility, have been shown to affect their availability. The importance of surface area as a variable for the slightly soluble reaction products was discussed by Huffman (71). In studies with the two dicalcium phosphates and tricalcium phosphate, Bouldin and Sample (19, 20), found that the availability coefficients of these materials in different granule sizes were dependent primarily upon geometric surface area of the granules. A fair correlation was found between the relative initial rates of solution of a number of phosphates (expressed as P./unit surface area/unit time) and the value of the materials as sources of phosphorus for plants (74). Rates of solution of a number of slightly soluble calcium phosphates were found proportional to their surface areas and were controlled by diffusion through a liquid film at the surface of the dissolving solid (73). Their rates of dissolution were in the same relative order as their solubilities. It was postulated that surface area influences the availability of those compounds whose rates of dissolution are controlled by diffusion through a surface film of liquid. Other experiments with five slightly soluble calcium phosphates dicalcium phosphate dihydrate (DCPD), anhydrous dicalcium phosphate (DCP), tricalcium phosphate (TCP), octacalcium phosphate (OCP), hydroxy-apatite (HAP) supported this postulate; the plant response was related primarily to the rates of solution or solubilities of the various compounds (94), and these rates were shown to be controlled by diffusion (73). The surface areas of many of the phosphates change in complex ways as a result of dissolution and of coating by new phases that form during their dissolution, (72, 74). Moreover, these new phases contribute to the change in solution phosphorus concentration through their own dissolution.

Fertilizers are commercially applied banded with or close to the seed. In some instances they may be broadcast. Response of a variety of crops to each of these modes of application of phosphorus fertilizers have been compared (30, 31, 86, 135, 156). Generally, in their early growth stages, crops extract a good deal more of their phosphorus from banded applications than from broadcast applications (87, 156). The proportion of plant phosphorus derived from the fertilizer in the later growth stages is similar for both modes of application (30, 31, 156). On acid soils banded water soluble phosphorus fertilizer was more available to several crops than broadcast applications (109,135, 146). On calcareous soils varying results were obtained on comparing the two modes of application of water soluble phosphorus fertilizers (87, 109, 135, 146). Some workers (109) found no difference between the two methods of application in added phosphorus availability. Other workers (14, 87, 146) found less phosphorus utilization from banded than from broadcast applications.

(2) Soil Factors

Soil reaction had a marked effect on the availability of added soluble and slightly soluble phosphates (55). Soil reaction was inversely related to the proportion of the plant phosphorus derived from applied basic rock phosphate, however, no such relationship existed for applied super-phosphate (55). Soil reaction influenced the type of reaction product formed when water soluble phosphorus was applied to soils (100). Mattingly and Widdowson (106) found that in some acid soils broadcast rock-phosphate was apparently more available than broadcast super-phosphate.

A number of workers found that association of non-phosphorus containing salts increased the availability of various sources of applied phosphorus (18, 50, 119, 133, 137, 147). The effect of high soluble salt concentration in enhancing the solubility of either the added source (147), or its reaction products (133), as well as an effect on the physiology of the plant (50, 119), have been offered to explain this effect.

Grunes (59) presented a comprehensive review on the effect of nitrogen on the utilization of soil and fertilizer phosphorus. Plant phosphorus uptake was increased by the addition of nitrogen to soils fertilized with either banded or broadcast applications of phosphorus (60). Addition of nitrogen to soils not fertilized with phosphorus had no effect on plant phosphorus absorption, despite growth responses of tops and roots to the added nitrogen (60). The ammonium ion was more effective than the nitrate ion in increasing the utilization of fertilizer phosphorus (119). Added nitrogen was most effective in this regard when it was in intimate association with the phosphorus fertilizer (119, 134).

Because of its rapid precipitation with calcium, phosphorus applied in water soluble fertilizers does not move far from the point of application in calcareous soils (67, 99). The phosphorus content of only a small volume of soil about the point of application was increased on addition of water soluble phosphorus compounds to calcareous soils (99). The water soluble phosphorus concentration within the zone of spread of added phosphorus in acid soils can be extremely high (15, 16). No information is available on the water soluble phosphorus concentration in zones of spread of phosphorus applied to calcareous soils, although it is probable that dicalcium phosphate dihydrate would be the initial reaction product (100).

(2) Plant Factors

Some workers have reported the utilization of applied phosphorus by some crops in preference to soil phosphorus (83, 111, 124). Jacques (84) found that superphosphate increased root growth of perennial rye-grass in the vicinity of the fertilizer applications. Duncan and Ohlrogge (43, 44) observed proliferation of the root system of corn in the phosphorus fertilized portion of the soil mass. They found a more marked root proliferation in the phosphorus fertilizer zone when nitrogen was also applied. Duncan and Ohlrogge (43), noted that branching of roots was not closer together in the fertilized soil. Root proliferation was caused rather by an increase in the length of the continually branching roots. They did not observe any difference between roots developed in fertilized and non-fertilized fractions of the soil mass. Cooke (29) showed that banded applications of superphosphate stimulated development of pea roots only in soil through which the fertilizer had diffused before precipitation. Blanchar and Caldwell (15, 16) observed a decrease in growth of corn roots in phosphorus fertilizer zones of acid soils. They showed that roots would not grow into that region of a mono-calcium phosphate fertilizer band which had a water soluble phosphorus concentration greater than 1000ppm. The first order root tip of corn was sensitive to bands of relatively low salt concentration which apparently killed the meristem (43). Second order roots were not affected by the same band. Duncan and Ohlrogge (43) suggested that the rapid rate of growth of first order roots penetrate the fertilizer salt too rapidly to permit protective intercellular adjustments in osmotic pressure resulting in the death of the meristem due to plasmolysis.

Factors other than those which controlled crop utilization of soil phosphorus were responsible for controlling crop utilization of added phosphorus from concentrated applications (87). Kalra and Soper (87) found that some crops which were good extractors of soil phosphorus, e.g. soybeans, utilized only a small quantity of applied phosphorus banded into a calcareous soil relative to other less efficient extractors of soil phosphorus, e.g. rape. These workers found that flax, oats and rape differed more in their utilization of applied phosphorus than in their utilization of soil phosphorus. They later showed that the widest variation in the utilization of added phosphorus by flax, oats, rape, and buckwheat occurred when they were provided with a concentrated application, i.e. a narrow band of mono-potassium phosphate solution or dicalcium phosphate dihydrate crystals applied as a point source (145). By varying the form of added phosphorus and its mode of application they inferred some phosphorus feeding habits of the four crops from fertilized systems. There was no phosphorus application which provided the optimum availability of applied phosphorus to all species. Spreading a solution of mono-potassium phosphate with an increased soil volume had no effect on applied phosphorus availability to rape or buckwheat but stimulated its availability to oats and flax approximately three and six fold respectively (145).

Soper and Kalra (145), suggested that differences in the inherent root properties of crops within the fertilizer zone caused the observed variation in applied phosphorus utilization by different species. A knowledge of the inherent root properties which control applied phosphorus utilization as well as the factors which influence these properties would contribute a great deal to understanding the utilization of applied phosphorus by specific crops under specific growing conditions.

CHAPTER III

EXPERIMENTAL

A. POT EXPERIMENTS

1. Materials & Methods:

Greenhouse Techniques

Soils:

Soil material, used in the four pot experiments, was collected from 0 - 15 cm depth. After air drying, the soil was passed through a 0.6 cm sieve and mixed thoroughly. Undecomposed organic debris, e.g. straw, old roots, etc., which would have interfered in the recovery of roots, was removed prior to potting. Representative samples of the soils were then taken for analysis, using standard laboratory procedures. Some characteristics of the soils are shown in Table 0.1. The amount of soil used per 2.3 litre glazed crock in each experiment was as follows:-

Experiment	Soil Mass
I	1800 g
II	1400 g
III & IV	2000 g

Crops:

Twenty flax (Linum usitatissimum, L. "Redwood") seeds, and ten each of rape (Brassica napus, L. "Tanka"), wheat (Triticum vulgare, L. Manitou"), and buckwheat (Fagopyrum esculentum, Moench) were planted 1.3 cm below the soil surface. A week after seeding plants were thinned to 12 flax and 4 each of rape, wheat, and buckwheat per pot.

TABLE 0.1

SOIL CHARACTERISTICS

Experiment	Soil Type	pH	Conductivity (mmhos/cm)	$CaCO_3$ equivalent (%)	$NaHCO_3$ extractable P (ppm)	Nitrate-N (ppm)	Exchangeable K (ppm)	Field Capacity (%)
I	Lakeland	7.6	0.4	18.9	8.4	1.5	200	28
II(Soil I)	Lakeland	7.5	0.9	13.1	12.9	7.4	620	40
II(Soil II)	Firdale	7.7	0.4	--	6.6	3.1	235	25
III & IV	Plumridge	8.2	0.3	14.9	4.8	12.5	82	23

Experimental Design:

Each experiment was arranged in the greenhouse in a randomized complete block design. Pots were randomized within each block and the position of each block was relocated weekly. Experiment I was replicated three times while the other experiments were replicated four times.

Growth Conditions:

Supplementary lighting from cool-white "Sylvania" fluorescent tubes provided an intensity of about 1000 ft-c and a 16 hour day length. Day temperature in the greenhouse ranged from 27°C to 32°C while the night temperature ranged from 21°C to 24°C.

Every other day each pot was weighed and sufficient distilled water added to rewet the soil to its field capacity moisture content. On alternate days the average loss in weight of a random sample of four pots of each crop was used as a guide for the addition of water. Sufficient quantities of $(NH_4)_2SO_4$, NH_4NO_3, $KNO_3K_2SO_4$ solutions were added to each pot to supply nitrogen, potassium, and sulphur according to Table 0.2. Nutrients applied at planting were added in the distilled water which was applied to increase the moisture content of the soil to its field capacity value. Other applications were added to the surface of the pots prior to the daily watering.

TABLE 0.2

ADDITION OF NUTRIENTS

Experiment	Time of Application after seeding	Nitrogen (ppm)	Potassium (ppm)	Sulphur (ppm)
I	Planting	40	--	40
	20 days	20	--	--
	40 days	20	--	--
II	Planting	50	--	20
III	Planting	62	100	30
IV	Planting	36	100	30
	20 days	20	--	--

Harvesting:

Crops were harvested after 50, 34, 32, and 34 days growth in experiment I, II, III, and IV respectively. Above ground portions were cut approximately 0.6 cm above the soil surface, cut into 1 cm lengths and air dried. They were finally dried at 70°C for 48 hours and weighed for yield determinations. Where more than 1g of tissue was produced per pot it was ground in a Wiley Mill in preparation for tissue analysis.

Roots were harvested in two portions, i.e. from the phosphorus application and from the remainder of the soil. In experiment I, roots were recovered from a soil core, 2 cm in diameter, which was taken from the vicinity of the point of application of the applied phosphorus. A mild steel probe of 2 cm internal diameter was used for this purpose. A vertical core was taken from the centre of each pot (including control pots) and that portion between 1 cm and 6 cm from the soil surface was retained, the remainder returned to the pot. This portion of the soil core was air dried and weighed. Roots were then recovered by rinsing them free of soil with distilled water. Roots were retained on a screen of 2mm mesh size. The soil suspension was retained for water soluble phosphorus determination. After drying and weighing the recovered roots, a measure of the average root intensity in the vicinity of the phosphorus application was obtained, in terms of mg of root per g of soil.

In experiments II, III and IV, roots were recovered from the entire phosphorus application. The phosphorus application in these experiments consisted of 40 mg of phosphorus as dicalcium phosphate dihydrate crystals mixed intimately with 20 g of soil in experiment II, and 22 g of soil in experiment III and IV. This mixture was enclosed in an impervious cylinder open at its top and bottom. The cylinder consisted of a length of acrylic tubing 3.5 cm long and 2.8 cm internal diameter. This phosphorus application was placed in the centre of the soil mass with its long axis vertical. After harvesting, a vertical core 5 cm in diameter was taken from the centre of each pot (including controls). The phosphorus application was then recovered intact from this soil core by cutting the roots passing out of the cylinder at either end with a scalpel. Roots were then washed from these cylinders in a similar manner as from the phosphorus applications taken from experiment I, saving the soil-water suspensions for phosphorus determinations.

The remainder of the root mass in each pot was recovered by washing the roots free of soil under tap water. Roots were retained on a screen of 2 mm mesh size.

Analytical Techniques

Tissue Analysis:

Above ground portions and roots (including those sampled separately from the vicinity of the application) were dried at 70°C for 48 hours, weighed and ground in a Wiley mill (if more than 1 g yield). Samples of tops and roots (1g) were wet ashed in a HNO_3-H_2SO_4-$HClO_4$ ternary acid mixture according to the procedure outlined by Jackson (80), and diluted to a final volume of 100ml. Aliquots were taken from these solutions for total phosphorus and radioactivity measurements. Total phosphorus was determined using the vanadomolybdophosphoric yellow colour method(79). Radioactivity determinations were made using a liquid DM6 GM tube (manufactured by 20th Century Electronics Ltd., New Addington, Croydon, Surrey, England) attached to a binary scalar, Nuclear Chicago Model 161A.

The activity of a 'standard' solution of the applied phosphorus was determined within 2 hours of determining the radioactivity present in tissue digests of the fertilized plants. Thus, knowing the specific activity (cpm per mg phosphorus) of the applied phosphorus at the time of analysis, the amount of radioactivity (cpm) in the above or below ground portions could be readily converted to amount of applied phsophorus (mg). Soil phosphorus absorbed by phosphorus fertilized plants was obtained by difference between the total and applied phosphorus utilizations.

Water Soluble Phosphorus Concentration of the Reaction Zone:

Soil water suspensions retained after root recovery from the phosphorus applications were diluted with distilled water in a 10:1 solution to soil ratio and shaken for 24 hours at 25°C. This was also done on the soil samples recovered from the phosphorus applications within uncropped pots in experiment I. The phosphorus concentration of the filtrate was determined using the chlorostannous-reducedmoly-bdophosphoric blue colour method (78).

Preparation of Radioactive Phosphorus Compounds:

Radioactive monopotassium phosphate (MKP) and dipotassium phosphate (DKP) used in experiment I, was prepared as follows:-
MKP and DKP crystals were each dissolved in a minimum of distilled water and to each solution sufficient carrier free P^{32} in the form of H_3PO_4 was added to create specific activities within each radioactive

solution of approximately 10μc per 20 mg of phosphorus. These solutions were then evaporated to dryness on a sand bath and the radioactive crystals so formed lightly crushed.

Radioactive dicalcium phosphate dihydrate, used in experiments II, III and IV, was prepared by the method of Bailar (6). Carrier free radio phosphorus (H_3PO_4) was added to the mixed $Na_2\ HPO_4$, KH_2PO_4 solution to yield a labelled product of specific activity 10μc per 40 mg of phosphorus.

Radioactive octacalcium phosphate used in experiment IV, was prepared as per personal communication, G. L. Gurney, TVA, Muscle Shoals, Alabama: Previously prepared radioactive DCPD crystals (10μc/40 mg P) were hydrolysed at 60 C under 0.5M sodium acetate solution. Hydrolysis was carried out in 4 oz glass jars (5 g DCPD per 100 mls sodium acetate). The acetate was decanted and replaced with fresh solution when its pH fell below 6.5. This procedure was repeated until a petrographic analysis showed that the flat platy DCPD crystals had been replaced by the long, needle-shaped crystals of OCP(10-12 days)

Radioactive hydroxy apatite used in experiment IV was prepared by the method of Clark (24). Radiophosphorus was incorporated into the H_3PO_4. The hydroxyapatite was washed within one week of preparation but was allowed to stand in the mother liquor until that time. Specific activity of the product was approximately 20μc per 40 mg of phosphorus.

The chemical analysis and X-ray diffractogram of the radioactive compounds, dicalcium phosphate dihydrate, octacalcium phosphate and hydroxy apatite, compared against those of the pure forms, showed that each was successfully prepared.

2. EXPERIMENT I

Soper and Kalra (145) found a large variability in phosphorus utilization by flax, oats, rape and buckwheat from monopotassium phosphate and dipotassium phosphate applications to a calcareous soil. In increasing utilization of applied phosphorus the four crops ranked in the order; flax, oats, rape and buckwheat. These workers noted that the ability of these crops to utilize applied phosphorus was not related to their abilities to utilize native soil phosphorus. Characteristic feeding habits of the four crops, for applied phosphorus, were studied by varying the mode of application. It was found that some species (rape and buckwheat) could make equal or better utilization of fertilizer phosphorus when it was applied as a concentrated source rather than when spread throughout a large soil volume. In contrast, other species (flax and oats) made better utilization of fertilizer phosphorus by increasing the soil volume through which it was spread. Thus, the greatest variation between crops in their absorption of added phosphorus occurred when applied as a concentrated source of water-soluble crystals. These workers suggested that differences among the crops in their root efficiencies for phosphorus absorption (mg phosphorus per gram root) or in the proliferation of their roots within the application accounted for the vast differences between them in their utilization of the applied phosphorus.

It was considered that information regarding root and soil properties within zones of spread of phosphorus applications was required to explain the large variability among crops in utilizing applied phosphorus. Hence, the intensity of flax, wheat, rape and buckwheat roots within phosphorus applications as well as the size and water soluble phosphorus concentrations of the reaction zones formed between the soil and applied phosphorus were studied. Root intensities together with measurements of applied phosphorus utilization by each crop enabled estimates to be made of the growth rate as well as the rate of phosphorus absorption of roots within the phosphorus applications, during crop growth.

Materials and Methods

Radioactive monopotassium phosphate (MKP) and dipotassium phosphate (DKP) crystals were labelled with P^{32}. Some characteristics of the soil used in this experiment are shown in Table 0.1.

Applications of each phosphorus carrier, supplying 20mg and 40mg of phosphorus, were applied 2.5cm below the soil surface, after the soil had been wet to its field capacity moisture content (28 per cent) and allowed to equilibrate for 48 hours. The radioactive crystals were placed in a small depression made with the tip of a glass rod (0.6cm diameter) at the centre of the pot. The crystals were transferred to the soil via a funnel to prevent spread of the application. Positioning the crystals at the centre of the pot enabled location of the site of application at harvest.

Flax, wheat, rape and buckwheat were grown on the four soil treatments (20mg and 40mg of phosphorus as MKP or DKP) as well as on a control, non-fertilized, treatment and replicated three times. Additions of nitrogen and sulphur were made at planting and during crop growth according to Table O.2.

Above and below ground portions of the four crops were harvested after 50 days growth. Below ground portions were recovered in two parts, i.e. from a small cylindrical volume (20cc approximately) in the vicinity of the site of application, and from the remainder of the soil mass. Water soluble phosphorus was determined on the soil taken from the vicinity of the phosphorus applications.

Uncropped pots were used to determine the size of the reaction zone of each application. Waxed cardboard containers of 10 cm inside diameter containing 800g of soil were used for this purpose. Each of the four applications was applied to the centre of a container of soil in the same way as it was applied to the cropped pots. Uncropped pots were duplicated and kept under the same experimental conditions as cropped pots for the 50 days during crop growth. When cropped pots were harvested, the uncropped pots were sectioned vertically through the point of application of the radioactive crystals. The container bottoms were not cut to prevent movement of the soil core halves after sectioning. No screen medical X-ray film, protected with plastic sheeting, was inserted between the soil core halves and exposed for two hours in a dark room. The exposed film was developed for 3 to 4 minutes in Kodak X-ray developer, rinsed with water, and fixed for 15 to 20 minutes in Kodak X-ray fixer. The film was finally rinsed in water and dried. The diameter of the darkened circular image on the exposed film was measured. Assuming spherical zones of spread of the four applications the volume of each reaction zone was calculated.

Results and Discussion

The soil was apparently phosphorus sufficient for the growth of wheat, rape, and buckwheat plants, since none of these crops showed growth responses to the application of potassium phosphates (Table 1.1). Flax did respond to phosphorus fertilization (Table 1.1). However, in field trials and greenhouse work in Manitoba, flax has consistently failed to respond to phosphorus fertilization on soils of similar or lower phosphorus status. Available potassium content of the soil (ammonium acetate extractable) was considered adequate for optimum growth of flax plants (Table 0.1). Consequently, potassium added in the phosphorus carrier was not considered responsible for the growth response of this crop. The growth response of phosphorus fertilized flax plants, therefore, was regarded as a chance occurrence rather than a definite trend.

Phosphorus utilization by rape or buckwheat plants from each concentrated application of added phosphorus was more than seven-fold that of either flax or wheat plants (Table 1.2). Generally, in order of increasing rate of utilization of added phosphorus the four crops ranked as follows: flax, wheat, rape, and buckwheat. Flax plants utilized only 5 per cent as much added phosphorus as did buckwheat plants (Table 1.2). Soper and Kalra (145) suggested two plausible explanations for species differences in their utilization of applied

TABLE 11

YIELD OF ABOVE AND BELOW GROUND PORTIONS OF FLAX, WHEAT, RAPE, AND BUCKWHEAT FERTILIZED WITH CONCENTRATED APPLICATIONS OF MONOPOTASSIUM PHOSPHATE AND DIPOTASSIUM PHOSPHATE CRYSTALS (g)

Crop		Treatment				
		Control	* MKP (20)	** MKP (40)	# DKP (20)	## DKP (40)
Flax	tops	3.47 a	4.72 b	4.80 b	4.81 b	4.49 b
	roots	1.02 a	1.55 bc	1.66 bc	1.86 c	1.44 b
Wheat	tops	3.14 a	3.11 a	3.17 a	2.83 a	2.99 a
	roots	0.58 a	0.60 a	0.59 a	0.53 a	0.56 a
Rape	tops	8.84 a	9.02 a	9.11 a	9.07 a	9.28 a
	roots	2.34 b	2.33 b	2.40 b	1.95 a	2.26 ab
Buck wheat	tops	16.05 a	15.99 a	17.58 a	17.14 a	17.83 a
	roots	--	--	--	--	--

Duncan's Multiple Range Test
Means of treatments followed by the same letter are not significantly different

* MKP(20) 20 mg of phosphorus as monopotassium phosphate
** MKP(40) 40 mg of phosphorus as monopotassium phosphate
\# DKP(20) 20 mg of phosphorus as dipotassium phosphate
\#\# DKP(40) 40 mg of phosphorus as dipotassium phosphate

TABLE 1.2

UTILIZATION OF APPLIED PHOSPHORUS
BY FLAX, WHEAT, RAPE AND BUCKWHEAT IN 50 DAYS FROM
CONCENTRATED APPLICATIONS OF MONOPOTASSIUM PHOSPHATE AND DIPOTASSIUM
PHOSPHATE CRYSTALS (mg)

Crop	Treatment MKP(20) #	MKP(40) ##	DKP(20) +	DKP(40) + +	'F' values Source	Rate
Flax	0.59 a	1.22 a	0.54 a	1.02 a	2.30	43.5**
Wheat	1.69 a	2.36 a	0.98 a	2.20 a	2.87	13.6*
Rape	12.31 b	16.24 b	12.79 c	17.83 b	0.31	5.78
Buckwheat	12.36 b	22.36 c	10.20 b	19.92 b	2.61	47.9**

Duncan's Multiple Range Test
Means of species followed by the same letter are not significantly different

top data only
* significant at 5 per cent level of probability
** significant at 1 per cent level of probability

\# 20 mg of phosphorus as monopotassium phosphate
\## 40 mg of phosphorus as monopotassium phosphate
\+ 20 mg of phosphorus as dipotassium phosphate
\++ 40 mg of phosphorus as dipotassium phosphate

phosphorus, i.e. large differences between species in their root efficiencies for phosphorus absorption from the applied phosphorus and/or large differences between species in the stimulation of their root growth in the vicinity of the phosphorus application. Another possible explanation is that normal root growth rates of species may differ sufficiently to account for the differences between them in added phosphorus utilization.

Differences between species in their normal root growth rates could not entirely account for the differences between them in their utilization of added phosphorus. For the three crops, for which the total root mass was recovered at harvest, there was no relationship between total root growth and added phosphorus utilization. Wheat plants which produced the smallest root mass (Table 1.1), utilized more added phosphorus than flax plants (Table 1.2), which produced three times the root mass of wheat plants (Table 1.1). Rape plants produced double the root mass of flax or wheat plants (Table 1.1). Thus, the apparently faster root growth rate of rape plants might have been partly responsible for the greater rate of utilization of added phosphorus by rape than by flax or wheat.

Table 1.3 shows the approximate volume of soil through which phosphorus from the four concentrated applications of potassium phosphates spread as determined by autoradiographs of soil cores sectioned through the point of application of the P^{32} labelled crystal sources. The 40DKP application which spread through the largest soil volume occupied less than 1 per cent of the total

TABLE 1.3

SIZE OF THE REACTION ZONES
BETWEEN SOIL AND THE ADDED PHOSPHORUS
OF CONCENTRATED APPLICATIONS OF MONOPOTASSIUM PHOSPHATE
AND DIPOTASSIUM PHOSPHATE

	Treatment							
	* MKP(20)		** MKP(40)		# DKP(20)		## DKP(40)	
	A	B	A	B	A	B	A	B
Average diameter of sphere of spread (cm)	1.7	1.6	2.0	2.0	2.0	2.0	2.4	2.7
Volume of sphere of spread (cc)	2.5	2.1	4.2	4.2	4.2	4.2	7.3	10.3
Average of 2 reps.	2.3		4.2		4.2		8.8	

* 20 mg of phosphorus as monopotassium phosphate
** 40 mg of phosphorus as monopotassium phosphate
\# 20 mg of phosphorus as dipotassium phosphate
\## 40 mg of phosphorus as dipotassium phosphate

volume of the soil in the pot. Utilization of phosphorus from these applications in 50 days could be regarded as a measure of the rate of utilization of phosphorus by that portion of the root system feeding from the small fertilized soil volume. Phosphorus utilization from each application in 50 days, therefore, was a function of the growth rate and the rate of phosphorus absorption of that portion of the root system within its zone of spread. In the present study, growth rate of the root system within the zone of spread of the phosphorus application, during the 50 day experimental period, was inferred from the measurement of the root intensity in the vicinity of the phosphorus application at the time of harvest (in terms of root mass per soil mass). The growth rate, during the experimental period, of the portion of root system of the four crops within the zone of spread of each phosphorus application could be compared by comparing these root intensities, which are presented in Table 1.4.

Large variability in the rate of utilization of applied phosphorus between crops was not fully explained by the growth rate of their roots within the zone of spread of each application. Growth rate, during the experimental period, within the zone of spread of each phosphorus application was evidently greatest for roots of rape. Intensity of rape roots in the vicinity of each application after the 50 day growth, was 2 to 4 fold the root intensity of any other crop in the vicinity of the phosphorus application (Table 1.4). The greater

TABLE 1.4

AVERAGE INTENSITY OF FLAX, WHEAT, RAPE AND BUCKWHEAT ROOTS IN THE VICINITY OF CONCENTRATED APPLICATIONS OF MONOPOTASSIUM PHOSPHATE OR DIPOTASSIUM PHOSPHATE CRYSTALS AFTER 50 DAYS GROWTH (mg root per g soil)

Crop	Control	Treatment * MKP(20)	** MKP(40)	# DKP(20)	## DKP(40)
Flax	0.29 a	0.27 a	0.45 a	0.40 a	0.25 a
Wheat	0.26 a	0.30 ab	0.49 b	0.21 a	0.21 a
Rape	0.48 a	1.63 b	1.93 b	0.86 a	0.71 a
Buckwheat	0.27 a	0.55 a	0.30 a	0.37 a	0.45 a

Duncan's Multiple Range Test

Means of treatments followed by the same letter are not significantly different.

* 20 mg of phosphorus as monopotassium phosphate
** 40 mg of phosphorus as monopotassium phosphate
\# 20 mg of phosphorus as dipotassium phosphate
\## 40 mg of phosphorus as dipotassium phosphate

utilization of applied phosphorus from each application by rape than by flax or wheat, therefore, could have been due to the greater growth rate of rape roots than flax or wheat roots within the zone of spread of each phosphorus application.

Similar intensities of flax, wheat, and buckwheat roots were measured in the vicinity of each phosphorus application after 50 days growth (Table 1.4). Apparently, there were no large differences between these crops in their root growth rates within the zones of spread of phosphorus applications during the experimental period. However, buckwheat utilized 7 to 20 times as much phosphorus from each application as did flax or wheat (Table 1.2). Consequently, the large variability in phosphorus utilization from each application, between flax, wheat, and buckwheat, must have been the result of a large variability between roots of these crops in their rates of applied phosphorus absorption.

Rate of phosphorus absorption by the portion of root system within the zone of spread of the phosphorus application, during the 50 day growth period was inferred from a measure of the applied phosphorus absorbed in to days per unit mass of roots within the zone after the 50 day growth period. The root mass within the zone after the 50 day growth period was approximated knowing the average root intensity in the vicinity of the application (mg root per g soil), shown in Table 1.4, and the approximate soil volume through which the application spread (cc), shown in Table 1.3, assuming a bulk density of 1.0. The apparent rate of applied phosphorus absorption was calculated for roots feeding on the applied phosphorus. (Table 1.5).

Utilization of applied phosphorus in 50 days per unit mass of flax, wheat, rape and buckwheat roots within each application (the apparent rate of phosphorus absorption from each application) suggested considerable variability between crops in their rates of applied phosphorus absorption during the experimental period. In general, in increasing apparent rate of phosphorus absorption from each application, the four crops ranked in the same position relative to one another, as when placed in order of increasing applied phosphorus utilization, i.e. flax, wheat, rape, and buckwheat, (Tables 1.5 and 1.2 respectively). It is suggested therefore, that variability in the rate of phosphorus absorption rather than in the growth rate of roots within phosphorus applications was probably the chief cause of the variability among these crops in their utilization of applied phosphorus.

The large variability between flax, wheat, rape and buckwheat roots in their apparent rate of phosphorus absorption from applied phosphorus, was possibly the result of large differences between them in their inherent rates of phosphorus adsorption from the solution phosphorus concentration within the phosphorus application. Similar variability has been reported between the inherent rates of phosphorus adsorption of the roots of other species when adsorption from the same solution phosphorus concentrations. These reports have been for both excised roots (2, 115), and roots of intact plants (4, 149, 151).

A solubilization of phosphorus compounds has also been suggested to occur in the vicinity of the root due to various root excretions (117)

TABLE 1.5

UTILIZATION OF APPLIED PHOSPHORUS IN
50 DAYS PER UNIT MASS OF FLAX, WHEAT, RAPE AND
BUCKWHEAT ROOTS WITHIN THE ZONES OF SPREAD OF CONCENTRATED
APPLICATIONS OF MONOPOTASSIUM PHOSPHATE AND DIPOTASSIUM PHOSPHATE
CRYSTALS AFTER 50 DAYS GROWTH
(mg P/gm root)

	Treatment			
Crop	* MKP(20)	** MKP(40)	# DKP(20)	## DKP(40)
Flax	1270 a	660 ab	400 b	570 ab
Wheat	2890 a	1250 a	1150 a	1290 a
Rape	3540 a	2100 a	3690 a	2960 a
Buckwheat	10300 a	19600 b	9040 a	5200 a

Duncan's Multiple Range Test
Means of treatments followed by the same letter are not significantly different.

* 20 mg of phosphorus as monopotassium phosphate
** 40 mg of phosphorus as monopotassium phosphate
\# 20 mg of phosphorus as dipotassium phosphate
\## 40 mg of phosphorus as dipotassium phosphate

as well as other root properties (41). Thus, the variability between flax, wheat, rape and buckwheat roots in their apparent rates of phosphorus absorption from the zones of applied phosphorus could have been the result of differences between them in their abilities to solubilize the reaction products formed between the soil and applied phosphorus. The phosphorus concentration of a water extract of soil taken from the vicinity of each phosphorus application after 50 days growth (10:1 solution:soil ratio equilibrated for 24 hours at 25°C.) was measured to determine whether the roots of any crop could solubilize the reaction products measurably. Water soluble phosphorus was determined, in the same manner on soil taken from the reaction zones of uncropped pots. These water soluble phosphorus concentrations are presented in Table 1.6. Water soluble phosphorus concentration measured within each reaction zone of flax, wheat, rape or buckwheat cropped pots was lower than within each reaction zone of uncropped pots (Table 1.6). Cropping apparently decreased the water solubility of the reaction products, the decrease being directly related to the amount of applied phosphorus extracted by cropping. Rape and buckwheat, which extracted more applied phosphorus from each application than flax or wheat (Table 1.2), caused greater decreases in the water soluble phosphorus concentration within each reaction zone than either flax or wheat (Table 1.6). Roots of flax, wheat, rape, or buckwheat did not appear to measurably solubilize the reaction products formed between this calcareous soil and added phosphorus. The variability therefore, in the apparent rates of phosphorus absorption by these roots were apparently due to inherent differences between them

TABLE 1.6

WATER SOLUBLE PHOSPHORUS CONCENTRATION
WITHIN ZONES OF SPREAD OF CONCENTRATED APPLICATIONS
OF MONOPOTASSIUM PHOSPHATE OR DIPOTASSIUM PHOSPHATE CRYSTALS
AFTER 50 DAYS CROPPING WITH FLAX, WHEAT, RAPE AND BUCKWHEAT
($M \times 10^4$)

Crop	* MKP(20)	** MKP(40)	# DKP(20)	## DKP(40)
No crop	5.1	8.2	1.7	2.4
Flax	5.9	6.3	1.1	2.5
Wheat	2.9	4.0	1.1	1.2
Rape	0.9	2.3	0.1	0.5
Buckwheat	1.5	1.5	0.3	0.8

* 20 mg of phosphorus as monopotassium phosphate
** 40 mg of phosphorus as monopotassium phosphate
\# 20 mg of phosphorus as dipotassium phosphate
\#\# 40 mg of phosphorus as dipotassium phosphate

in their rates of phosphorus absorption from the same phosphorus concentration.

Rate of application apparently had no marked effect, during the 50 day growth period, on the growth rate of flax, wheat, rape, or buckwheat roots within the MKP or DKP applications. Similar intensities of flax, wheat, rape and buckwheat roots after 50 days growth were found in the vicinity of the 20 mg and 40 mg rates of phosphorus applied as MKP or DKP (Table 1.4). With one exception rate of application did not influence the rate of phosphorus absorption by roots of any crop from the zones of applied MKP or DKP. Except for the phosphorus absorption by buckwheat roots from applied MKP, the apparent rates of phosphorus absorption by roots of each crop from the 20mg rate did not differ significantly from their apparent rate of phosphorus absorption from the 40mg rate of MKP or DKP (Table 1.5). Consequently, those root properties of flax, wheat, rape and buckwheat which control their rates of phosphorus utilization from concentrated applications, i.e. growth rate and rate of phosphorus absorption of their roots, were not seriously affected by the rate of application of MKP or DKP. Apparently, the availability of reaction products formed between the soil and the applied phosphorus were essentially unaffected by the rate of application of MKP or DKP. It was concluded, therefore, that the amount of reaction products formed rather than their type was affected by altering the rate of MKP or DKP.

Rate of application influenced the rate of utilization of phosphorus from MKP and DKP by each crop during the 50 day growth period. Flax, wheat, and buckwheat utilized approximately twice as much phosphorus from the 40mg rate as from the 20mg rate of MKP or DKP during the 50 day growth period (Table 1.2).

Rape utilized only 30 - 40 percent more phosphorus from the 40mg than it did from the 20mg rate of MKP or DKP during the 50 day growth period (Table 1.2). There was a direct proportionality between rate of application and the size of the MKP and DKP reaction zones. The volume of soil through which the phosphorus of MKP or DKP spread was approximately doubled by doubling their rates of application (Table 1.3). However, it could not be deduced from the present data whether the indirect effect of rate of application on the size of the reaction zone or its direct effect on the amount of reaction product was responsible for the greater availability of the higher rates of MKP and DKP.

Evidently the phosphorus carrier had no marked effect, during the 50 day growth period, on the growth rate of flax or buckwheat roots within the MKP and DKP applications. The intensity of flax or buckwheat roots after 50 days growth in the vicinity of MKP applications did not differ significantly from their intensity in the vicinity of DKP applications of equivalent amounts of phosphorus (Table 1.4). On the other hand, phosphorus carrier apparently did influence the growth rate of wheat and rape roots within zones of spread of the MKP and DKP applications during the 50 day growth period. The intensity of wheat roots in the vicinity of the 40MKP application was approximately double the intensity of wheat roots in the vicinity of the 40DKP application (Table 1.4). The intensity of rape roots in the vicinity of both MKP applications was approximately four fold their intensity in the vicinity of DKP applications of equivalent amounts of phosphorus (Table 1.4). Phosphorus carrier, had no apparent effect during the 50 day growth period on the rate of phosphorus absorption by wheat or rape roots within zones of spread of the MKP or DKP applications. Apparent rates of phosphorus absorption by wheat or rape roots within zones of applied phosphorus did not differ significantly between MKP and DKP at equivalent rates of applied phosphorus (Table 1.5). On the contrary, the rates of phosphorus absorption by flax or buckwheat roots, during the 50 day growth period were affected but in a minor way, by phosphorus carrier. Flax roots showed a greater apparent rate of phosphorus absorption from the 20MKP application than from the 20 DKP application (Table 1.5). Similarly, buckwheat roots showed a greater apparent rate of phosphorus absorption from the 40MKP application than from the 40DKP application (Table 1.5). Consequently, those root properties controlling the rate of utilization of phosphorus by flax, wheat, rape, and buckwheat from concentrated applications, i.e. growth rate and rate of phosphorus absorption, were affected by phosphorus carrier. In general, MKP zones seemed to present better conditions for roots of each crop to utilize applied phosphorus than did DKP zones. It was concluded, therefore, that the reaction products formed between the soil and MKP were more available to these four crops than the reaction products formed between the soil and DKP.

Each crop used similar amounts of phosphorus from the two sources at each rate of applied phosphorus. (Table 1.2). Thus, in spite of the better availability of the MKP reaction products the two carriers were of similar availability to each crop. Applied phosphorus as DKP spread through approximately double the soil volume as did equivalent amounts of phosphorus applied as MKP (Table 1.3). It was concluded, therefore, that size of the reaction zone as well as the availability of the reaction products affected the utilization of MKP and DKP applications by these four crops. Hence, the better availability of MKP than of DKP reaction products could have been offset by the smaller reaction zones of MKP applications than of DKP applications.

It is further suggested that the size of the reaction zone rather than the amount of reaction product formed with the soil was that reaction zone property which controlled phosphorus utilization from the different rates of MKP and DKP. Water soluble phosphorus concentration of soil taken from the vicinity of the MKP and DKP applications in cropped and uncropped pots, 50 days after application and seeding of the cropped pots, were higher for MKP than for DKP applications (Table 1.6). The phosphorus absorption by flax, wheat, rape and buckwheat roots from the MKP and DKP applications suggested the formation of reaction products of greater plant availability within MKP than within DKP reaction zones. Formation of more soluble reaction products between calcareous soils and MKP than between calcareous soils and DKP has been reported (148). Consequently, their water solubility might have been that property of these reaction products which controlled phosphorus absorption by roots within reaction zones and hence their availability to various crops. Solution phosphorus concentration affects the growth rate (5, 101, 144), and the rate of phosphorus absorption of roots of intact plants (4, 101). It also influences the rate of phosphorus absorption of excised roots (2, 115). That phosphorus availability from concentrated applications of water soluble phosphates is controlled through the effect of solution phosphorus concentration on growth rate and/or rate of phosphorus absorption of roots within its zone of spread therefore, seems quite plausible.

Growth rates of wheat and rape roots were stimulated significantly within zones of spread of MKP or DKP. The intensity of wheat roots after 50 days growth in the vicinity of the 40MKP application was approximately double the intensity of roots in their untreated control pots (Table 1.4). The intensity of rape roots in the vicinity of 20MKP and 40MKP applications was approximately four fold the intensity of rape roots in their untreated control pots (Table 1.4). On the other hand, growth rates of flax or buckwheat roots were apparently unaffected by the phosphorus applications. It could be that growth of small portion of the root systems of these crops cannot be enhanced. It seems possible that the growth rate of flax or buckwheat roots within the phosphorus application could not be enhanced above the growth rate of the remainder of their root systems. It has been reported that some crops require nitrogen to be mixed with applied phosphorus before their root growth rates within zones of phosphorus applications are stimulated (43, 44). On the other hand, the present method of measuring root stimulation within zones of applied phosphorus might not have been sufficiently sensitive to detect the growth stimulations of flax or buckwheat roots.

Rates of phosphorus absorption by roots of all four crops were stimulated within the zones of spread of MKP or DKP. The apparent rate of phosphorus absorption by roots of each crop from MKP and DKP applications was at least 40 fold the apparent rate of phosphorus absorption by roots of their unfertilized plants i.e. their controls (Tables 1.5 and 1.7). There was a considerable variation between the crops in the stimulation of the rate of phosphorus absorption of their roots within zones of spread of MKP or DKP. While the maximum stimulation of the rate of P absorption by flax roots was approximately 100 fold their rate of phosphorus absorption from soil, the stimulation for buckwheat roots was up to 1000 fold their rate of phosphorus absorption from unfertilized soil. (Table 1.5). Hence, either the growth rate or the rate of phosphorus absorption of roots or both these root properties of each crop were stimulated within zones of spread of MKP and DKP applications. The extent of these stimulations however, depended on the crop. These results suggested that the rate of utilization of phosphorus from concentrated applications depended on plant properties rather than properties of the applied phosphorus, e.g. reaction products between soil and added phosphorus. Consequently, properties of the reaction zone must have had their effect on the rate of utilization of applied phosphorus indirectly through their effects on the growth rate and/or the rate of phosphorus absorption of the roots within the reaction zone.

Summary and Conclusions

Applied phosphorus (MKP and DKP) utilization by flax, wheat, rape and buckwheat in 50 days was controlled chiefly by the rate of phosphorus

TABLE 1.7

UTILIZATION OF SOIL PHOSPHORUS
IN 50 DAYS PER UNIT MASS OF FLAX, WHEAT,
RAPE, OR BUCKWHEAT ROOTS PRODUCED IN 50 DAYS BY
PLANTS FERTILIZED WITH CONCENTRATED APPLICATIONS OF
MONOPOTASSIUM PHOSPHATE AND DIPOTASSIUM PHOSPHATE
(mg P/gm root)

		Treatment			
Crop	Control	* MKP(20)	** MKP(40)	# DKP(20)	## DKP(40)
Flax	11.9 b	9.0 a	9.1 a	7.8 a	8.8 a
Wheat	20.4 b	16.2 a	16.3 a	18.2 ab	16.2 b
Rape	9.8 b	7.6 a	6.9 a	7.4 a	5.7 a
Buckwheat	--	--	--	--	--

Duncan's Multiple Range Test
Means of treatments followed by the same letter
are not significantly different

* 20 mg of phosphorus as monopotassium phosphate
** 40 mg of phosphorus as monopotassium phosphate
\# 20 mg of phosphorus as dipotassium phosphate
\## 40 mg of phosphorus as dipotassium phosphate

absorption by their roots from reaction zones formed between soil and applied phosphorus. Root growth rate within the reaction zones also affected the rate of utilization of applied phosphorus by rape as well as wheat to a minor degree.

Rate of phosphorus utilization by each of the four crops from different rates of a particular water soluble phosphorus carrier was controlled by the size of the reaction zone. Rate of phosphorus utilization by each of the four crops from different water soluble phosphorus carriers was controlled by the type of reaction product formed as well as the size of the reaction zone.

An hypothesis was developed to explain the rate of phosphorus utilization by a crop from concentrated applications of water-soluble phosphates. It was concluded that the water solubility of their reaction products formed with soil is likely that property which controls their availability. Rate of utilization of applied phosphorus depends indirectly on this property of the reaction products through its effect on the growth rate and rate of phosphorus absorption of roots within the reaction zone.

3. EXPERIMENT II

Crop utilization of applied phosphorus was found to be related to the rate of absorption of applied phosphorus by that portion of the root system within the phosphorus application (experiment I). However, one of the crops tested, rape, utilized nearly as much applied phosphorus as did a crop whose roots absorbed applied phosphorus at a much greater rate, buckwheat. Root growth of rape was stimulated in the vicinity of phosphorus applications whereas buckwheat roots were apparently not stimulated. An experiment was subsequently undertaken to study the effect of increased root growth within a phosphorus application on applied phosphorus utilization by a variety of crops, (flax, wheat, rape, and buckwheat).

Phosphorus was applied as a concentrated application to two soil treatments, i.e. to a small fractional soil volume. In one treatment, root growth within the pot was funneled through the phosphorus application, i.e. funneled treatment. In the other, root distribution within the pot was not controlled, i.e. non-funneled treatment. Growth rate of roots in the phosphorus application were thus varied.

Growth rates of flax, wheat, rape and buckwheat roots within monopotassium phosphate and dipotassium phosphate applications were inferred from root masses recovered from their zones of spread after 50 days growth (experiment I). The accuracy of measuring these root masses depended upon the accuracy of locating and sampling the zone of spread of applied phosphorus. The accuracy of the root growth measurement within the phosphorus application was improved, in this experiment, by applying phosphorus to a predetermined fraction of the soil volume within a pot. In order to immobilize the applied phosphorus within this fractional soil volume, a phosphorus compound which was only slightly water soluble, dicalcium phosphate dihydrate, was intimately mixed with the required volume of soil and the mixture placed within an impervious cylinder, open at either end to permit root growth into the phosphorus application.

It was suggested that the utilization of phosphorus by flax, wheat, rape, and buckwheat from concentrated application of monopotassium phosphate and dipotassium phosphate was affected by the size of the reaction zone between soil and applied phosphorus. Lewis and Racz (99) and Olsen and Watanabe (122) showed the effects of soil properties on the size of the reaction zone formed between soil and applied phosphorus, e.g. texture (122) and inorganic carbonate content (99). In the present sutdy two soils were utilized i.e. calcareous and a non-calcareous. Since phosphorus was applied to the same volume of each soil, the effect of soil properties on applied phosphorus availability other than their effects on the size of the reaction zone, could be studied.

Materials and Methods

Some characteristics of the two soils used in this experiment are shown in Table 0.1.

A concentrated application of phosphorus was added to each of two soil treatments on the two soils. To one of these treatments, root growth was funneled through the application. The normal rooting pattern of the other treatment was not altered. Flax, wheat, rape, and buckwheat plants were grown on these two soil treatments which are represented diagramatically in figure 2.1 as well as on a control treatment of both soils. The experiment was replicated four times, yielding a total of 96 pots.

To 800g of the 1400g soil mass, which was used in each pot, was added sufficient water to wet it to the field capacity moisture content. The soil was then allowed to equilibrate for 48 hours. To

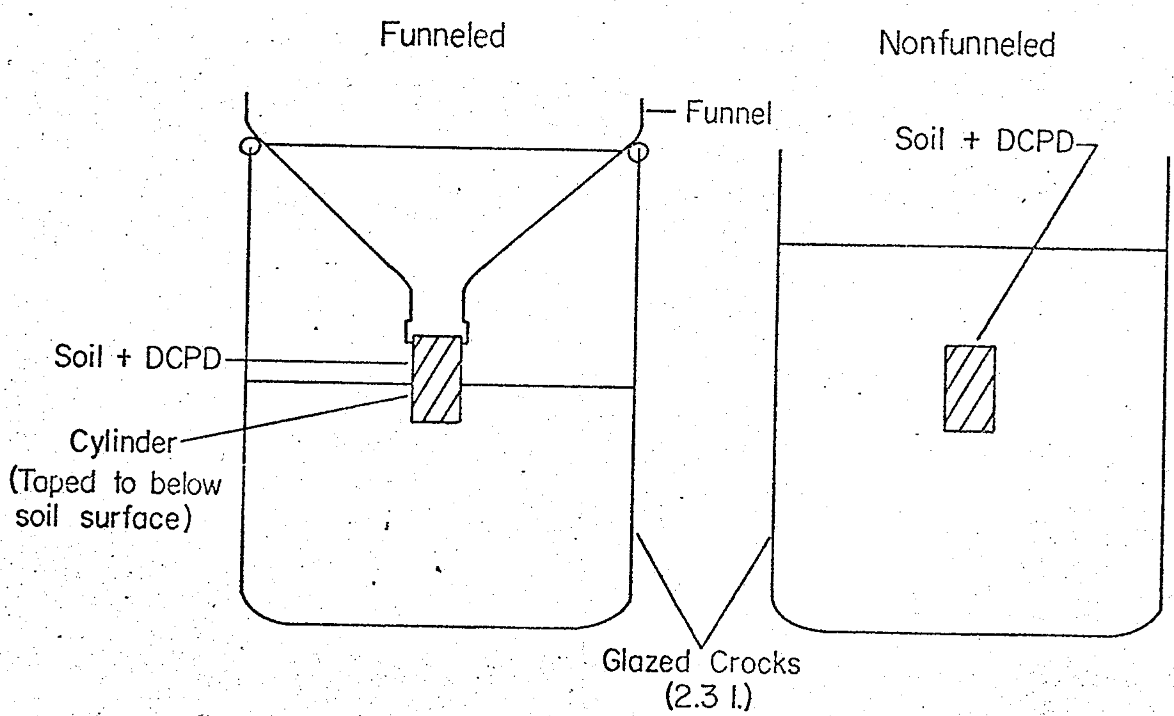


Figure 2.1. Diagramatic Representation of Funneled and Non-Funneled Treatments.

a 2 cm depression made in the centre of each pot a length of acrylic tubing, 3.5 cm long and of 2.8cm internal diameter, was vertically positioned. The 32 cylinders used in the funneled treatment had been previously taped to stemless polyethylene funnels, of base diameter 3.2cm, top diameter 16cm and of 1 litre capacity, cut from three quart plastic milk jugs. Each cylinder within this treatment was taped to below the soil level to eliminate the effect of light on root growth. The funnel rested on the lip of the pot. There was sufficient space between the funnel and the pot to allow addition of water to the bottom portion of the soil mass.

To the acrylic cylinder within each control pot was added 20g of the 0.5mm fraction of the appropriate soil. To the cylinders in the other two treatments was added 20g of the 0.5mm soil fraction with which had been intimately mixed 40mg of phosphorus as dicalcium phosphate dihydrate (DCPD). The applied phosphate compound was labelled during its synthesis, with P^{32} (10 μc per 40mg phosphorus). After addition of the soil-radioactive DCPD mixture to these cylinders, water was applied in a gentle stream to its contents to overcome scattering of the application when the remaining 600g was added to the pot.

Above and below ground portions of plants were harvested after 34 days growth. Roots were recovered in two portions, i.e. those from within the cylinders and the remainder. The water-soluble phosphorus concentration of soil within the cylinder from each pot was determined.

Total phosphorus contents of above and below ground portions were determined for each pot. Applied phosphorus contents of above and below ground portions of fertilized plants were also determined.

Results and Discussion

The root mass recovered from the phosphorus application was the product of the number of roots entering the phosphorus application and their growth rate after entry. The total root mass recovered from the non-funneled treatment of each crop with two exceptions did not differ significantly from the root mass recovered from the control treatment. (Table 2.1). A similar mass of roots, therefore, should have entered the cylinder of the non-funneled treatment as entered the cylinder of the control treatment for each crop. However, a larger root mass of each crop was recovered from the cylinder of the non-funneled treatment than was recovered from the cylinder of the control, after 34 days growth (Table 2.2). Since similar root masses should have entered the cylinders of these treatments it was concluded that the growth rate of roots within the cylinder of the non-funneled treatment was stimulated during cropping, presumably due to the phosphorus application. Growth rates of roots of the four crops were apparently stimulated in this manner within the phosphorus application.

Root growth stimulations of the four crops within the non-funneled treatment were related to one another in a similar ratio on both soils (figure 2.2). Thus, it appears that the root growth stimulation of these crops within the phosphorus application was a function of the crop. There was a marked variability in root growth

TABLE 2.1

EFFECT OF PHOSPHORUS FERTILIZATION
AND OF INCREASED ROOT GROWTH RATE IN THE PHOSPHORUS
APPLICATION ON THE YIELDS OF ABOVE AND BELOW GROUND PORTIONS
OF FLAX, WHEAT, RAPE, AND BUCKWHEAT GROWN ON A FIRDALE AND A LAKELAND
SOIL IN 34 DAYS
(g)

Soil* Treatment** Crop		C	I N-F	F	C	II N-F	F
Flax	tops	.50a	.61b	.82c	1.01a	1.10a	1.04a
	roots	.26a	.33b	.59c	.31a	.37a	.54b
Wheat	tops	.64a	.87b	1.63c	.96a	1.07a	1.62b
	roots	.43a	.52a	1.02b	.46a	.51a	.98b
Rape	tops	1.67a	2.56b	3.43c	2.47a	3.15b	4.14c
	roots	.49a	.71b	1.24c	.63a	.67a	1.65b
Buckwheat	tops	4.83a	5.26a	5.18a	5.89a	6.18ab	6.35b
	roots	.74a	.79a	1.09b	1.04a	.94a	1.37b

Duncan's Multiple Range Test
Treatments followed by the same letter are not significantly different

* I Firdale (non-calcareous)
** II Lakeland (calcareous)
C Control
N-F non-funneled treatment
F funneled treatment

TABLE 2.2

MASS OF FLAX, WHEAT, RAPE AND BUCKWHEAT ROOTS RECOVERED FROM THE CYLINDER OF A CONTROL, NON-FUNNELED AND FUNNELED ON A FIRDALE AND A LAKELAND SOIL (mg)

Soil*	I			II		
Treatment** Crop	C	N-F	F	C	N-F	F
Flax	4	7	36	2	4	24
Wheat	7	17	51	3	8	54
Rape	10	57	100	12	34	72
Buckwheat	18	43	47	16	24	41

* I Firdale soil (non-calcareous)
II Lakeland soil (calcareous)

** C Control
N-F Non-funneled treatment
F Funneled treatment

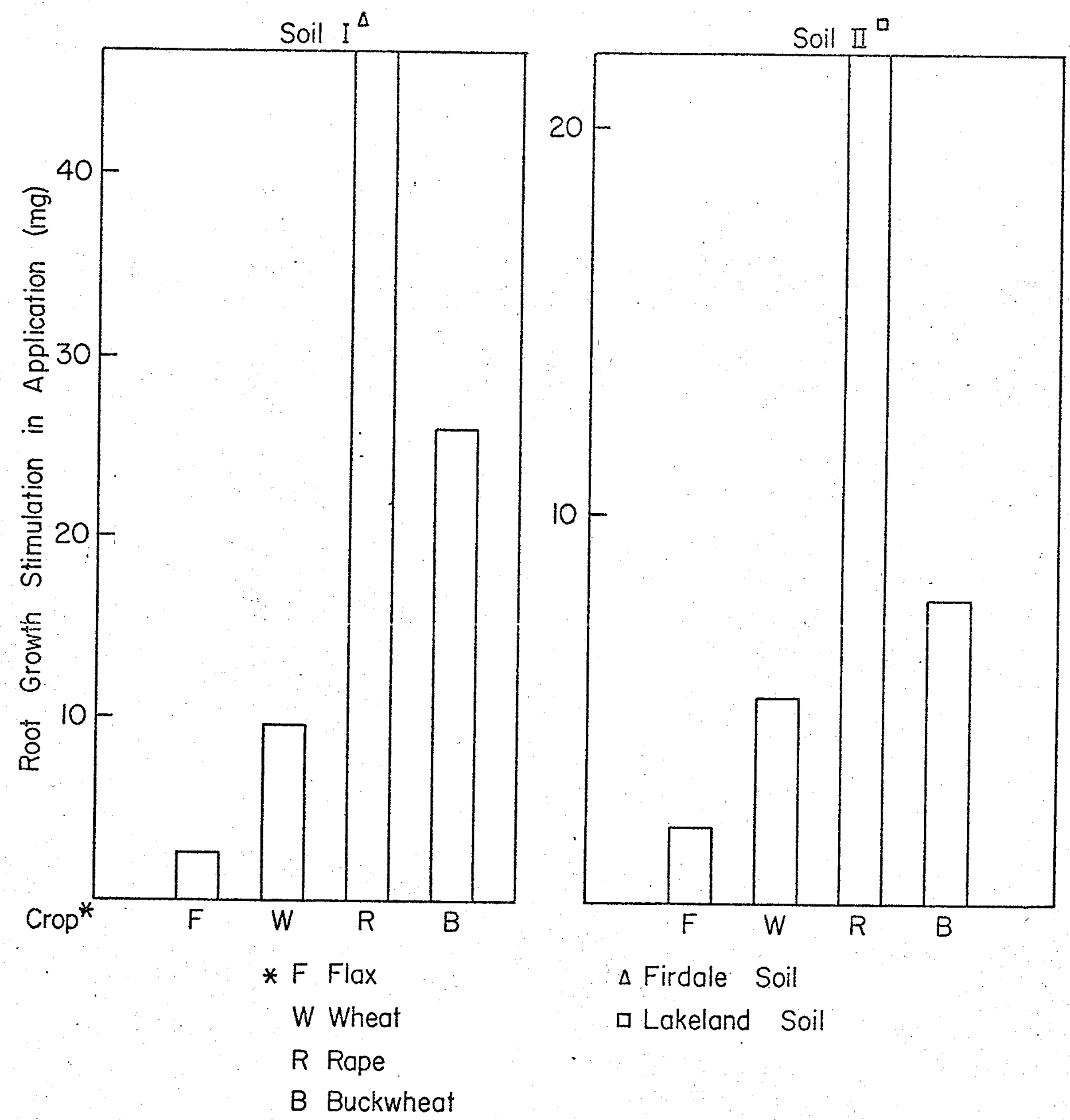


Figure 2.2. Growth Stimulation of Flax, Wheat, Rape and Buckwheat Roots in a Small Phosphorus Fertilized Soil Volume of a Firdale and a Lakeland Soil.

stimulation among the crops. Rape roots were stimulated at least 2 fold and up to 20 fold the growth of any other crop (figure 2.2). Roots of the four crops were stimulated within the phosphorus application of both soils in the order; rape > buckwheat > wheat > flax (figure 2.2).

Funneling roots through the phosphorus application was designed to increase the root mass which fed from the applied phosphorus. This treatment affected the crops quite differently in this regard. There was an approximately 2 fold or smaller increase in the root mass recovered from the cylinder of the funneled over that recovered from the cylinder of the non-funneled treatment for rape and buckwheat (Table 2.2). On the other hand, there was a 3 - 6 fold increase in the root mass recovered from the zone of applied phosphorus due to funneling flax or wheat roots through the applied phosphorus (Table 2.2). Since the root systems of each crop were funneled through the same volume of fertilized soil, the proportional increase in the number of roots which entered the zone of applied phosphorus, due to funneling, should have been similar for each crop. The total root system of each crop was stimulated on the funneled treatment over that of the control treatment (Table 2.1). This was presumably a growth response to the large amount of applied phosphorus utilized from the funneled treatment (figure 2.3). The root system produced on the funneled treatment was approximately double the root system produced on the control treatment of both soils for flax, wheat and rape (Table 2.1). The increased total root growth of these crops

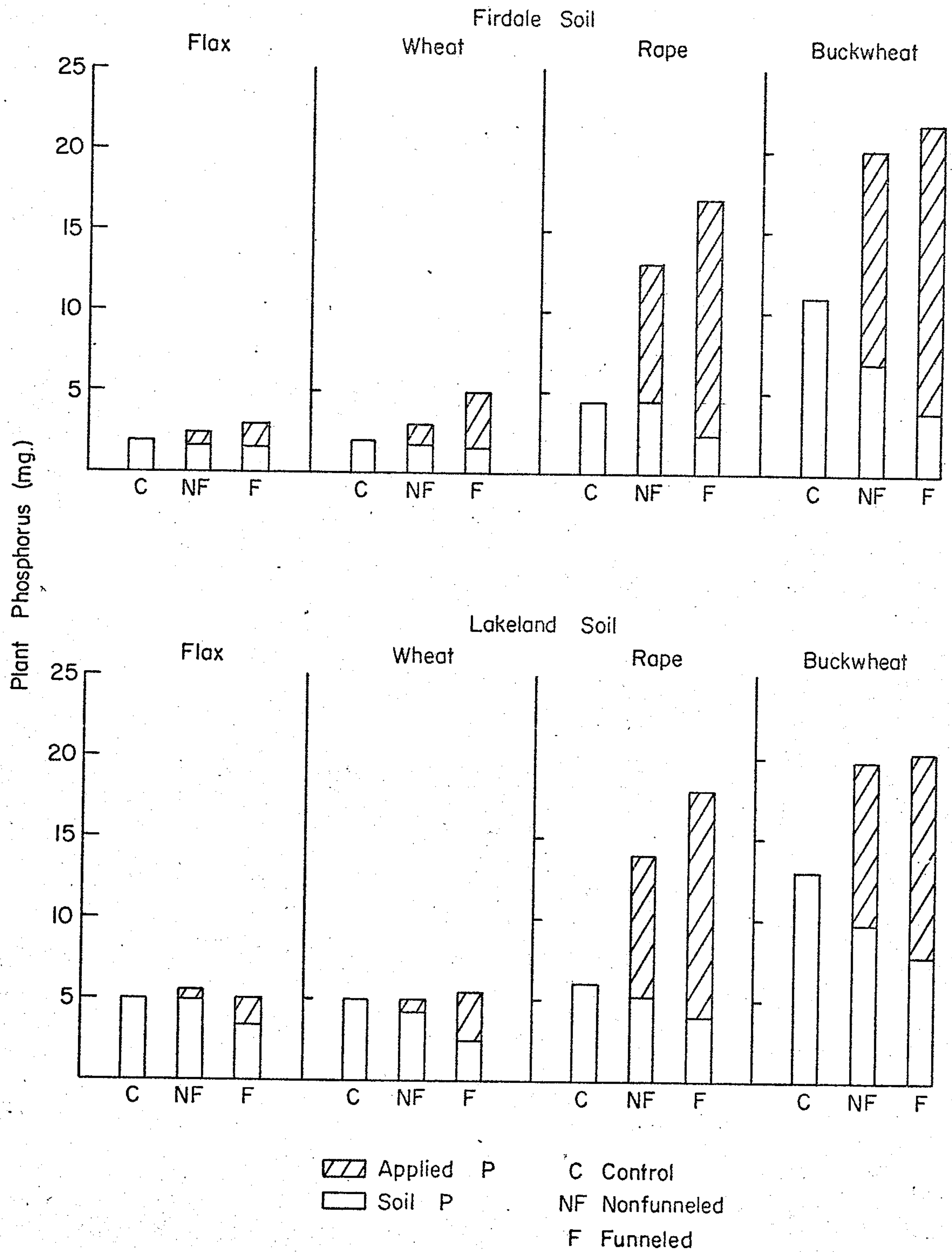


Figure 2.3. Phosphorus Uptake in 34 Days by Flax, Wheat, Rape and Buckwheat from a Control and from Two Phosphorus Fertilized Treatments Which Have Different Root Masses Feeding From the Small Phosphorus Fertilized Soil Volume.

should have resulted in a similar proportional increase in the number of their roots which entered the zone of applied phosphorus. It is suggested therefore that the different effect of the funneled treatment on the root mass feeding on the applied phosphorus was probably due to a difference in the effect of funneling on the growth rate of roots after entry into the zone of applied phosphorus.

Root growth rate was stimulated within the zone of applied phosphorus of the non-funneled treatment for each crop. The extent of the stimulatory effect on root growth due to the applied phosphorus was apparently not the same for the funneled and non-funneled treatments for all crops. The growth stimulation of roots in the zone of applied phosphorus of the funneled treatment relative to their growth stimulation in the non-funneled treatment was apparently less for rape than for flax or wheat. The quantity of phosphorus absorbed from the phosphorus fertilized treatments was greater for rape than for flax or wheat (figure 2.2). Thus it was more likely that the plant phosphorus requirement (or the 'sink' for phosphorus absorption in the plant) for rape rather than that for flax or wheat was provided by phosphorus fertilized treatments. The smaller apparent stimulation in the growth rate of rape roots than of flax or wheat roots due to funneling could have been the result of a greater depletion of the 'sink' for phosphorus absorption of rape than of the 'sink' for phosphorus absorption of flax or wheat.

Root growth within the phosphorus application of soil 1 was stimulated approximately double the extent of the stimulation within the phosphorus application of soil 2, for each crop (figure 2.2). This could have been the result of better root growth conditions within the phosphorus application of soil 1 than within the phosphorus application of soil 2. The water soluble phosphorus concentration within the application of the non-funneled treatment however, was lower in soil 1 than in soil 2 after cropping with each crop (table 2.4). Both soils contained sufficient nutrients, other than phosphorus, for optimum growth of the four crops. Thus, root growth conditions within the phosphorus applications of these two soils did not appear responsible for the different root growth stimulations within their applications .

The phosphorus supplying power of soil 1 was, as expected, significantly less than the phosphorus supplying power of soil 2. Each crop extracted less phosphorus from the control treatment of soil 1 than from the control treatment of soil 2 (figure 2.3). Hence, root growth stimulations of each crop within the phosphorus application were less on the soil of higher phosphorus supplying power, i.e. soil 2. It appeared, therefore, that the extent of root growth stimulation of these crops within the phosphorus application was affected inversely by the soil phosphorus supplying power. Increasing soil phosphorus supplying power to the plant could decrease growth stimulation of its roots within a phosphorus application through its effect on depleting the plant 'sink' for phosphorus absorption.

Applied phosphorus utilization by flax and wheat was increased 3-5 fold by funnelingroots through the phosphorus application (Table 2.3). Only small proportional increases in applied phosphorus utilization

TABLE 2.3

APPLIED PHOSPHORUS UTILIZATION
BY FLAX, WHEAT, RAPE AND BUCKWHEAT IN
34 DAYS FROM A FUNNELED AND NON-FUNNELED TREATMENT
(mg)

Soil* Treatment** Crop	I N-F	I F	** N-F	** F
Flax	0.35a	1.20b	0.28a	1.16b
Wheat	1.42a	3.70b	0.56a	3.17b
Rape	8.50a	14.03b	8.58a	13.77b
Buckwheat	12.38a	17.73b	9.44a	11.99b

Duncans Multiple Range Test
Means of Treatments on each soil follwed by the same letter are not significantly different.

* I Firdale (non-calcareous)
II Lakeland (calcareous)
** N-F non-funneled treatment
F funneled treatment

TABLE 2.4

WATER SOLUBLE PHOSPHORUS CONCENTRATION
IN THE PHOSPHORUS APPLICATION OF A FIRDALE AND A
LAKELAND SOIL AFTER 34 DAYS GROWTH OF FLAX, WHEAT, RAPE
AND BUCKWHEAT
($M \times 10^4$)

Soil*	I		II	
TreatmentII**	N-F	F	N-F	F
Flax	7.2	7.3	9.6	7.4
Wheat	7.5	7.1	9.9	--
Rape	7.6	7.8	9.2	7.0
Buckwheat	11.2	14.0	9.1	8.7

* I Firdale soil (non-calcareous)
II Lakeland soil (calcareous)

** N-F non-funneled treatment
F funneled treatment

resulted due to funneling roots of rape and buckwheat through the phosphorus application (Table 2.3). The smaller proportional increase in applied phosphorus utilization by rape and buckwheat due to funneling than by flax or wheat could have been due to a greater decrease in the availability of the applied phosphorus to the former two crops, during cropping. The water-soluble phosphorus concentration within the phosphorus application of both soils, was determined after cropping with flax, wheat, rape and buckwheat. Cropping with rape and buckwheat did not decrease the water-soluble phosphorus concentration within the phosphorus application of either soil any more than flax or wheat (Table 2.4). On the contrary, buckwheat had a slight stimulatory effect on the water-soluble phosphorus concentration within the phosphorus application of the non-calcareous soil (soil 1), relative to the other crops (Table 2.4). Thus, rape and buckwheat did not appear to decrease the applied phosphorus availability much more than flax or wheat.

Increases in the applied phosphorus utilization by flax, wheat, rape and buckwheat due to funneling their roots through the application were associated with similar proportionate increases in root growth within the phosphorus application. The 3-5 fold increases in applied phosphorus utilization by flax and wheat were associated with 3-6 fold increases in their root growths within the phosphorus application (Table 2.2). The small proportional increases in applied phosphorus utilization by rape and buckwheat were associated with 2 fold or smaller increases in their root growths within the phosphorus application (Table 2.2). Thus, root growth within the phosphorus application directly affected the utilization of applied phosphorus bythese four crops.

Roots of the four crops did not differ in the water-soluble phosphorus concentration which they maintained within the phosphorus application of the calcareous soil (Table 2.4). As was found in experiment 1, none of the crops appeared to measurably solubilize the reaction products produced between the applied phosphorus and the calcareous soil. On the other hand, buckwheat roots maintained a higher phosphorus concentration within the phosphorus application on the non-calcareous soil than did the other crops (Table 2.4). Buckwheat utilized as much as, or more than the applied phosphorus utilized by any of the other crops (Table 2.3). Hence, this crop should have depleted the applied phosphorus supply by as much as any of the other crops. Buckwheat roots, therefore, appeared to solubilize the reaction products formed between the applied DCPD and the non-calcareous soil.

Summary and Conclusions

The growth rate of flax, wheat, rape and buckwheat roots were stimulated within the concentrated applications of phosphorus on two soils. These increases in their root growth rate within phosphorus applications increased crop utilization of applied phosphorus.

The extent of the root growth stimulation within the phosphorus application depends on the crop. In increasing root growth stimulation within the phosphorus application the four crops ranked in the order;' flax, wheat, buckwheat and rape.

The extent of the growth stimulation of flax, wheat, rape and buckwheat roots within the phosphorus application was inversely affected by the soil phosphorus supplying power.

Buckwheat roots maintain a higher water-soluble phosphorus concentration within the reaction zone of dicalcium phosphate dihydrate and a non-calcareous soil than flax, wheat or rape.

4. EXPERIMENT III

Flax, wheat, rape, and buckwheat roots showed a greater growth stimulation within a phosphorus application of a soil of low phosphorus supplying power than they did within a similar phosphorus application on a soil of high phosphorus supplying power. An experiment was conducted to demonstrate the effect of soil phosphorus supplying power on the phosphorus utilization from a concentrated application of phosphorus, keeping other soil factors constant. The soil phosphorus supplying power was varied by mixing 0, 50 and 200ppm of phosphorus as dicalcium phosphate dihydrate crystals intimately with a soil of low phosphorus supplying power.

Materials and Methods

The soil used in this experiment (Plumridge) was chosen on the basis of its low phosphorus supplying power and its light texture. The latter property assisted root recovery. Some characteristics of the soil are shown in Table 0.1.

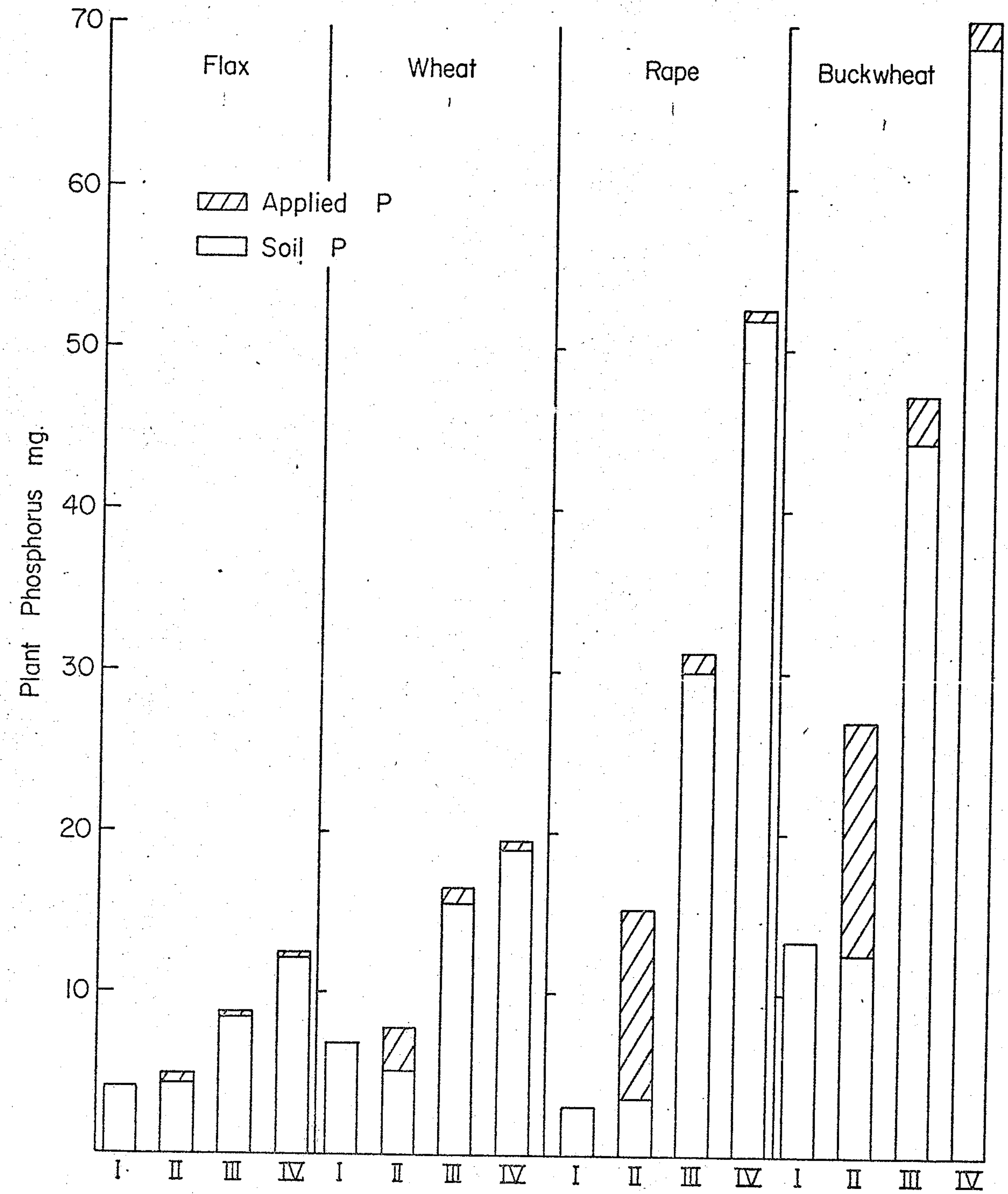
Three levels of phosphorus supplying power of the Plumbridge soil were achieved by mixing 0, 50 or 200ppm of phosphorus as dicalcium phosphate dihydrate (DCPD) intimately with 2Kg portions of the soil. The DCPD was incorporated into air dry soil by the process of progressive geometric dilution.

A concentrated application of phosphorus, occupying a specific soil volume (a cylinder 3.5 cms long and 2.8 cm diameter) was applied to the centre of the 2Kg soil mass in each pot. This application consisted of placing a mixture of 0.222g of radioactive DCPD (10 μc P^{32}/40mg P) and 22g of soil within an acrylic cylinder at the centre of each pot at the required depth. The cylinder was open at its top and bottom. A cylinder was similarly positioned in the control treatment to which 22g of soil only was added. Soil added to the cylinders had been crushed to pass through a 0.5mm sieve. Flax, wheat, rape and buckwheat were grown as test crops and the experiment was replicated four times, i.e. a total of 64 pots.

Nitrogen, potassium and sulphur were added to each pot at planting according to Table 0.2. Above and below ground portions of the crops were harvested 32 days after seeding. Roots were recovered from each pot in two portions, i.e. those from within the cylinder and the remainder. The water-soluble phosphorus concentration of soil recovered from the cylinder of each pot, was determined. Total phosphorus contents of above and below ground portions were determined for each pot. Phosphorus derived from the concentrated applications was also determined within the above and below ground portions of the fertilized plants.

Results and Discussion

Mixing DCPD crystals intimately with the soil had the desired effect of increasing the inherently low phosphorus supplying power of this soil. Each crop took up more phosphorus from treatments III and IV than from treatment II (figure 3.1). Mixing 50ppm of



I Control
II Concentrated application of phosphorus in 2Kg Soil
III Concentrated application in 2Kg Soil and 50ppm P as DCPD
IV Concentrated application in 2Kg soil and 200ppm P as DCPD

Figure 3.1. Phosphorus Uptake in 32 Days by Flax, Wheat, Rape and Buckwheat from Soil and From a Small Soil Volume Fertilized with Phosphorus at Three Soil Phosphorus Supplies

phosphorus as DCPD into the soil (treatment III) approximately doubled the phosphorus supply to plants already supplied with a concentrated application of phosphorus. Treatment III of each crop took up approximately twice as much phosphorus as treatment II (figure 3.1). Mixing 200ppm of phosphorus as DCPD into the soil (treatment IV) had approximately double the effect of the 50ppm application of phosphorus (treatment III) in increasing the phosphorus supply to flax, wheat, rape, and buckwheat plants already supplied with a concentrated application of phosphorus (treatment II), (figure 3.1).

Increasing the phosphorus supply to flax, wheat, rape and buckwheat decreased their utilization of phosphorus from the concentrated application. The amount of applied phosphorus which was taken up by each crop from the three treatments decreased in the order; II, III, IV (figure 3.1). There was a similar water-soluble phosphorus concentration within the phosphorus application of each of the treatments after cropping with flax, wheat, rape or buckwheat (table 3.1). Thus, utilization of applied phosphorus was apparently restricted by the plant rather than by the potential availability of the applied phosphorus.

Total root growth of none of the crops was increased by the concentrated application of phosphorus. The root mass recovered from treatment II did not differ significantly from the root mass recovered from the control for each crop (Table 3.2). However, a significantly greater root mass was recovered from the cylinder of treatment II than from the cylinder of the control for wheat, rape, and buckwheat (Table 3.3). The root mass recovered from the cylinder

TABLE 3.1

WATER SOLUBLE PHOSPHORUS CONCENTRATION
IN THE ZONE OF APPLIED PHOSPHORUS OF A PLUMRIDGE
SOIL AFTER 32 DAYS GROWTH OF FLAX, WHEAT, RAPE AND BUCKWHEAT
AT THREE LEVELS OF SOIL PHOSPHORUS SUPPLY
($M \times 10^{-4}$)

Treatment* Crop	II	III	IV
Flax	7.7	7.7	7.5
Wheat	6.9	8.1	6.2
Rape	4.8	8.6	8.2
Buckwheat	7.4	8.9	7.4

* II Concentrated application of phosphorus in 2Kg soil
III Concentrated application in 2Kg of soil + 50ppm of P as DCPD
IV Concentrated application in 2Kg soil + 200ppm of P as DCPD

TABLE 3.2

EFFECT OF SOIL PHOSPHORUS SUPPLYING POWER ON THE YIELD OF ABOVE AND BELOW GROUND PORTIONS OF FLAX, WHEAT, RAPE, AND BUCKWHEAT PLANTS FERTILIZED WITH A CONCENTRATED APPLICATION OF PHOSPHORUS (g)

Treatment* Crops		I	II	III	IV
Flax	tops	.91a	.98ab	1.12bc	1.23c
	roots	.20a	.29ab	.32b	.22ab
Wheat	tops	1.49a	1.63a	2.78b	2.80b
	roots	.37a	.37a	.48a	.47a
Rape	tops	1.12a	2.83b	4.31c	4.98d
	roots	.45a	.51a	.70ab	1.00b
Buckwheat	tops	6.46a	7.21ab	8.41c	8.20bc
	roots	1.05a	1.07a	1.24a	1.17a

Duncan's Multiple Range Test
Treatment means followed by the same letter are not significantly different.

* I Control
II Concentrated application of phosphorus in 2Kg soil
III Concentrated application in 2Kg soil + 50 ppm P as DCPD
IV Concentrated application in 2Kg soil + 200ppm P as DCPD

of treatment II did not differ significantly from the root mass recovered from the cylinder of the control for flax. However, the mass of flax roots recovered from the cylinder of treatment II was approximately double the mass recovered from the cylinder of the control (Table 3.3). As was found in experiment II, the growth rate of roots of each crop was stimulated within the zone of applied phosphorus. The amount of stimulation, however, varied greatly among the crops. The order of stimulation of roots of the four crops was the same as previously found; rape $>$ buckwheat $>$ wheat $>$ flax (Table 3.3). Similarly, the rate of phosphorus absorption by roots of the four crops was apparently stimulated within the phosphorus application. The apparent rate of phosphorus absorption by roots from the phosphorus application of treatment II was greater than their apparent rate of phosphorus absoprtion from the remainder of the soil mass for each crop (Table 3.4). Thus, the four crops stimulated the growth and rate of phosphorus absorption by their roots within the concentrated application of phosphorus at low soil phosphorus supply, the extent of these stimulations varying greatly among the crops.

When supplied with 2 - 3 fold increases in the soil phosphorus supply, the growth rates of flax, rape and buckwheat roots were not stimulated within the zone of applied phosphorus. The root masses recovered from the cylinders of treatments III and IV were not significantly different from the root mass recovered from the cylinder of the control for these three crops (Table 3.3). Apparently growth

TABLE 3.3

THE MASS OF FLAX, WHEAT,
RAPE AND BUCKWHEAT ROOTS RECOVERED
FROM THE CYLINDER AFTER 32 DAYS GROWTH AT
THREE LEVELS OF SOIL PHOSPHORUS SUPPLY
(mg)

Treatment* Crop	I	II	III	IV
Flax	2.2a	4.3a	2.1a	3.1a
Wheat	3.6a	14.3b	8.9b	8.6b
Rape	4.5a	55.8b	6.3a	5.4a
Buckwheat	5.1a	34.1b	10.4a	7.5a

Duncan's Multiple Range Test
Means of treatments followed by the same letter are not significantly different.

* I Control
II Concentrated application of phosphorus in 2Kg soil
III Concentrated application in 2Kg soil + 50ppm of P as DCPD
IV Concentrated application in 2Kg soil + 200ppm of P as DCPD

stimulation of flax, rape and buckwheat roots was adversely affected by increasing the total phosphorus supply to these plants. Growth stimulations of roots of these crops within the phosphorus application, therefore, could have been plant responses to a low phosphorus supply.

The mass of wheat roots recovered from the cylinder of treatments III and IV were significantly greater than the control but less than treatment II (Table 3.3). Apparently increasing the soil phosphorus supply to wheat had only a slight adverse effect on the growth stimulation of its roots in the phosphorus application. This could have been due to the fact that only a portion of the growth response of wheat roots within the phosphorus application was a plant response to low phosphorus supply. The remainder of the growth stimulation of wheat roots within the phosphorus application could have been a root growth response to the high phosphorus supply.

Increases in total phosphorus absorption by each crop, due to increases in the soil phosphorus supplying power, were associated with increases in the rate of phosphorus absorption by their roots from the soil mass (excepting the phosphorus application). The phosphorus absorbed in 32 days per unit mass of root recovered from the soil mass external to the phosphorus application was greater in treatments III and IV than in treatment II for each crop (table 3.4). Similarly, decreases in applied phosphorus absorption by each crop, due to increases in the soil phosphorus supplying power, were associated with decreases in the rate of phosphorus absorption by

TABLE 3.4

APPARENT RATES OF PHOSPHORUS ABSORPTION OF FLAX, WHEAT, RAPE, AND BUCKWHEAT ROOTS FROM THE SOIL MASS AND FROM A CONCENTRATED APPLICATION AT THREE LEVELS OF SOIL PHOSPHORUS SUPPLY, i.e. PHOSPHORUS UTILIZED FROM EACH SOURCE IN 32 DAYS PER UNIT MASS OF ROOTS RECOVERED FROM THE RESPECTIVE SOURCE (mg phosphorus/g root/32 days)

Treatment*		I	II	III	IV
Crop	P source				
Flax	Soil mass	21a	15a	26a	56b
	application		86b	90b	50a
Wheat	Soil mass	19a	14a	33b	40b
	application		177b	96a	53a
Rape	Soil mass	7a	7a	44b	53b
	application		206b	190b	116a
Buckwheat	Soil mass	13a	12a	36b	59c
	application		431b	283a	214a

Duncan's Multiple Range Test
Means of treatments followed by the same letter are not significantly different

* I Control
II Concentrated application of phosphorus in 2Kg soil
III Concentrated application in 2Kg soil + 50ppm P as DCPD
IV Concentrated application in 2Kg soil + 200ppm P as DCPD

their roots from the phosphorus application. Increasing the soil phosphorus supply by 2 and 3 fold decreased the applied phosphorus absorbed per unit mass of roots recovered from the phosphorus application for wheat and buckwheat (Table 3.4). Only on increasing the soil phosphorus supply by 3 fold was the applied phosphorus absorbed per unit mass of roots recovered from the phosphorus application decreased for flax and rape. Thus, increasing the soil phosphorus supplying power to these four crops increased the rate of phosphorus absorption of their roots from the soil external to the phosphorus application while simultaneously decreasing their rates of phosphorus absorption from within the phosphorus application.

The 3 fold increase in soil phosphorus supply to flax and wheat plants decreased the rates of phosphorus absorption by their roots from the phosphorus application to approximately their rates of phosphorus absorption from the reaminder of the soil mass (Table 3.4). On the other hand, the 3 fold increase in soil phosphorus to rape and buckwheat plants failed to decrease the rates of phosphorus absorption of their roots from the phosphorus application to their rates of phosphorus absorption from the remainder of the soil mass (Table 3.4). Asher and Loneragan (4) suggested that the rate of phosphorus absorption by plants is limited by a maximal capacity of individual plant parts for phosphorus accumulation. The present results suggest, therefore, that a three fold increase in the phosphorus supplying power of this soil to the four crops provided sufficient phosphorus for its maximum accumulation by flax and wheat plants but not by rape or buckwheat plants. Consequently, the large variability among crops in the total phosphorus taken up from high soil phosphorus supplies (treatments III and IV) are probably indicative of the large variability among the crops in the capacity of their 'sinks' for phosphorus absorption. In this regard, rape and buckwheat appear to have much larger 'sinks' for phosphorus absorption than flax or wheat (figure 3.1). This large variability among crops in their 'sink' size could be one reason for the large variability among crops in their root behavior within phosphorus applications, i.e. roots of a crop with a large 'sink' for phosphorus absorption being stimulated in growth and rate of phosphorus absorption more than roots of a crop with a small 'sink'.

Conclusion

The extent of growth and phosphorus absorption by roots near a concentrated application of phosphorus are stimulated to a greater extent in soils of low phosphorus supply than in soils of high phosphorus supply.

5. Experiment IV

The reaction products formed between soil and applied phosphorus are the compounds from which plants extract their applied phosphorus. Provided that the rate of dissolution of these compounds is greater than the rate of absorption of applied phosphorus, then the rate of applied phosphorus utilization is probably controlled by the phosphorus concentration maintained by the reaction products. The objective of this experiment was to study the effect of phosphorus concentration within the reaction zone on the utilization of applied phosphorus by flax, wheat, rape and buckwheat.

The rate of phosphorus utilization from a concentrated application can be described by the growth rate as well as the rate of phosphorus absorption of the roots within the reaction zone. The effect of phosphorus concentration within the reaction zone on the rate of applied phosphorus utilization was studied, therefore, by comparing the growth rates and rates of phosphorus absorption of roots of these crops within zones of various water-soluble phosphorus concentrations. Three phosphorus concentrations within the reaction zone were maintained by mixing calcium phosphate compounds, of varying solubility products in water, with a small fractional soil volume, i.e. hydroxyapatite, pK_{sp} 115.5 at 25°C (24), octacalcium phosphate, K_{sp} 1.25×10^{-47} at 25°C (113) and dicalcium phosphate dihydrate, K_{sp} 2.77×10^{-7} at 25° C (112).

Cropping with flax, wheat, rape, and buckwheat, appreciably decreased the water soluble phosphorus concentration within concentrated applications of phosphorus, presumably due to crop removal of applied phosphorus (experiment I). Crops which extracted a large proportion of the applied phosphorus (rape and buckwheat) decreased the phosphorus concentration more than crops which extracted only a small proportion of the applied phosphorus (flax and wheat). Knowledge of the effect of reaction zone phosphorus concentration on the rate of applied phosphorus utilization by these crops might give some indication of their rates of utilization of applied phosphorus during cropping.

Materials and Methods

The Plumridge soil, used in experiment III was also used in this study. Hydroxyapatite (HA), $Ca_{10}(PO_4)_6 \cdot (OH)_2$, pK_{sp}:115.5 at 25°C (24), octacalcium phosphate (OCP), $Ca_4H(PO_4)_3 \cdot 3H_2O$, K_{sp}:1.25×10^{-47} at 25°C (113), and dicalcium phosphate dihydrate (DCPD), $CaHPO_4 \cdot 2H_2O$, K_{sp}: 2.77×10^{-7} at 25°C (112) were labelled with radio phosphorus during their preparation, 10µc/40mg of phosphorus for DCPD and OCP and 20µc/40mg of phosphorus for HA. Amounts of these radio active compounds equivalent to 40 mg of phosphorus were intimately mixed with 22g of soil which had been crushed to pass through a 0.5mm sieve. The soil-DCPD, soil-OCP or soil-HA mixture was then placed in an acrylic cylinder at the centre of the 2Kg soil mass within the pot. The cylinder was of the same dimensions as that used in experiments II and III. 16 pots of each of these 3 treatments were set up as well as 16 control pots. The control pot contained a cylinder similarly positioned at the centre of the soil mass but which contained 22g of soil only. Flax, wheat, rape and buckwheat were used as test crops. The experiment was replicated four times. Nitrogen, potassium and sulphur were added at planting according to Table 0.2.

The above and below ground portions of the four crops were harvested 34 days after seeding. The roots were recovered in two portions; i.e. those within the cylinder and the remainder. The water-soluble phosphorus concentration of the soil within the cylinder of each pot was determined. Total phosphorus contents of above and below ground portions were determined for each pot. Applied phosphorus content of above and below ground portions of fertilized plants were also determined.

Results

It was demonstrated in experiment III that flax, wheat, rape, and buckwheat made better utilization of phosphorus from a concentrated application when the phosphorus supplying power of the soil was low. In order to study the effect of reaction zone phosphorus concentration on their applied phosphorus utilization, measurable utilization of phosphorus by these crops from the phosphorus application was required. Accordingly, a soil of low phosphorus supplying power was used in this experiment.

In spite of the low phosphorus supply from the soil, flax and wheat could not enhance their phosphorus supply from the concentrated applications of hydroxyapatite, octacalcium phosphate or dicalcium phosphate dihydrate (figure 4.1). Thus, the growth of above and below ground portions of neither crop responded to any of these phosphorus applications (Table 4.1). The concentrated application of hydroxapatite did not increase the phosphorus supply to rape or buckwheat (figure 4.1). However, their total phosphorus supply was increased by the octacalcium

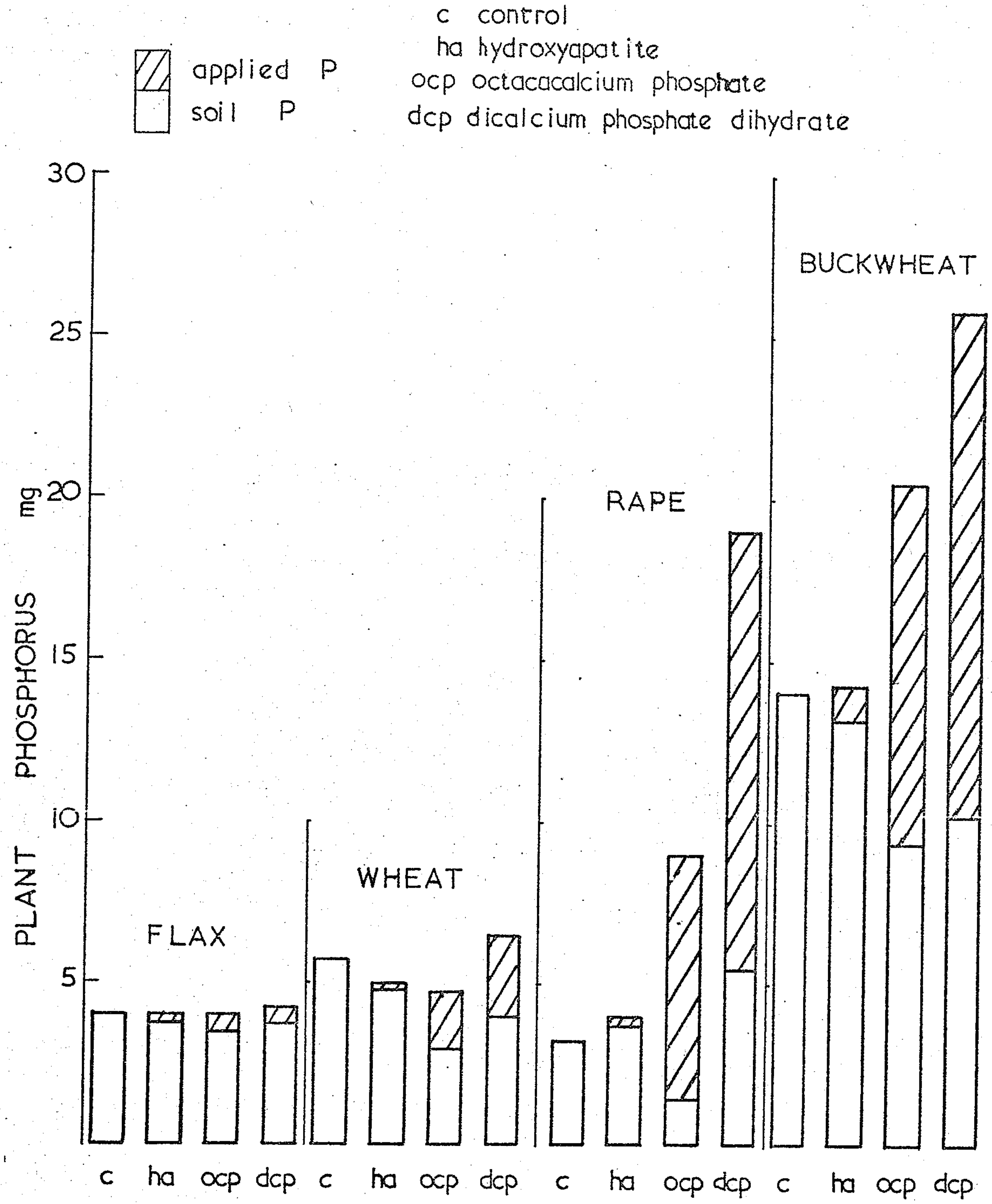


Figure 4.1. Phosphorus Uptake in 34 Days by Flax, Wheat, Rape, and Buckwheat from a Plumridge Soil and From a Small Soil Volume Fertilized with Hydroxyapatite, Octacalcium Phosphate or Dicalcium Phosphate Dihydrate.

TABLE 4.1

YIELD OF ABOVE AND BELOW
GROUND PORTIONS OF FLAX, WHEAT,
RAPE, AND BUCKWHEAT SUPPLIED WITH A
CONCENTRATED APPLICATION OF HYDROXYAPATITE,
OCTACALCIUM PHOSPHATE AND DICALCIUM PHOSPHATE DIHYDRATE
(g)

Treatment Crop		Control	HA*	OCP#	DCPD##
Flax	tops	1.03ab	0.99a	1.01ab	1.12b
	roots	.32a	.35a	.34a	.38a
Wheat	tops	1.17a	1.06a	0.94a	1.31a
	roots	.40a	.31a	.27a	.38a
Rape	tops	1.10a	1.43a	2.72b	3.34b
	roots	.32a	.46a	.48a	.73b
Buckwheat	tops	8.42ab	8.01a	8.33a	9.58b
	roots	1.17a	1.66b	1.58b	1.14a

Duncan's Multiple Range Test
Means of treatments followed by the same
letter are not significantly different.

* Concentrated application of Hydroxyapatite
\# Concentrated application of Octacalcium phosphate
\## Concentrated application of Dicalcium phosphate dihydrate

phosphate and dicalcium phosphate dihydrate applications (figure 4.1). Growth response to the increased phosphorus supply occurred for rape and buckwheat. Only the top growth of rape was increased by the concentrated application of octacalcium phosphate, while both top and root growth were increased by the dicalcium phosphate dihydrate application (Table 4.1). The dicalcium phosphate dihydrate treatment supplied approximately double the quantity of phosphorus to rape, as the octacalcium phosphate treatment (figure 4.1). Apparently the above ground portion of rape was first increased by increasing its total phosphorus supply. Growth of its below ground portion was eventually increased as its phosphorus supply was further increased.

In contrast, root growth of buckwheat was significantly increased due to the concentrated applications of hydroxyapatite and octacalcium phosphate, while its top growth was increased by the dicalcium phosphate dihydrate application (Table 4.1). Phosphorus uptake by buckwheat on the three fertilized treatments, increased in the order; hydroxyapatite, octacalcium phosphate, dicalcium phosphate dihydrate (figure 4.1). Apparently, increasing the phosphorus supply to buckwheat, first increased its root growth. On further increasing its phosphorus supply top growth, rather than root growth, was increased.

Flax utilized only a small quantity of phosphorus from the three applications (figure 4.1). Hence it was expected that this crop would have had the least effect of the four crops in lowering the phosphorus concentration within these applications. This was in fact the case (Table 4.2). The water soluble phosphorus concentration to which roots were initially exposed on entering the zone of applied phosphorus was therefore greater than 7.6×10^{-4}M, 3.4×10^{-4}M and 1.3×10^{-4}M for dicalcium phosphate dihydrate, octacalcium phosphate and hydroxyapatite application, respectively (Table 4.2).

Phosphorus utilization by wheat, rape and buckwheat from the concentrated applications increased in the order of increasing water-soluble phosphorus concentration, i.e. hydroxyapatite, octacalcium phosphate, dicalcium phosphate dihydrate (figure 4.2). Flax utilized equally as much phosphorus from octacalcium phosphate as from dicalcium phosphate dihydrate but considerably less from hydroxyapatite (figure (4.2).

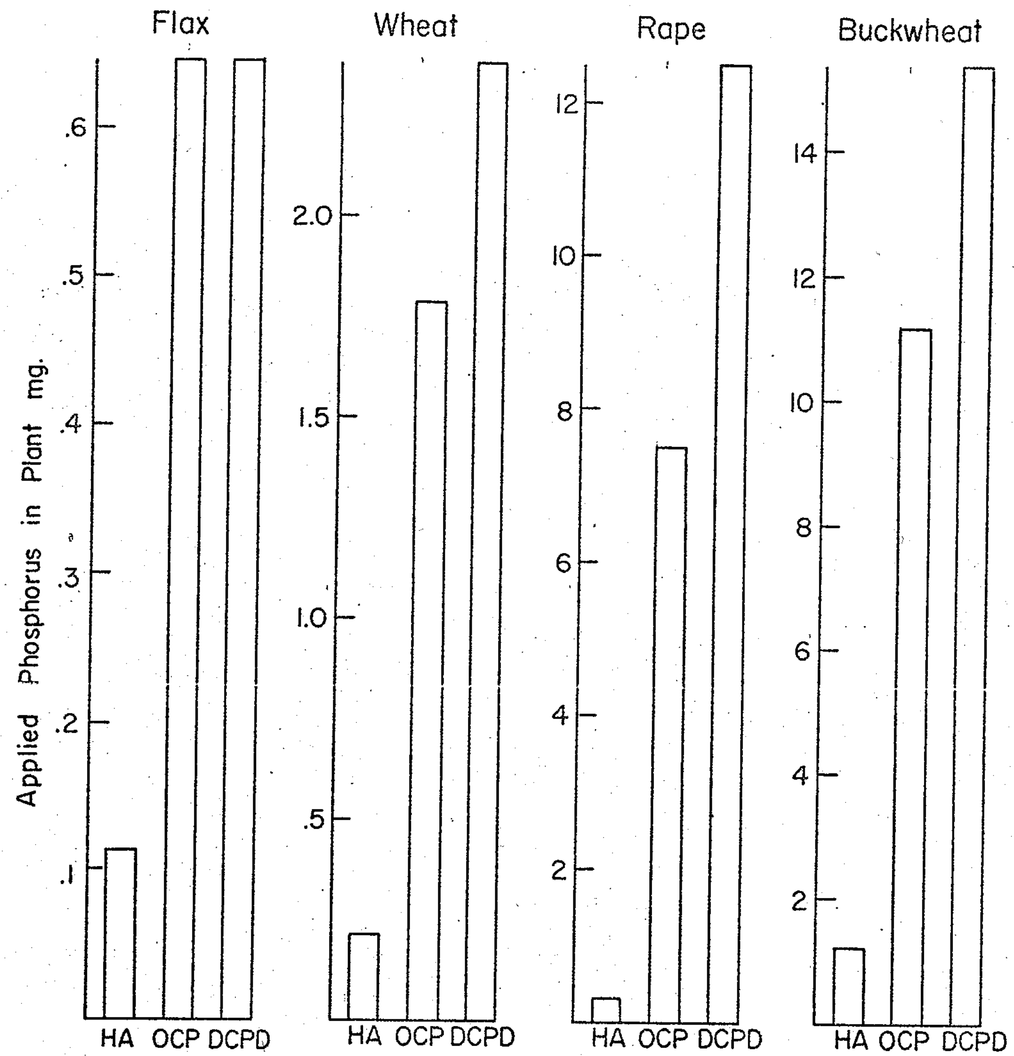
As was found in experiment III, the growth rate and rate of phosphorus absorption by flax, wheat, rape, and buckwheat roots were stimulated within the dicalcium phosphate dihydrate application of this soil relative to the growth rate and rate of phosphorus absorption by the remainder of their root systems (Tables 4.3 and 4.4 respectively). Decrease in applied phosphorus utilization due to decreasing the phosphorus concentration of the application was associated with a decrease in the stimulation of one or both these root properties of each crop. Root growth of each crop was not significantly stimulated within the hydroxyapatite application (Table 4.3). However, root growth of each crop was stimulated to a similar extent within the zones of applied octacalcium phosphate and dicalcium phosphate (Table 4.3). The rate of phosphorus absorption from dicalcium phosphate dihydrate did not differ significantly from the rate of phosphorus absorption from octacalcium phosphate for flax or wheat roots (Table 4.4). However, the rate of phosphorus absorption, by roots of each of these crops, from hydroxyapatite, was significantly lower than the rate of absorption from dicalcium phosphate dihydrate (Table 4.4). The rate of phosphorus absorption from the three applications decreased as the water solubility of the applied phosphorus decreased for rape and buckwheat roots, i.e. DCPD $>$ OCP $>$ HA (Table 4.4).

TABLE 4.2

WATER SOLUBLE PHOSPHORUS CONCENTRATIONS OF SOIL TAKEN FROM CONCENTRATED APPLICATIONS OF HYDROXYAPATITE, OCTACALCIUM PHOSPHATE AND DICALCIUM PHOSPHATE DIHYDRATE AFTER CROPPING WITH FLAX, WHEAT, RAPE AND BUCKWHEAT ($x10^4$M)

Treatment Crop	HA*	OCP#	DCPD##
Flax	1.3	3.4	7.6
Wheat	0.9	2.0	7.6
Rape	1.0	0.9	5.9
Buckwheat	0.8	0.9	6.8

HA Hydroxyapatite
OCP Octacalcium phosphate
DCPD Dicalcium phosphate dihydrate



HA - Hydroxyapatite OCP Octacalcium Phosphate
DCPD - Dicalcium Phosphate Dihydrate

Figure 4.2. Phosphorus Uptake in 34 Days by Flax, Wheat, Rape and Buckwheat From a Small Soil Volume Fertilized with Hydroxyapatite, Octacalcium Phosphate and Dicalcium Phosphate

TABLE 4.3

THE MASS OF FLAX, WHEAT, RAPE, AND BUCKWHEAT ROOTS RECOVERED FROM CONTROL, HYDROXYAPATITE, OCTACALCIUM PHOSPHATE AND DICALCIUM PHOSPHATE DIHYDRATE CYLINDERS (mg).

Treatment* Crop	Control	HA	OCP	DCPD
Flax	4.8a	6.2a	14.2b	11.9ab
Wheat	4.3a	5.5a	12.3ab	16.6b
Rape	8.5a	20.5a	84.8b	86.1b
Buckwheat	9.5a	14.5a	27.0b	29.1b

Duncan's Multiple Range Test
Means of treatments followed by the same letter are not significantly different.

* Control
HA Concentrated application of Hydroxapatite
OCP Concentrated application of Octacalcium phosphate
DCPD Concentrated application of Dicalcium phosphate dihydrate

TABLE 4.4

APPARENT RATES OF PHOSPHORUS ABSORPTION OF FLAX, WHEAT, RAPE, AND BUCKWHEAT ROOTS FROM THE SOIL AND CONCENTRATED APPLICATION OF HYDROXYAPATITE, OCTACALCIUM PHOSPHATE AND DICALCIUM PHOSPHATE DIHYDRATE, i.e. PHOSPHORUS UTILIZED FROM EACH SOURCE IN 34 DAYS PER UNIT MASS OF ROOTS RECOVERED FROM THE RESPECTIVE SOURCE
(mg phosphorus/g root/34 days)

Treatment Crop	Psource	Control	HA*	OCP#	DCPD##
Flax	soil	12	9	10	11
	application		20a	51ab	64b
Wheat	soil	14	10	11	14
	application		35a	151b	178b
Rape	soil	10	8	3	7
	application		13a	88b	151c
Buckwheat	soil	12	9	6	8
	application		72a	416b	527c

Duncan's Multiple Range Test
Means of treatments followed by the same letter are not significantly different.

* Concentrated application of hydroxyapatite
\# Concentrated application of octacalcium phosphate
\## Concentrated application of dicalcium phosphate dihydrate

Discussion and Conclusions

As the water solubility of the calcium phosphate compounds within the zone of applied phosphorus decreased, the stimulation of growth and rate of phosphorus absorption of roots feeding on the applied phosphorus decreased. Thus, it was concluded that the type of reaction products formed within the zone of spread of applied phosphorus, in calcareous soils, would significantly affect the availability of pelleted applications of phosphorus, to each of the crops studied. It was further concluded, that as the water solubility of the soil-fertilizer reaction products of calcareous soils decreased, due to crop phosphorus removal, the availability of the applied phosphorus decreased. This effect of crop phosphorus removal on the availability of applied phosphorus was probably greater for rape and buckwheat than for flax or wheat since rape and buckwheat utilized a greater proportion of the applied phosphorus than flax or wheat.

During the 34 days cropping rape and buckwheat decreased the water solubility of the OCP application to that of the HA application (Table 4.2). While there was no growth stimulation of rape or buckwheat roots within the HA application, there was a significant growth stimulation within the OCP application (Table 4.3). These results suggest that growth stimulation of rape and buckwheat roots within phosphorus applications probably occur in the early growth stages of these crops, prior to significant crop removal of applied phosphorus.

B. EXCISED ROOT EXPERIMENTS

1. General - Materials and Methods

Two experimental techniques using excised flax, wheat, rape and buckwheat root tissue were employed. A technique similar to that used by Noggle and Fried (115) was used to study the kinetics of phosphorus absorption from pure solutions.

Seeds were pregerminated in distilled water for 24 hours and placed on wire screens covered with cheese cloth. The screens were supported 1 cm above aerated nutrient solution. The nutrient solution contained:

1M $Ca(NO_3)_2$	5mls/litre
1M $MgSO_4$	2mls/litre
1M KNO_3	5mls/litre
NaH_2PO_4	to 3ppm of phosphorus

Fe as Sequestrene 138 Fe, Iron Chelate,-sodium ferric ethylenediamine di-(O-hydroxyphenylacetate)

The solution was changed frequently. Seedlings were grown under artificial light of approximately 1000 ft-c intensity and a day length of 16 hours. Day temperatures ranged from 27°C-32°C and night temperatures 21°C to 24°C. Roots were excised after 10-14 days growth, rinsed four times, and placed in distilled water. Solutions of KH_2PO_4 (10^{-6}M, 10^{-5}M, 0.5×10^{-4}M, 10^{-4}M, 0.5×10^{-3}M, and 10^{-3}M) were prepared and the pH of each adjusted to pH 4 (56).

The solutions were labelled with P^{32}, 100 μc/litre, except for the $10^{-6}M$, $0.5 \times 10^{-5}M$ and $10^{-5}M$ phosphorus concentrations which were labelled with 10 μc/litre. Two experiments were conducted using the technique to be described below. One consisted of a study of phosphorus sorption by flax, rape, and buckwheat roots from solutions of $10^{-6}M$, $10^{-5}M$, $10^{-4}M$, and $10^{-3}M$ phosphorus as KH_2PO_4 for intervals up to 100 minutes. The other was a study of the kinetics of short-term phosphorus sorption by roots of four crops (flax, wheat, rape, and buckwheat) from solutions of $10^{-6}M$, $0.5 \times 10^{-5}M$, $10^{-5}M$, $0.5 \times 10^{-4}M$, $10^{-4}M$, $0.5 \times 10^{-3}M$ and $10^{-3}M$ KH_2PO_4 for periods of 10 minutes, and for 2, 4, 6, and 8 minutes also from the $10^{-6}M$ and $10^{-3}M$ solutions.

Approximately 1g fresh weight of roots of each species was used for each sorption. Roots were placed in beakers and covered with distilled water. Prior to the sorption period, the water was decanted and the labelled solution (approximately 150 ml) added.

Two complete sets of phosphorus sorptions were carried out similtaneously. One set was rinsed with distilled water after the sorption period. This was designed to remove labelled phosphorus solution adsorbed to the roots. The other set of roots was rinsed with non-radioactive phosphorus solution of the same concentration used during sorption. This rinsing was designed to remove exchangeable as well as adsorbed label from the roots.

After rinsing, roots were transferred to pre-weighed aluminium planchettes and dried under an Infra-Red lamp. When roots were dry, the planchettes were re-weighed to obtain the dry weight of roots used in the sorption. Samples were counted under an end window Geiger Muller tube. 1ml aliquots of the radioactive solutions used in the sorption were used as standards. Thus, knowing the specific activity of the standard (counts per minute per millimole of phosphorus) phosphorus sorbed by the roots could be calculated from the amount of radioactivity they had sorbed, (counts per minute).

To study exchangeable and releasable phosphorus of excised flax, wheat, rape, and buckwheat roots, seeds were pre-germinated for 24 hours and grown through wire screens as in other excised root studies. Phosphorus was with-held from the growth medium so that the only phosphorus present was that of the seed reserves. A 10^{-4}M $CaSO_4$ solution (aerated) was used as the growth medium, since tissue breakdown has been reported in the absence of the Ca^{++} ion (154). The solution was renewed regularly.

After 6 to 10 days growth on the $CaSO_4$ solution, a pre-weighed mass of freshly excised roots was packed into a column of 2cm internal diameter, shown in Fig. 5.1. An outlet tube of 0.5cm internal diameter was fitted to the base of the column. A sieve to retain the roots was supported approximately 0.5 cm from the bottom of the column.

A close-fitting hard rubber stopper sealed the top of the column. There were three openings through this stopper, one each for water and phosphorus solution inlets and one to allow adjustment of the solution volume in contact with the root mass (void volume). Each inlet line was fitted with a stopcock for on-off control of solution flow and for rapid change-over from one solution to another. Since solution flow

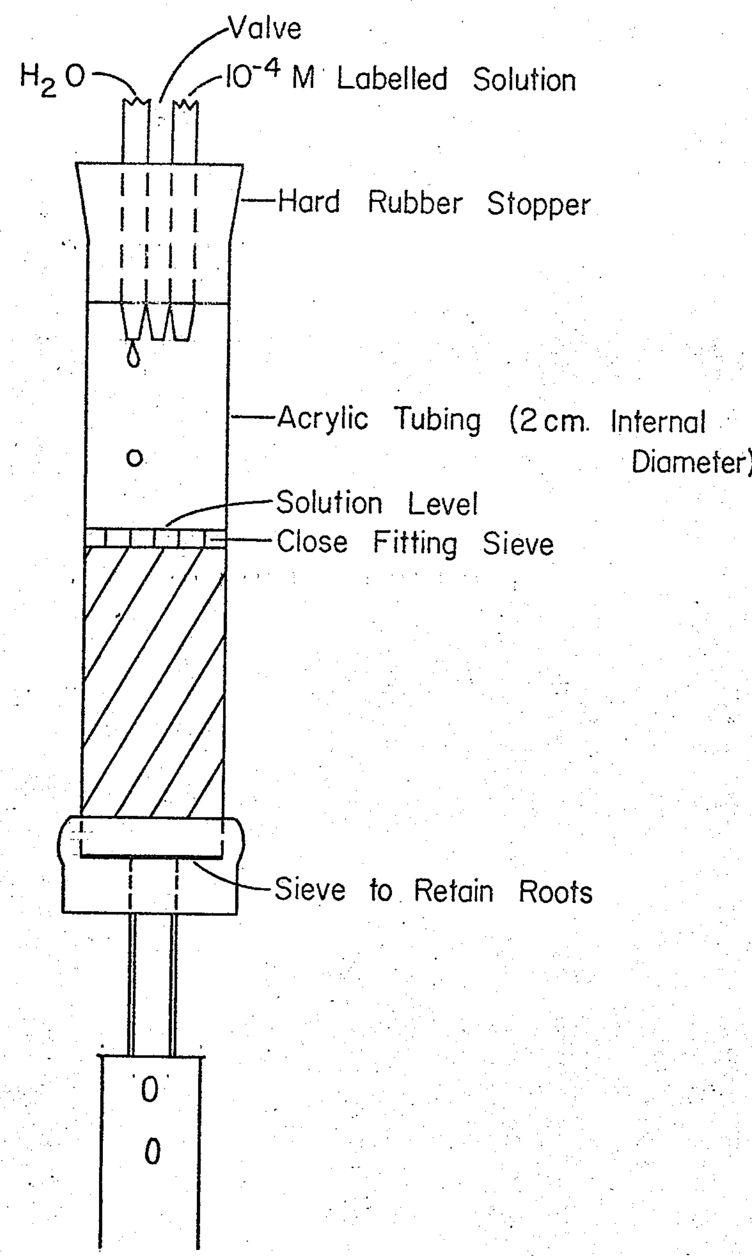


Figure 5.1. Diagramatic Representation of Column Used For the Study of Exchangeable or Releasable Phosphorus

rates depended on gravity feed, solution reservoirs were chosen which provided a large solution surface area so that the flow rate remained reasonably constant during the sorption study. Solution flow rates were controlled by adjusting the reservoir solution surface height above that of the column outlet. Approximately 1m of heavy glass walled capillary tubing, of 0.5mm internal diameter between the reservoir and the column inlet also contributed to the maintenance of a constant flow rate of~1ml per minute.

The eluent from the column was collected continuously in 12 x 75mm test tubes. For each sorption experiment, flow of each solution through the column was pre-adjusted to a common rate.

A pre-weighed mass of freshly excised roots, usually 5g or 10g, was packed carefully into the column under water so as not to damage the roots. A sieve, which fitted neatly inside the column was placed on top of the root mass to maintain a constant void volume and to ensure that roots would remain covered with the bathing solution. Entrapped air was bled from the inlet lines. The void volume , i.e. the volume of solution in contact with the roots, was then adjusted. Finally all joints were covered with silicone grease to maintain airtight seals.

Water was first passed over the root mass (approximately 3 void volumes) to remove traces of phosphorus released from the cut root end or from damaged tissue.

At the completion of the sorption experiment, several fractions of the eluent were weighed to determine the average flow rate. The void volume was also measured at the completion of the experiment. Thus, the time of contact between solution and root mass was obtained: Time of contact = Void Volume/Flow Rate.

The concentrations of both radiophosphorus and total phosphorus were determined on each eluent fraction. The concentration of radiophosphorus was determined on a 1 ml sample spread on an aluminum planchette, dried under an IR lamp, and counted under an end-window GM tube. Total phosphorus concentrations were determined using procedures outlined by Jackson (78), depending on the concentration ranges. These methods were scaled down since only 1 to 2 ml aliquots were available for the test.

2. EXPERIMENT V

A study was made of the use of excised root tissue in phosphorus absorption measurements. The ultimate objective of the excised root studies was to compare the rates of phosphorus absorption of excised flax, wheat, rape, and buckwheat roots from phosphorus concentrations of 10^{-6}M to 10^{-3}M with their apparent rates of phosphorus absorption from concentrated applications of water-soluble phosphates. Noggle and Fried (115) analysed, kinetically, the sorption of radioactive phosphorus by millet, barley, and alfalfa roots, from P^{32} labelled phosphorus solutions, which was not removed by post-sorption rinsing with distilled water. Thus, they considered that the fraction of the sorbed labelled phosphorus, in the form of carrier-phosphate complex, assumed to be exchangeable with the external solution, was a portion of the phosphorus actively absorbed by the root. Helder (66) suggested the existence of a large exchangeable phosphorus pool in the root. On the basis of the possible existence of an exchangeable pool of phosphorus in the root, other than the carrier-phosphate complex, a preliminary comparative study of post-sorption root treatment was undertaken. Two post-sorption root treatments were compared, i.e. rinsing with distilled water or rinsing with a non-labelled phosphorus solution of the same concentration as the P^{32} labelled sorption solution.

The carrier hypothesis has received most attention in studies of phosphorus absorption. Other theories have been put forward, however, with some supporting evidence (66, 104). Recent isolation of functional ion carriers from biological systems has given more support for the carrier theory (125). Helder (66) suggested that true phosphorus absorption was preceded by an exchange reaction between phosphorus in the root and phosphorus in the solution. Phosphorus absorption studies, particularly those using excised roots (2, 61, 115), have utilized radiophosphorus, P^{32}, to label the sorption solution. This enabled otherwise undetectible amounts of sorbed phosphorus to be accurately determined. In such a system the existence of an exchange reaction, as suggested by Helder (66), would give rise to the deposition of P^{32}, from the solution, into an exchangeable phosphorus fraction within the root tissue. Hence, this would result in an over-estimate of the rate of true phosphorus absorption. Consequently, the measurement of rates of phosphorus absorption from solutions labelled with P^{32} could be seriously in error, should an exchange reaction between root and solution phosphorus exist. Whether P^{32} sorbed by excised root tissue from solutions labelled with P^{32} was, in fact, due to true phosphorus absorption or was the result of an exchange reaction between root and solution phosphorus was, another objective of this experiment.

Results and Discussion

Figures 5.2, a, b, c, and d show the amount of phosphorus sorbed by flax, rape, and buckwheat roots for periods of up to 100 minutes, from phosphorus concentrations of 10^{-6}M, 10^{-5}M, 10^{-4}M, and 10^{-3}M respectively. Lines I and II in these figures represent phosphorus sorptions determined by post-sorption rinsing with distilled water and phosphorus solution (of the concentration used during sorption), respectively.

Flax, rape and buckwheat roots continued to sorb phosphorus from all phosphorus concentrations up to 100 minutes, which was the longest sorption period studied. Their rates of phosphorus sorption from these concentrations however, decreased somewhat during the 100 minute sorption period, i.e. the plot of phosphorus sorption against sorption time was curvilinear. Increasing the phosphorus concentration in the sorbing solution increased their rates of phosphorus sorption during the sorption period studied. However, the ten-fold increments in phosphorus concentration did not result in such large increments in their rates of phosphorus sorption.

The rate of phosphorus sorption by flax roots from each phosphorus concentration was less than the rate of phosphorus sorption by rape or buckwheat roots. There was not a great deal of difference between rape and buckwheat roots in their rates of phosphorus absorption from low phosphorus concentration (10^{-6}M figure 5.2 a). From higher phosphorus concentrations (10^{-5}M, 10^{-4}M and 10^{-3}M), buckwheat roots

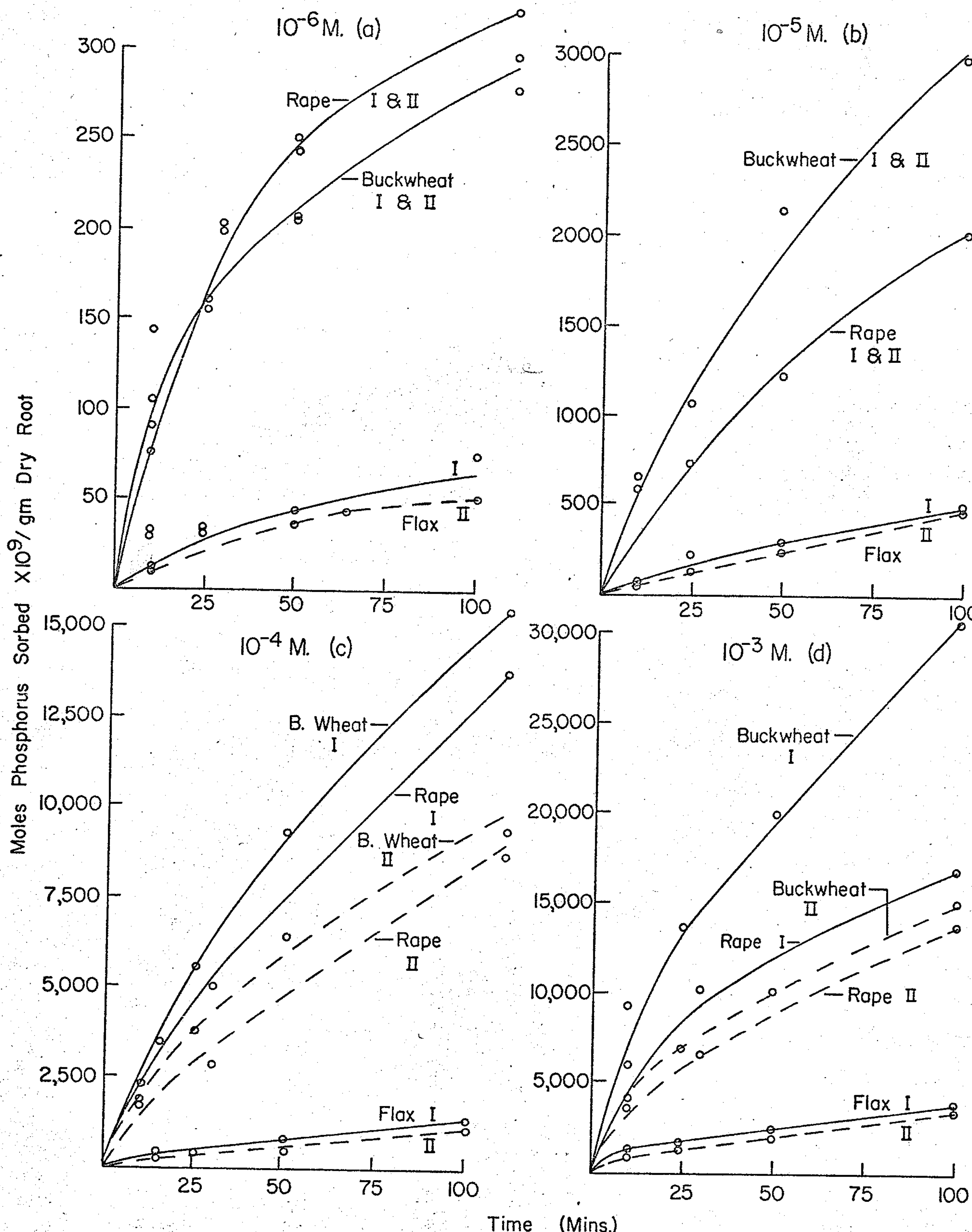


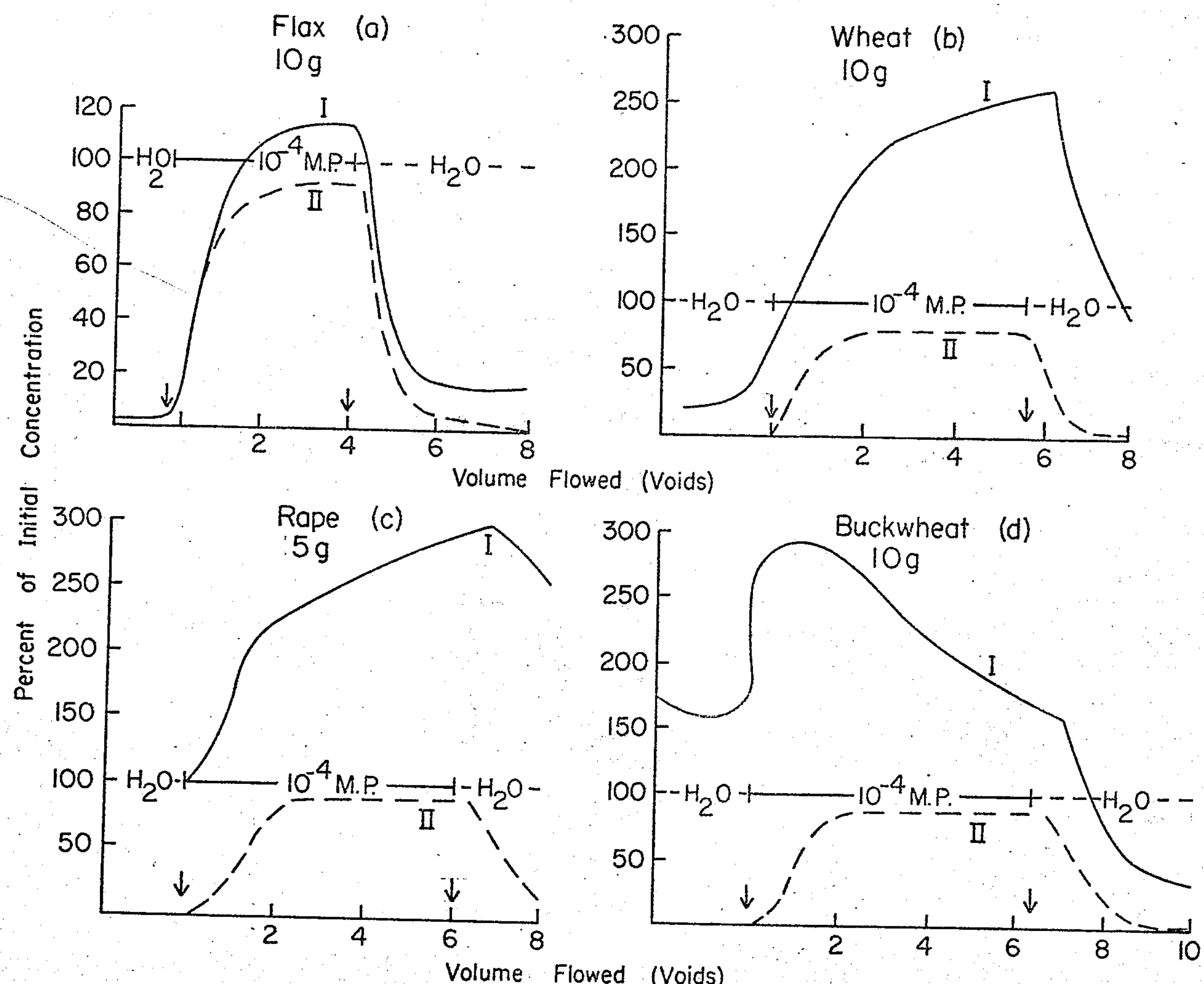
Figure 5.2. Phosphorus Sorption by Excised Roots After Post Sorption Rinsing With Distilled Water (line I) and After Post Sorption Rinsing with Non-Labelled Phosphorus Solution (line II)

sorbed phosphorus at a greater rate than rape roots (figures 5.2 b, c, and d).

A comparison of lines I and II in figures 5.2, a, b, c, and d shows the effect of post-sorption treatment on the measured phosphorus sorption by flax, rape and buckwheat roots, from the four phosphorus concentrations. Post-sorption root treatment had a small but measureable effect on the phosphorus sorbed from each concentration by flax roots. Phosphorus sorption by rape or buckwheat roots from low phosphorus concentrations (10^{-6}M, 10^{-5}M) was not affected by post-sorption root treatment. However, it had a marked effect on their phosphorus sorptions from higher phosphorus concentrations (10^{-4}M and 10^{-3}M).

Some of the phosphorus which was sorbed by rape and buckwheat roots from 10^{-4}M and 10^{-3}M phosphorus concentrations (after rinsing with distilled water) was removed by rinsing with phosphorus solutions. The portion of the sorbed phosphorus removed by rinsing with phosphorus solution could have existed in a pool of phosphorus within the tissue which was readily exchangeable with phosphorus in the external solution. The presence of cation exchange reactions occuring between excised roots and bathing solutions was shown by Epstein (47). Later these reactions were found to be non-rate-limiting steps in the absorption of cations (48). The existence of an exchange reaction between phosphorus in roots and bathing solution was suggested by Helder (66), for intact plants. Approximately half the labelled phosphorus sorbed in 100 minutes by buckwheat roots from a 10^{-3} phosphorus solution was removed by rinsing with non-labelled phosphorus solution (figure 5.2 d). The existence of such a large pool of exchangeable phosphorus in excised root tissue is questionable. An experiment was subsequently designed to measure the exchangeable and/or releasable phosphorus of excised flax, wheat, rape, and buckwheat roots. A mass of freshly excised flax, wheat, rape or buckwheat roots(5-10g) was packed into a column depicted in figure 5.1, and bathed in a small volume (7.5-12.5ml) of 10^{-4}M phosphorus solution, labelled with radiophosphorus (P^{32}). The bathing solution was replenished at a constant rate, while maintaining a constant volume of solution in contact with the root tissue, i.e. void volume. Total phosphorus concentration as well as the radiophosphorus concentration of the eluted solution were monitored at regular intervals, depending on the flow rate (2-5 min). The P^{31} and P^{32} concentrations of the bathing solution were expressed as a percentage of their initial concentrations, prior to root contact. The concentrations of P^{31} (lineI) and P^{32} (line II) expressed in this manner are presented in figures 5.3a, b, c, and d.

The root mass was rinsed, prior to bathing with the phosphorus solution, with a volume of distilled water. Roots of the four crops released phosphorus to this rinsing water (Figures 5.3 a, b, c, and d). This release continued even after several hours of rinsing which suggested that it was not just phosphorus released due to tissue damage during excision.



Contact time for flax, wheat, rape and buckwheat roots was approximately 14, 13, 15 and 13 minutes respectively.

Figure 5.3. P^{31} Concentration (line I) and P^{32} Concentration (line II) of a 10^{-4}M Labelled KH_2PO_4 Solution After Contact With a Mass of Excised Roots for 14, 13, 15, and 13 Minutes.

Phosphorus continued to be released from the roots during bathing with the phosphorus solution. Even during short periods of root contact the phosphorus concentration of the bathing solution was increased considerably (Line I Figures 5.3 a, b, c, and d).

A greater quantity of phosphorus was released to the phosphorus solution than to the presorption rinsing water (Figures 5.3 a, b, c, d). This could have been due to the fact that the release of phosphorus from excised roots was stimulated by the presence of phosphorus in the external medium. Such a suggestion was put forward by Helder (66) to explain similar results with roots of intact plants.

During bathing with phosphorus solution, release of phosphorus from flax roots remained reasonably constant (figure 5.3 a). The rate of phosphorus release from wheat and rape roots increased during sorption (figure 5.3 b and c), and decreased from buckwheat roots (figure 5.3 d). These results possibly suggest that the amount of phosphorus available for release from excised root tissue varies with plant species. Apparently, more phosphorus was available for release from wheat and rape roots than from buckwheat roots. The slower rate of release of phosphorus from flax roots than from roots of the other species could have been due to a smaller amount of phosphorus available for release from flax than from wheat, rape, or buckwheat roots.

The root mass sorbed P^{32} from the bathing solution (lines II, figures 5.3 a, b, c and d). This sorption could have been due to an exchange reaction between root and solution phosphorus, or due to true phosphorus absorption by the roots. Flax and buckwheat roots removed a similar amount of P^{32} from the bathing solution in a similar contact time. (figures 5.3 a and d). In a previous experiment the rate of P^{32} sorbed by excised buckwheat roots from a 10^{-4}M concentration was 10 fold or greater, the rate of P^{32} sorbed by flax roots (figure 5.2 c). In that study roots were grown, prior to excision, in a nutrient solution containing phosphorus. In the present study roots were grown in phosphorus free medium. Thus, conditions of root growth, or presorption phosphorus supply to the roots could have been responsible for the difference in the relative rates of P^{32} sorption by these two species.

The increase in the P^{31} concentration of the bathing solution (line I) was greater than its decrease in the P^{32} concentration, after root contact (figure 5.3 a, b, c and d). Apparently, the release of phosphorus from these roots was greater than their absorption of phosphorus. Russell and Bishop (138) reported that organic and inorganic phosphorus are released from actively growing roots. Results of the present study did not indicate whether the release was of organic or inorganic phosphorus.

3. Experiment VI

A pot experiment on a calcareous soil indicated that phosphorus utilization by flax, wheat, rape, and buckwheat from concentrated applications of MKP and DKP crystals was controlled chiefly by the rates of phosphorus absorption of their roots. In the same study, it was concluded that availability of the applied phosphorus to each of these crops is controlled by the water solubility of the reaction products formed between the soil and the added phosphorus.

Two absorption sites or carriers are believed to function in transporting phosphorus from the external solution into the absorbing root (61). This hypothesis has enabled an accurate description of phosphorus absorption by roots of any crop from any phosphorus concentration. An analysis of the kinetics of phosphorus absorption by excised millet, barley, and alfalfa roots showed a large variation in the rate of phosphorus absorption by their roots, from phosphorus concentrations of 10^{-6}M to 10^{-3}M (115). Assuming phosphorus absorption at two sites to be controlled by metabolically produced phosphate ion carriers, absorption of phosphorus by excised millet, barley, and alfalfa roots from the range of phosphorus concentrations, 10^{-6}M to 10^{-3}M, enabled Noggle and Fried (115) to calculate constants which described their rate of phosphorus absorption from any concentration. A similar study was undertaken using excised flax, wheat, rape, and buckwheat roots in an attempt to explain the large variability in their apparent rates of phosphorus absorption from concentrated applications of water soluble phosphates.

In determining the rates of phosphorus absorption by excised flax, wheat, rape, and buckwheat roots from labelled P^{32} solutions the root tissue was rinsed with non-labelled phosphorus solutions at the end of the sorption period. Kinetics of the apparent phosphorus absorption (sorbed P^{32}), measured in this way was analysed in a similar manner as did Noggle and Fried (115) for excised millet, barley, and alfalfa roots.

The carrier theory has proved most useful in kinetic studies of phosphorus absorption (61). This theory has compared the process of phosphorus absorption with that of an enzyme catalysed reaction; the carrier (R) for phosphorus being the enzyme, and phosphate ions (P) the substrate. Carrier, which is considered metabolically produced and located somewhere within the root, functions in transporting phosphorus from the external medium, $P_{(outside)}$, into the root, $P_{(inside)}$, via an active intermediate in the root, RP. Thus, phosphorus absorption can be represented by the following two equations;

$$R + P_{(outside)} \underset{K_2}{\overset{K1}{\rightleftharpoons}} RP \qquad (1)$$

$$RP \underset{K_4}{\overset{K_3}{\rightleftharpoons}} R' + P_{(inside)} \qquad (2)$$

where, K_1, K_2, K_3, K_4, are the rate constants for each reaction, and R' is another form of the carrier. Reaction (2) is considered essentially irreversible. Hence, absorbed phosphorus cannot be transported back to the external medium. As for all enzyme catalysed reactions the breakdown of the enzyme-substrate complex, RP, is considered the rate limiting step in phosphorus absorption.

At steady state, $P_{(inside)}$ is produced at a constant rate which is proportional to the concentration of RP. In the present study, labelled phosphorus associated with the carrier was not considered to be removed by post-sorption rinsing with non-labelled phosphorus solution. Hence, phosphorus absorbed by the root (V) consisted of $P_{(inside)}$ as well as phosphorus associated with the carrier (RP) and can be represented by equation (3).

$$V = k_3 \, [RP] . t + RP \qquad (3)$$

An increase in the external phosphorus concentration, $P_{(outside)}$, causes an increase in the concentration of RP. Consequently, at infinite external phosphorus concentration R will be completely saturated with phosphorus. Thus, all the R will be in the form of RP, i.e. $[RP] = [\lesssim R]$, where $\lesssim R$ is the total amount of carrier which will combine with phosphorus, and maximum sorption of phosphorus (V_{max}) will occur as shown in equation (4):

$$V_{max} = k_3 [\lesssim R] .t + [\lesssim R] \qquad (4).$$

A velocity equation for steady state uptake may be derived from equations (1) and (2), which is analagous to the steady state analysis described by Michaelis and Menten (110) for the kinetic studies of enzyme reactions:

$$V = -K_m \cdot V/[P] + V_{max}. \qquad (5)$$

where K_m is the Michaelis and Menten constant and $[P]$ is the phosphorus concentration

The Michaelis and Menten equation, equation (5), describes the rate of phosphorus absorption from any phosphorus concentration, and can be calculated by substitution for K_m and V_{max}. This study was designed principally to determine these constants for flax, wheat, rape, and buckwheat roots so that their phosphorus sorption velocities from any phosphorus concentration could be calculated.

From the form of equation (5) it is obvious that the plot of V against $V/[P]$ should be a straight line if a single first order reaction were involved; the slope of this line being $-K_m$ and the ordinate intercept, V_{max}.

Steady-state uptake measurements of phosphorus by excised flax, wheat, rape, and buckwheat roots, when plotted in this way, were curvilinear (figure 6.1 a, b, c, and d). Hofstee (70) showed how these curved lines may be resolved into two linear components by the use of graphical methods. As found by Hagen and Hopkins (61), absorption of phosphorus appeared to be the result of two first order simultaneous reactions. This being the case, then the plot of V against V/P can be described by the equation:

$$y^2 = ax^2 + bxy + cx + dy$$

which is an hyperbola rotated anti-clockwise with respect to the axes such that both asymptotes intersect the Y-axis. The asymptotes are then, by definition, the two straight lines into which each curve can be resolved. Using four points taken from the experimentally-determined plot of V against V/P, equations to the asymptotes were obtained, (figure 6.1 a, b, c, d).

The reaction which predominated at high phosphorus concentration was defined by line "a" while that predominating at lower phosphorus concentrations was defined by line "b". $V_{max.a}$ and $V_{max.b}$ were determined directly from the ordinate intercepts of lines "a" and "b". $K_{m.a}$ and $K_{m.b}$ were determined by calculating the slopes of lines "a" and "b". Their values are presented in Table 6.1.

Table 6.1 shows the constants controlling phosphorus absorption by excised flax, wheat, rape, and buckwheat roots during 10 minutes sorption. Cursory inspection of the maximum phosphorus sorption velocities via carrier 'a' and carrier 'b' ($V_{max\ a}$ and $V_{max\ b}$ respectively) indicate a large variability between roots of the four crops. The maximum sorption

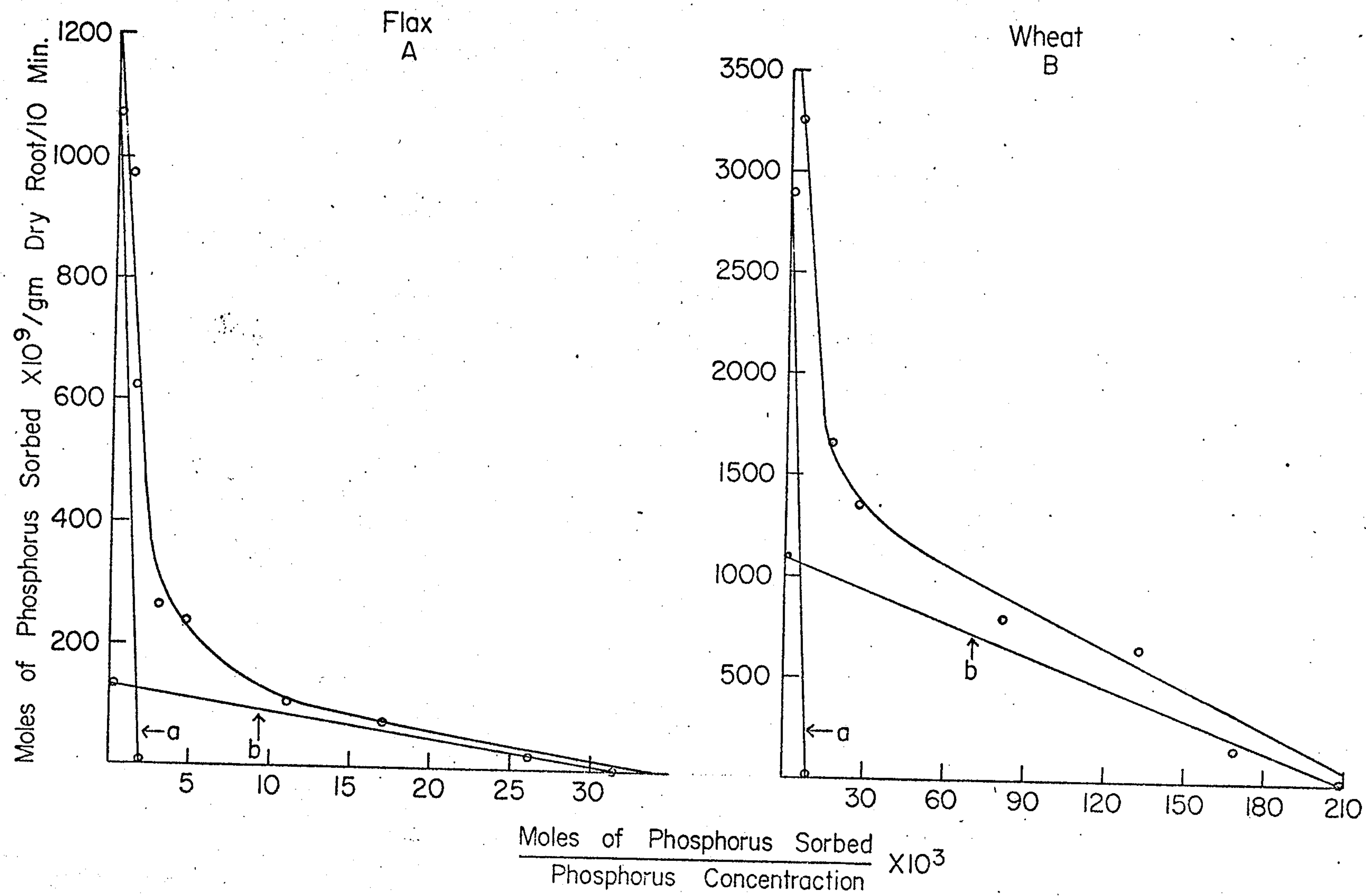


Figure 6.1. Phosphorus Sorption by Excised Roots in 10 Minutes Resolved Into Two First Order Reactions (line a and line b)

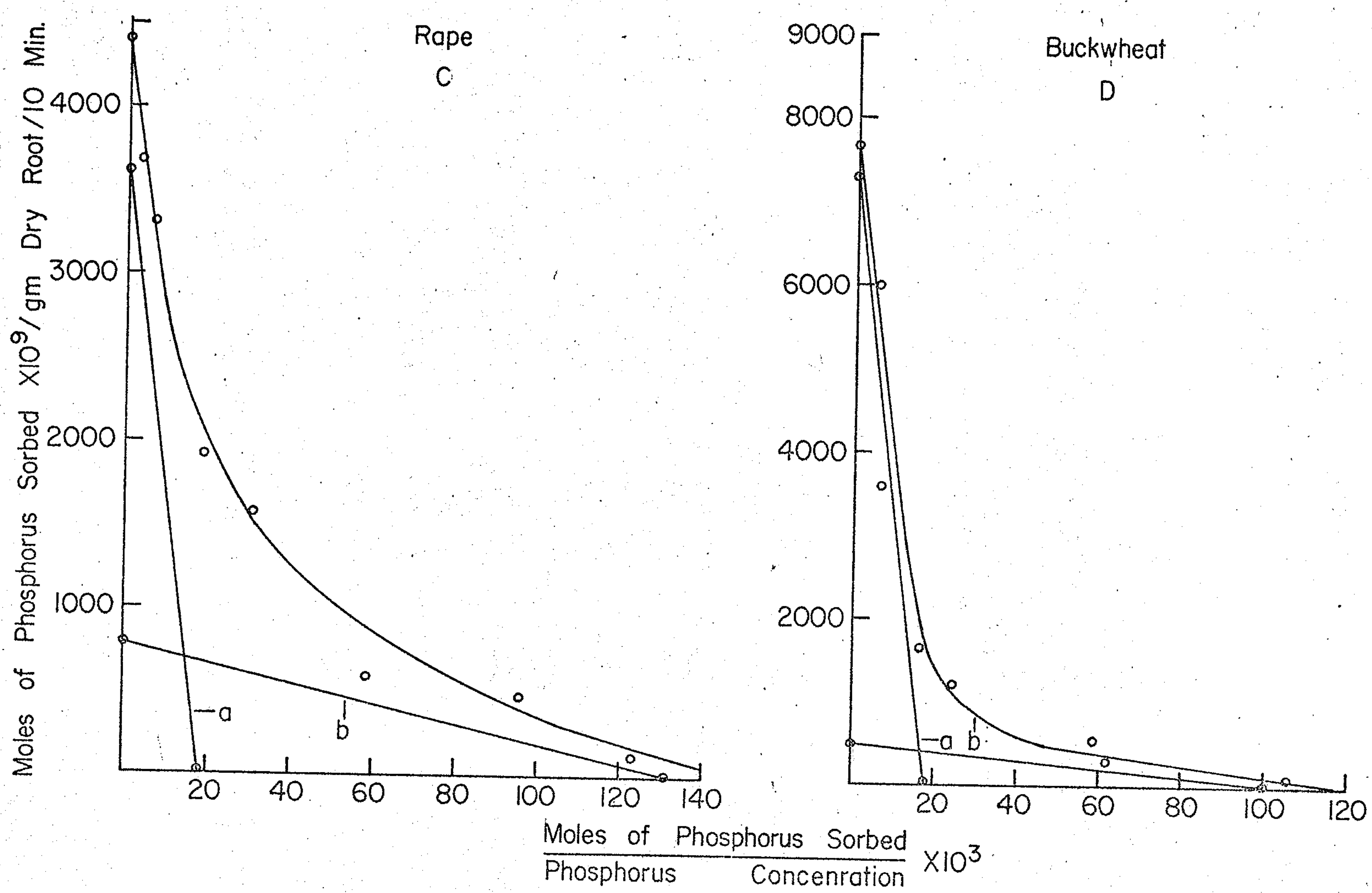


Figure 6.1 (continued)

TABLE 6.1

Crop	Maximum Sorption Velocities $V_{max\ a}$ (moles Px10^9/ g root/10 min)	$V_{max\ b}$	Apparent Dissociation Constants K_{ma}x10^4	K_{mb}x10^6	Rate Constants K_{3a} moles Px10^3/ mole RP/sec	K_{3b}	Concentratio of Carriers ΣR_a molesx10^8/g	ΣR_b
Flax	1097	133	6.2	4.0	3.6	6.4	34.7	2.7
Wheat	2887	1093	3.4	5.2	3.9	6.3	86.4	22.9
Rape	3615	784	2.0	6.0	1.8	6.5	174	16.0
Buckwheat	7430	500	4.2	5.0	4.4	4.7	204	13.1

velocities of wheat, rape and buckwheat roots via carrier 'b' did not differ greatly, although wheat was somewhat higher than the other two crops. The maximum sorption velocity of flax roots via carrier 'b' was considerably less than that for any of the other species. Maximum sorption velocities of the four crops via carrier 'a' increased in the order; flax, wheat, rape, and buckwheat. This was also the order of increasing apparent rates of phosphorus absorption of their roots from concentrated applications of phosphorus to soil (experiments I, II, III, and IV).

The effect of the dissociation constant of the carrier-phosphorus complex on the rate of phosphorus absorption via carrier 'a' and carrier 'b' (K_{ma} and K_{mb} respectively) can be best viewed from figure 6.2. Figure 6.2 is the plot of the percent of carrier 'a' and carrier 'b' of flax, wheat, rape, and buckwheat roots which is functional in phosphorus absorption over the concentration range 10^{-7} -10^{-2}M. Sorption velocity via each carrier for roots of each species from a number of phosphorus concentration in the range 10^{-7}-10^{-2}M was determined by sutstitution of [P] $K_m$and V_{max} in the Michealis and Menten equation (equation 5).

$$V = -K_m \, V/_P + V_{max} \qquad (5).$$

These sorption velocities, expressed as a percentage of the maximum sorption velocity, were then plotted against the phosphorus concentration, i.e. figure 6.2.

Noggle and Fried (115) showed that, for the three species which they studied, the 'b' reaction was responsible for most of the phosphorus

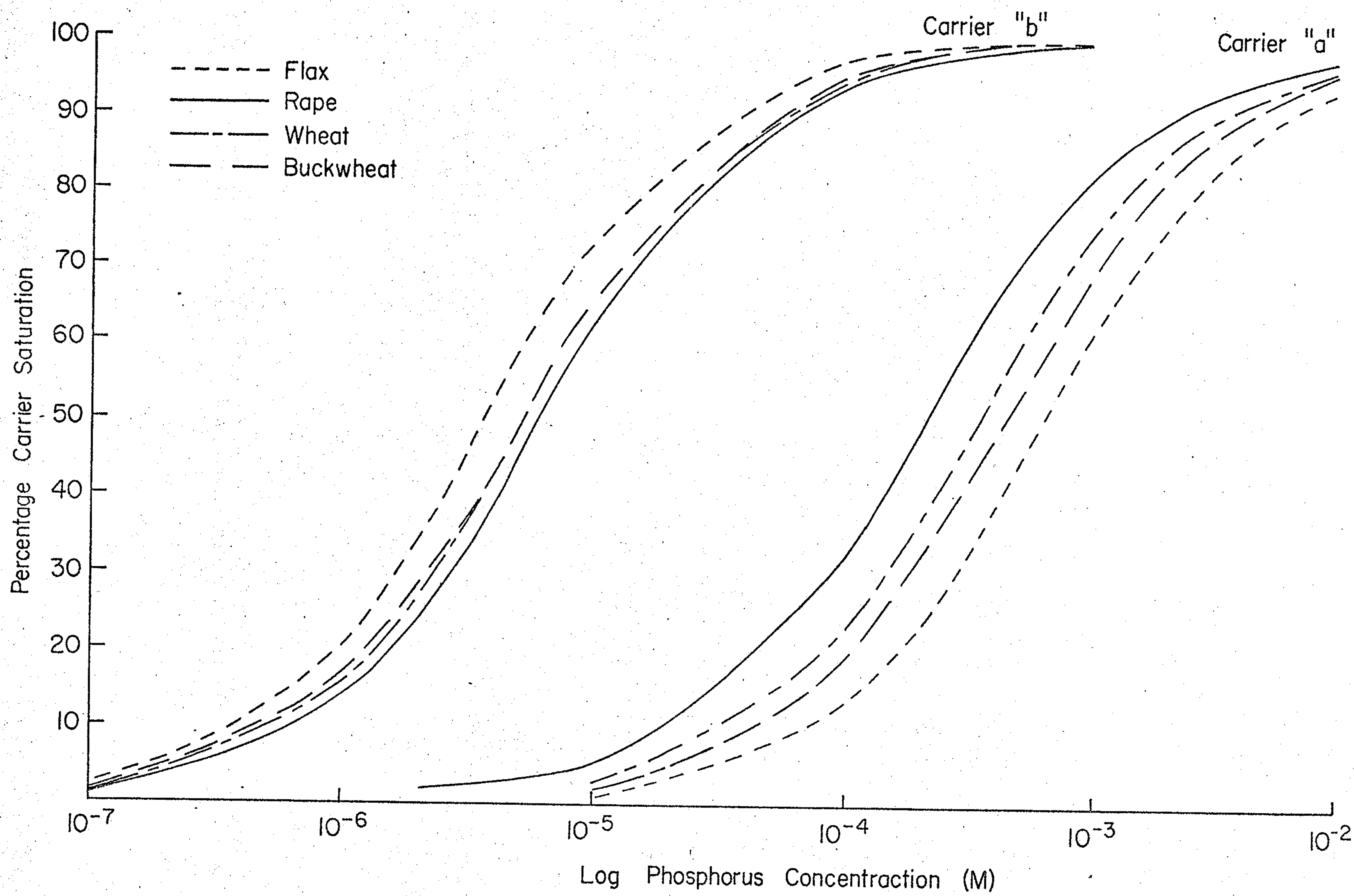


Figure 6.2. Effect of Phosphorus Concentration on the Proportions of the Phosphate Ion Carriers Functional in Phosphorus Absorption

absorbed from 10^{-6}M concentration. This was also shown to be true for flax, wheat, rape, and buckwheat roots (figure 6.2). A plot of phosphorus sorption by roots of each crop from 10^{-6}M against time yielded a straight line up to 10 minutes (figure 6.3a). The equation of this straight line can be represented in the same form as equation (3). Comparing this line with equation (3) it can be seen that the ordinate intercept was a measure of the amount of carrier 'b' functional in phosphorus absorption at 10^{-6}M phosphorus concentration, i.e. R_bP. An approximation of k_3 for reaction 'b' was obtained by dividing the slope of the line by the ordinate intercept. By substituting k_{3b} and V_{maxb} into equation (4) ΣR_b was obtained for each species. These are shown in Table 6.1. Noggle and Fried (115) found total saturation of carrier 'b' at phosphorus concentration of 5×10^{-4}M or higher. In the present study total saturation of carrier 'b' was considered to occur at phosphorus concentration of 10^{-3}M or higher. Hence, phosphorus sorption by roots of each crop from a 10^{-3}M concentration was plotted against time. Once again a steady state uptake of phosphorus was observed up to 10 minutes (figure 6.3 b). The ordinate intercept of this line was a measure of the phosphorus in combination with both carriers, i.e. $\Sigma R_b + R_aP$. Since R_b had been calculated, R_aP (the amount of carrier 'a' functional in phosphorus absorption at 10^{-3}M of phosphorus) could be found by subtraction. Phosphorus sorption from 10^{-3}M could be expressed in equation (6);

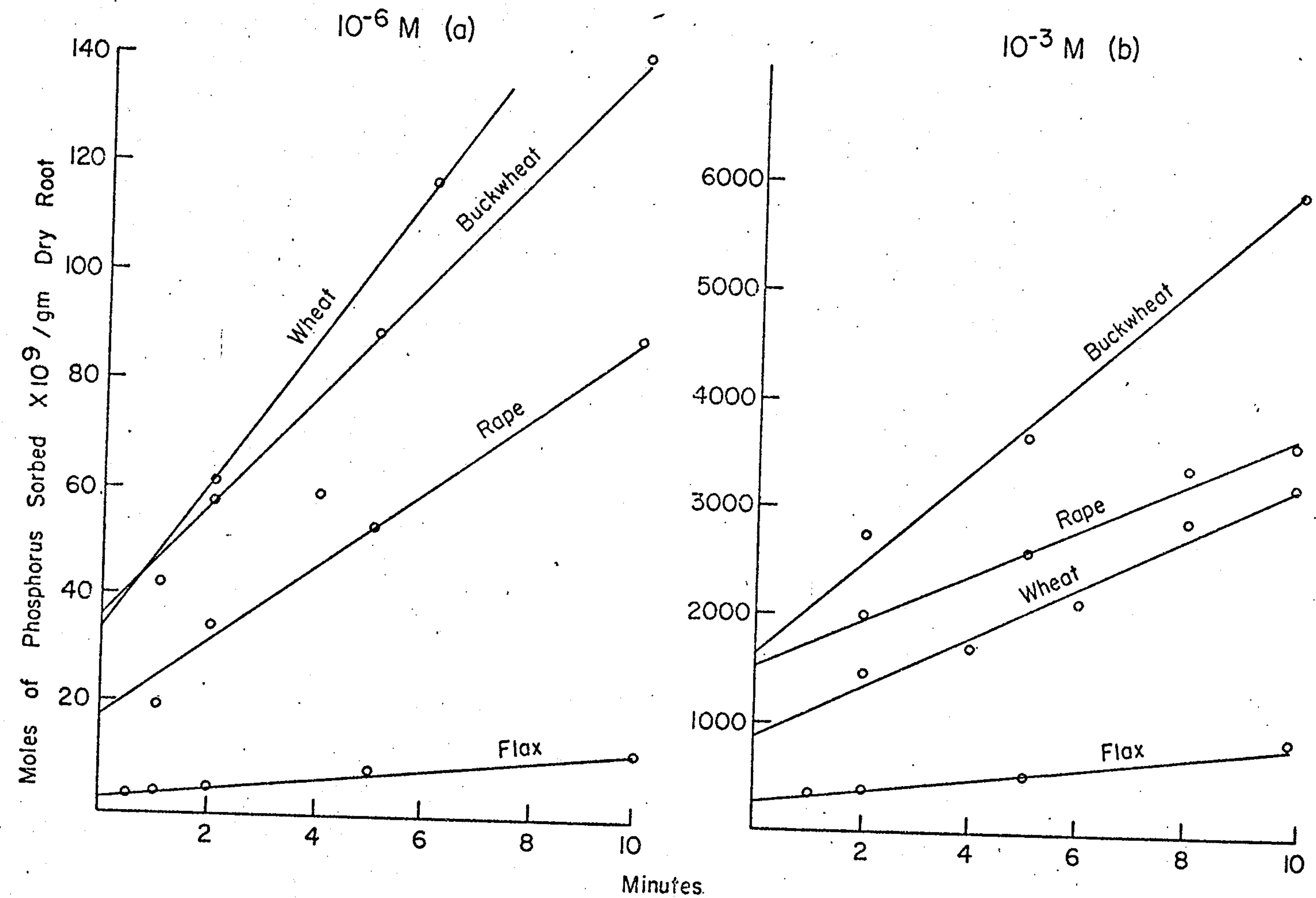


Figure 6.3. Short Term Phosphorus Sorption by Excised Roots

$$V = \left(\left[R_aP\right] \cdot k_{3a} + \left[\Sigma R_b\right] \cdot k_{3b} \right) \cdot t + R_aP + \Sigma R_b \qquad (6)$$

Since R_aP, ΣR_b, and k_{3b} were known, as well as sorption, V, for a specific time, e.g. 10 minutes, k_{3a} could be calculated. Substitution of k_{3a} and $V_{max\ a}$ into equation (4) enabled calculation of ΣR_a for the roots of each crop. These are also presented in Table 6.1.

K_{ma} and K_{mb} affected the proportion of carrier 'a' and carrier 'b' respectively which was functional in absorbing phosphorus from a particular phosphorus concentration. Their effects on phosphorus absorption can be readily seen from the plot of percentage saturation of carrier against phosphorus concentration i.e. figure 6.2. At phosphorus concentration of 10^{-4}M, 94 percent or more of carrier 'b' was functional in phosphorus absorption by excised flax, wheat, rape, and buckwheat roots (figure 6.2). Thus, for practical purposes carrier 'b' of flax, wheat, rape, and buckwheat roots could be considered completely functional in phosphorus absorption from phosphorus concentrations of 10^{-4}M or higher. Apparently, phosphorus concentrations greater than 10^{-4}M increased phosphorus absorption by flax, wheat, rape, and buckwheat roots, mainly through an increase in the phosphorus absorption by carrier 'a'. At phosphorus concentration of 10^{-2}M, 94 percent or more of carrier 'a' was functional in phosphorus absorption by excised flax, wheat, rape, and buckwheat roots (figure 6.2). Hence, for practical purposes both carriers of these roots could be considered completely functional in phosphorus absorption from phosphorus concentrations of 10^{-2}M or higher.

The apparent dissociation constant of the carrier 'b'—phosphorus complex (K_{mb}) did not vary markedly between the four crops (Table 6.1). The dissociation constant of the carrier 'a'—phosphorus complex (K_{ma}) varied slightly among the four species. K_{ma} of flax roots was greater than the K_{ma} of the other crops (Table 6.1). Thus, from phosphorus concentrations of up to 10^{-2}M, the proportion of carrier 'a' functional in phosphorus absorption was smaller for flax roots than for roots of the other three crops (figure 6.2).

The rate constant of phosphorus absorption via carrier 'b' did not vary greatly among crops (Table 6.1). The reaction rate constant of phosphorus absorption via carrier 'a' was similar for flax, wheat and buckwheat roots, being approximately double that of rape roots (Table 6.1). The variability among species in the maximum rate of phosphorus absorption via either carrier was not accounted for by the variability in the rate constant at either site (k_3). The concentration of phosphate ion carriers in root tissue was quite variable among the four species (Table 6.1). Thus, it was concluded, that the observed variability in the maximum velocities of phosphorus absorption at both sites was a direct effect of the concentration of carrier 'a' and carrier 'b' within the root tissue (Table6.1).

A comparison was made of the rates of phosphorus absorption of flax, wheat, rape, and buckwheat roots from the water-soluble phosphorus concentrations found in zones of spread of monopotassium phosphate and dipotassium phosphate. Phosphorus concentrations within zones of spread of these compounds, 50 days after application, ranged from 1.7×10^{-4}M to 8.2×10^{-4}M. Using the Michaelis and Menten equation (equation 5), and substituting for K_m and V_{max} for roots of each crop, their rates of phosphorus absorption from these two phosphorus concentrations were calculated at each carrier. The rates of phosphorus absorption presented in Table 6.2 are the sum of the rates at each carrier for roots of the four crops. Also presented in Table 6.2 are the averages, for roots of each crop, of the apparent rate of phosphorus absorption from zones of applied monopotassium phosphate and dipotassium phosphate which were found in experiment I over the 50 day growing period.

Table 6.2 shows that as the rate of phosphorus absorption by excised roots of these crops increased their apparent rates of phosphorus absorption from zones of applied phosphorus also increased. The apparent rate of phosphorus absorption from zones of applied phosphorus were calculated on the basis of the crop utilization of applied phosphorus in 50 days per unit mass of roots recovered from the application zone. Since there was some variability between crops in the growth rate of roots within zones of spread of MKP and DKP applications, lack of a close correlation between the two rates of phosphorus absorption was not surprising.

TABLE 6.2

Crop	Average apparent rate of phosphorus absorption from MKP & DKP applications* (mgP/g root/50 days)	Rates of phosphorus absorption from phosphorus solutions moles $x10^9$/g root/10 min.)	
		$1.7x10^{-4}M$	$8.2x10^{-4}M$
Flax	0.6	370	760
Wheat	1.5	2020	3140
Rape	2.9	2420	3700
Buckwheat	9.8	2630	5420

* Data taken from experiment I

SUMMARY AND CONCLUSIONS

Workers in Manitoba have observed variability among crop species in their utilization of phosphorus added to calcareous soils. They noted that variability was greatest when phosphorus was applied as a 'pellet-type' application. Thus it would seem that crops vary greatly in their ability to feed from concentrated sources of phosphorus. This study was an investigation of root properties of four crops, flax, wheat, rape, and buckwheat which were known to vary in their utilization of applied phosphorus.

It seems plausible that differential root growth of various crops within the applied phosphorus reaction zone could account for part of the variability in applied phosphorus utilization. A comparative study of root development of the four crops within the applied phosphorus reaction zone showed that root growth of none of the crops was adversely affected by conditions within the reaction zone. On the contrary the roots of all crops were found under certain conditions to grow preferentially within the reaction zone.

It was demonstrated that increasing the root mass of a particular crop feeding from the reaction zone increased its absorption of applied phosphorus. Thus, root development of a particular crop within the reaction zone significantly affects utilization of applied phosphorus. Preferential root growth of the four test crops within the reaction zone was found to be a function of the solubility of the reaction products formed within the reaction zone as well as the soil phosphorus availability. Preferential root growth occurred within zones of dicalcium phosphate dihydrate and octacalcium phosphate but was absent within zones of hydroxyapatite. When soil phosphorus availability was low, roots of the four crops grew preferentailly within the reaction zone. When soil phosphorus availability was increased preferential root growth was absent for flax, rape, and buckwheat and was diminished for wheat.

A marked variability was found among crops in the extent of preferential root growth within the applied phosphorus reaction zone. The extent of preferential root growth in the reaction zone for the test crops increased in the order; flax, wheat, buckwheat, and rape. Differential utilization of applied phosphorus by the four test crops however, could not be explained solely by preferential root growth within the reaction zone of the applied phosphorus. Thus roots of the test crops varied in the amount of applied phosphorus absorbed per unit mass of tissue.

The maximum velocity of phosphorus absorption by excised roots of the four crops increased in the order; flax, wheat, rape, and buckwheat. This was also the crop order for increasing apparent rate of phosphorus absorption by the root from the reaction zone of applied phosphorus, i.e. applied phosphorus absorbed by the crop per unit mass of roots recovered from the reaction zone. Thus, part of the variability among crops in their utilization of applied phosphorus could have been due to variability in the inherent rates of phosphorus absorption of their roots from the reaction zone.

Phosphorus absorption by the root is believed to be mediated by metabolically produced phosphate ion carriers. A kinetic study of short term phosphorus absorption by excised root tissue enabled calculations of the number of phosphate ion carriers produced per unit mass of root as well as the efficiency of the carrier in the absorption of phosphate ions. A large variability was found among the four test crops in the concentration of the phosphate ion carrier within their root tissue. This variability was chiefly responsible for the variability in the rate of phosphorus absorption by roots of the four test crops.

BIBLIOGRAPHY

1. Alberda, T. "The Influence of some External Factors on Growth and Phosphorus Uptake of Maize Plants of Different Salt Conditions." Rec. Trav. Bot. Neerlandais 41:542. 1948.

2. Andrew, C. S. "A Kinetic Study of Phosphate Absorption by Excised Roots of Stylosanthes humilis, Phaseolus lathyroides, Desmodium uncinatum, Medicago sativa, and Hordeum vulgare." Aust. J. Agr. Res. 17:611-624. 1966.

3. Arnon, D. I. "The Physiology and Biochemistry of Phosphorus in Green Plants". Soil and Fertilizer Phosphorus in Crop Nutrition. Academic Press, New York. pp. 1-42. 1953.

4. Asher, C. J., and Loneragan, J. F. "Response of Plants to Phosphate Concentration in Solution Culture: II. Rate of Phosphate Absorption and its Relation to Growth." Soil Sci. 103:311-318. 1967.

5. Asher, C. J., and Loneragan, J. F. "Response of Plants to Phosphate Concentration in Solution Culture: I. Growth and Phosphorus Content." Soil Sci. 103:225-233. 1967.

6. Bailar, J. C. Jr. "Calcium hydrogen orthophosphate-2-hydrate". Inorganic Synthesis 4:20-21. 1953.

7. Baker, D. F., and Woodruff, C. M. "Influence of Volume of Soil per Plant upon Growth and Uptake of Phosphorus by Corn from Soils treated with Different Amounts of Phosphorus." Soil Sci. 94: 409-412. 1962.

8. Barber, D. A., and Loughman, B. C. "The Effect of Micro-organisms on the Absorption of Inorganic Nutrients by Intact Plants: II. Uptake and Utilization of Phosphate by Barley Plants Grown under Sterile and Non-sterile conditions." J. Exp. Bot. 18:170-176. 1967.

9. Barber, S. A., Walker, J. M., and Vasey, E. H. "Mechanisms for the Movement of Plant Nutrients from the Soil and Fertilizer to the Plant Root." Agr. and Food Chem. 11:204-207. 1963.

10. Barrow, N. J. "Relationship between Uptake of Phosphorus by Plants and the Phosphorus Potential and Buffering Capacity of the Soil - an Attempt to Test Schofield's Hypothesis." Soil Sci. 104:99-106. 1966.

11. Beaton, J. D. and Read, D. W. L. "Effects of Temperature and Moisture on Phosphorus Uptake from a Calcareous Saskatchewan Soil treated with Several Pelleted Sources of Phosphorus." Soil Sci. Soc. Amer. Proc. 27:61-65. 1963.

12. Bennett, O. L., Longnecker, T. C., and Grey, C. "A Comparison of the Efficiency of Eighteen Sources of Phosphorus Fertilizers on Houston Black Clay." Soil Sci. Soc. Amer. Proc. 18:408-412. 1954.

13. Biddulph, O., and Woodridge, C. G. "The Uptake of Phosphorus by Bean Plants with Particular Reference to the Effects of Iron." Plant Physiol. 27:431-444. 1952.

14. Blanchar, R. W., and Caldwell, A. C. "Phosphorus Availability of Monocalcium and Diammonium Phosphates in Calcereous Soils." J.Agr. Food Chem. 13:171-173. 1965.

15. Blanchar, R. W., and Caldwell, A. C. "Phosphate-Ammonium-Moisture Relationships in Soils: I.Ion Concentration in Static Fertilizer Zones and Effects on Plants." Soil Sci. Soc. Amer. Proc. 30: 39-43. 1966.

16. Blancher, R. W., and Caldwell, A. C. "Phosphate-Ammonium-Moisture Relationships in Soils II. Ion Concentration in Leached Fertilizer Zones and Effects on Plants." Soil Sci. Soc. Amer. Proc. 30: 43-58. 1966.

17. Bouldin, D. R., and Black, C. A. "Phosphorus Diffusion in Soils". Soil Sci. Soc. Amer. Proc. 18:255-259. 1954.

18. Bouldin, D. R., and Sample, E. C. "The Effect of Associated Salts on the Availability of Concentrated Superphosphate." Soil Sci. Soc. Amer. Proc. 22:124-129. 1958.

19. Bouldin, D. R., and Sample, E. C. "Calcium Phosphate Fertilizers: III.The Effect of Surface Area on the Availability Coefficients of the Dicalcium Phosphates." Soil Sci. Soc. Amer. Proc. 23: 276-281. 1959.

20. Bouldin, D. R., and Sample, E. C. "Calcium Phosphate Fertilizers: IV.The Relation Between Solubility in Soils and Availability Coefficients of Dicalcium and Fused Tricalcium Phosphates." Soil Sci. Soc. Amer. Proc. 23:281-285. 1959.

21. Bowen, G. D., and Rovira, A. D. "Microbial Factors in Short-term Phosphate Uptake Studies with Plant Roots." Nature (London) 211:665-666. 1966.

22. Bray, R. H. "A Nutrient Mobility Concept of Soil-Plant Relationships." Soil Sci. 78:9-22. 1954.

23. Carter, O. G., and Lathwell, D. J. "Effects of Temperature on Orthophosphate Absorption of Excised Corn Roots." Plant Physiol. 42:1407-1412. 1967.

24. Clark, J. S. "Solubility Criteria for the Existence of Hydroxyapatite." Can. J. Chem. 33:1696-1700. 1955.

25. Clark, J. S., and Peech, M. "Solubility Criteria for the Existence of Calcium and Aluminum-bound Phosphate in Soils." Soil Sci. Soc. Amer. Proc. 19:171-174. 1955.

26. Clarkson, T. "Effect of Aluminum on Uptake and Metabolism of Phosphorus by Barley Seedlings. Plant Physiol. 41(1):165-172. 1966.

27. Clarkson, D. T. "Interactions between Aluminum and Phosphorus on Root Surfaces and Cell Wall Material." Plant and Soil 27:347-356. 1967.

28. Cole, C. V., and Olsen, S. R. "Phosphorus Solubility in Calcareous Soils: I. Dicalcium Phosphate Activities in Equilibrium Solutions." Soil Sci. Soc. Amer. Proc. 23:116-118. 1959.

29. Cooke, G. W. "Recent Advances in Fertilizer Placement: II. Fertilizer Placement in England." J. Sci. Food Agric. 9:429-440. 1954.

30. Cooke, G. W. "Placement of Fertilizers for Sugar Beet." J. Agr. Sci. 41:174-178. 1951.

31. Cooke, G. W., Jackson, M. V., Widdowson, F. V., Wilcox, J. C., and Goodway, N. D. "Fertilizer Placement for Horticultural Crops". J. Agr. Sci. 47:249-256. 1956.

32. Cornforth, I. S. "Relationships between Soil Volume used by Roots and Nutrient Accessibility." J. Soil Sci. 19:291-301. 1968.

33. Crossett, R. N. "Autoradiography of P^{32} in Maize Roots." Nature (London) 213:312-313. 1967.

34. Crossett, R. N. "Effect of Light upon the Transolaction of Phosphorus by Seedlings of Hordeum vulgare (L)." Aust. J. Biol. Res. 21:225-233. 1968.

35. Crossett, R. N. "The Site of Phosphorus Accumulation in Maize Roots." Aust. J. Biol. Sci. 21:1063-1067. 1968.

36. Crossett, R. N. and Loughman, B. C. "The Absorption and Translocation of Phosphorus by Seedlings of Hordeum vulgare (L)." New Phytol. 65:459-468. 1966.

37. Cunningham, R. K. "Cation-anion Relationships in Crop Nutrition: III. Relationships Between the Ratios of Sum of the Cations: Sum of the Anions and Nitrogen Concentration in Several Plant Species." J. Agric. Sci. 63:109-111. 1964.

38. Dean, L. A., and Gledhill, V. H. "Influence of Soil Moisture on Phosphate Absorption as Measured by an Excised Root Technique." Soil Sci. 82:71-79. 1956.

39. Dion, H. G., Dehm, J. E., and Spinks, J. W. T. "Study of Fertilizer Uptake using Radioactive Phosphorus: IV. The Availability of Phosphate Carriers in Calcareous Soils." Sci. Agr. 29:512-526. 1949.

40. Dion, H. G., Dehm, J. E., and Spinks, J. W. T. "Tracer Studies with Phosphate Fertilizers." Can. Chem. Proc. Ind. 34:905-909. 1950.

41. Drake, M. and Steckel, J. E. "Solubilization of Soil and Rock Phosphate as Related to Root Cation Exchange Capacity." Soil Sci. Soc. Amer. Proc. 19:449-450. 1955.

42. Drake, M., Vengris, J. and Colby, W. G. "Cation Exchange Capacity of Plant Roots." Soil Sci. 72:139-147. 1951.

43. Duncan, W. G., and Ohlrogge, A. J. "Principles of Nutrient Uptake from Fertilizer Bands: II. Root Development in the Band." Agron. J. 50:605-608. 1958.

44. Duncan, W. G. and Ohlrogge, A. J. "Principles of Nutrient Uptake from Fertilizer Bands:III. Band Volume, Concentration, and Nutrient Composition." Agron. J. 51:103-106. 1959

45. Edwards, D. G. "Cation Effects on Phosphate Absorption from Solution by Trifolium subterraneum." Aust. J. Biol. Res. 21:1-12. 1968.

46. Elgabaly, M. M. and Wiklander, L. "The Mechanism of Anion Uptake by Plant Roots: I. Uptake of Chloride from Cl^- Resin Systems and its Relation to the Electrical Properties of Root Surfaces." Soil Sci. 93:281-285. 1962.

47. Epstein, E. "Mineral Nutrition of plants: Mechanisms of Uptake and Transport." Ann. Rev. Plant Physiol. 7:1-24. 1956.

48. Epstein, E., and Leggett, J. E. "The absorption of Alkaline earth cations by barley roots: Kinetics and Mechanism." Amer. J. Bot. 41:785-791. 1954.

49. Fawcett, R. G., and Quirk, J. P. "Effect of Water-Stress on the Absorption of Soil Phosphorus by Wheat Plants." Nature (London) 188:687-688. 1960.

50. Ferguson, W. S., and Hedlin, R. A. "Effect of Soluble Salts on Plant Response to and Absorption of Phosphorus." Can. J. Soil Sci. 43:210-218. 1963.

51. Franklin, R. E. "Influence of the Suspension Effect on Uptake of Anions by Excised Roots." Soil Sci. 100:207-209. 1965.

52. Fried, M. and Broeshart, H. "The Soil-Plant System in Relation to Inorganic Nutrition." Academic Press, New York and London, p. 40. 1967.

53. Fried, M., and Dean, L. A. "A Concept Concerning the Measurement of Available Soil Nutrients." Soil Sci. 73:263-271. 1952.

54. Fried, M. Hagen, C. E., Saiz Del Rio, J. F., and Leggett, J. E. "Kinetics of Phosphate Uptake in the Soil-Plant System." Soil Sci. 84:427-437. 1957.

55. Fried, M. and Mackenzie, A. J. "Rock Phosphate Studies with Neutron Irradiated Rock Phosphate." Soil Sci. Soc. Amer. Proc. 14:226-231. 1949.

56. Fried, M., and Noggle, J. C. "Multiple Site Uptake of Individual Cations by Roots as Affected by Hydrogen Ion." Plant Physiol. 33:139-144. 1958.

57. Fried, M., and Shapiro, R. E. "Soil-Plant Relationships in Ion Uptake." Ann. Rev. Plant Physiol. 12:91-112. 1961.

58. Graham, E. R. "Availability of Natural Phosphates According to Energy Changes." Soil Sci. Soc. Amer. Proc. 19:26-29. 1955.

59. Grunes, D. L. "Effect of Nitrogen on the Availability of Soil and Fertilizer Phosphorus to Plants." Advances in Agronomy, XI:369-395. 1959.

60. Grunes, D. L., Viets, F. Jr., and Shih, S. H. "Proportionate Uptake of Soil and Fertilizer Phosphorus by Plants as Affected by Nitrogen Fertilization: I. Growth Chamber Experiment." Soil Sci. Soc. Amer. Proc. 22:43-48. 1958.

61. Hagen, C. E., and Hopkins, H. T. "Ionic Species in Orthophosphate Absorption by Barley Roots." Plant Physiol. 30:193-199. 1955.

62. Hagen, C. E., Leggett, J. E., and Jackson, P. C. "The Sites of Orthophosphate Uptake by Barley Roots." Proc. Nat. Acad. Sci. U.S. 43:496-506. 1957.

63. Hai, T. V. and Laudelout, H. "Phosphate Uptake by Intact Rice Plants by the Continuous Flow Method at Low Phosphate Concentrations." Soil Sci. 101:408-417. 1966.

64. Handley, R., Metwally, A., and Overstreet, R. "Divalent Cations and the Permeability to Sodium of the Root Meristem of Zea mays." Plant and Soil 22:200-206. 1965.

65. Helder, R. J. "Growth as a Determining Factor for the Intake of Anions by Maize Plants." Proc. Kon. Ned Akad. Wetensch. 54:275. 1951.

66. Helder, R. J. "Exchange and Circulation of Labelled Ions in Young Intact Plants." Radioisotopes in Scientific Research, Vol. IV. Proc. Ist UNESCO Int. Conf., Paris. 1957. Pergamon Press, London, New York and Paris. 369-379. 1958.

67. Heslep, J. M., and Black, C. A. "Diffusion of Fertilizer Phosphorus in Soils." Soil Sci. 78:389-401. 1954.

68. Hevesy, G. "Interaction between the Phosphorus Atoms of the Wheat Seedling and the Nutrient Solution." Ark. f. Botanik 33A, No. 2. 1946.

69. Hoagland, D. R., and Martin, J. C. "A Comparison of Sand and Solution Cultures with Soils as Media for Plant Growth." Soil Sci. 16:366-388. 1923.

70. Hofstee, B. H. J. "On the Evaluation of the Constants V_m and K_m in Enzyme Reactions." Science 116:329-331. 1952.

71. Huffman, E. O. "Reactions of Phosphate in Soils: Recent Research by TVA." Proc. Fert. Soc. 71:5-35. 1962.

72. Huffman, E. O., Cate, W. E., and Deming, M. E. "Rates and Dissolution Mechanisms of Some Ferric Phosphates." Soil Sci. 90:8-15. 1960.

73. Huffman, E. O., Cates, W. E., Deming, M. E., and Elmore, K. L. "Rates of Solution of Calcium Phosphates in Phosphoric Acid Solutions." J. Agr. Food Chem. 5:266-275. 1957.

74. Huffman, E. O., Cate, W. E., Deming, M. E., and Elmore, K. L. "Rates and Mechanisms of Dissolution of some Iron and Aluminium Phosphates." Trans. 7th Int. Congr. Soil Sci. Madison, Wisconsin, U.S.A. Vol. II:404-412. 1960.

75. Humphries, E. C. "The Absorption of Ions by Excised Root Systems. II. Observations on Roots of Barley Grown in Solutions Deficient in P,N, or K." J. Exp. Bot. 2:344. 1951.

76. Hyde, A. H. "Nature of the Calcium Effect in Phosphate Uptake by Barley Roots." Plant and Soil XXIV: 328-331. 1966.

77. Islam, M. A. "The Role of Solid Phase in Phosphorus Nutrition of Plants." Soil Sci. 79:115-122. 1955.

78. Jackson, M. L. "Soil Chemical Analysis." Prentice Hall Inc. Englewood Cliffs, N. J. 141-144. 1958.

79. Jackson, M. L. "Soil Chemical Analysis." Prentice - Hall, Inc., Englewood Cliffs, N.J. pp. 151-154. 1958.

80. Jackson, M. L. "Soil Chemical Analysis." Prentice - Hall, Inc., Englewood Cliffs, N.J. 333-334. 1958.

81. Jackson, P. C., and Hagen, C. E. "Products of Orthophosphate Absorption by Barley Roots." Plant Physiol. 34:326-339. 1959.

82. Jackson, P. C., Hendricks, S. B., and Vasts, B. M. "Phosphorylation by Barley Root Mitochondria and Phosphate Absorption by Barley Roots." Plant Physiol. 37:8-17. 1962.

83. Jacob, W. C., Van Middelem, C. H., Nelson, W. L., Welch, C. D., and Hall, N. S. "Utilization of Phosphorus by Potatoes." Soil Sci. 68:113-120. 1949.

84. Jacques, W. A. "Root-development in some common New Zealand Pasture Plants. II Perennial Rye-grass (Lolium perenne), cocksfoot (Dactylis glomerata), and white clover (Trifolium repens). Effect of fertilizer placement on the yield of roots and herbage." New Zealand J. Sci. Technol. A25 91-117. 1943.

85. Jeffrey, D. W. "Phosphate Nutrition of Australian Heath Plants: I. The Importance of Proteoid Roots in Banksia (Proteaceae)." Aust. J. Bot. 15:403-411. 1967.

86. Kalra, Y. P. "A Comparative Study of Phosphate Uptake by Several Field Crops." M.Sc. Thesis. University of Manitoba. 1966.

87. Kalra, Y. P., and Soper, R. J. "Efficiency of Rapè, Oats, Soybeans and Flax in Absorbing Soil and Fertilizer Phosphorus at Seven Stages of Growth." Agron. J. 60:209-212. 1968.

88. Larkum, A. W. D., and Loughman, B. C. "Anaerobic Phosphate Uptake by Barley Plants." J. Expt. Bot. 20:12-24. 1969.

89. Larsen. S. "The Use of p^{32} in Studies on the Uptake of Phosphorus by Plants." Plant and Soil 4:1-10. 1952.

90. Larsen, S. and Sutton, C. D. "The Influence of Soil Volume on the Absorption of Soil Phosphorus by Plants and on the Determination of Labile Soil Phosphorus." Plant and Soil 18:77-84. 1963.

91. Laties. G. G. "Active Transport of Salt in Plant Tissue." Ann. Rev. Plant Physiol. 10:87-112. 1959.

92. Lawton, K. "Plant Nutrition and the Utilization of Fertilizer Phosphorus." Phosphorus and its Compounds: J.R. Van Wazer Vol. II. Technology, Biological Functions and Applications. Interscience, New York, 1961. pp. 1461-1545.

93. Leggett, J. E., Galloway, R. A., and Gauch, H. G. "Calcium Activation of Orthophosphate Absorption by Barley Roots." Plant Physiol. 40:897-902. 1965.

94. Lehr, J. R., and Brown, W. E. "Calcium Phosphate Fertilizers: II. A Petrographic Study of their Alteration in Soils." Soil Sci. Soc. Amer. Proc. 22:29-32. 1958.

95. Lewis, D. G., and Quirk, J. P. "Phosphate Diffusion in Soil and Uptake by Plants: IV. Computed Uptake by Model Roots as a Result of Diffusive Flow." Plant and Soil 26:454-468. 1967.

96. Lewis, D. G., and Quirk, J. P. "Phosphate Diffusion in Soil and Uptake by Plants: I. Self-Diffusion of Phosphate in Soils. II. Phosphate Uptake by Wheat Plants." Plant and Soil 26:99-128. 1967.

97. Lewis, D. G., and Quirk, J. P. "Diffusion of Phosphate to Plant Roots." Nature (London) 205:765-766. 1965.

98. Lewis, D. G., and Quirk, J. P. "Phosphate Diffusion in Soil and Uptake by Plants: III. P^{31}-Movement and Uptake by Plants as Indicated by P^{32} Autoradiography." Plant and Soil 26:445-453. 1967.

99. Lewis, E. T., and Racz, G. J. "Phosphorus Movement in Some Calcareous and Non-Calcareous Manitoba Soils." Can. J. Soil Sci. 49:305-312. 1969.

100. Lindsay, W. L., and Taylor, A. W. "Phosphate Reaction Products in Soil and Their Availability to Plants." 7th Int. Congr. Soil Sci., Madison, Wisconsin, U.S.A. Vol. IV. 580-585. 1960.

101. Loneragan, J. F. and Asher, C. J. "Responses of Plants to Phosphate Concentration in Solution Culture: II. Rate of Phosphate Absorption and its Relation to Growth." Soil Sci. 103:311-318. 1967.

102. Loughman, B. C. "The Mechanism of Absorption and Utilization of Phosphorus by Barley Plants in Relation to Subsequent Transport to the Shoot." New Phytol. 65:388-397. 1966.

103. Loughman, B. C., and Russell, R. S. "The Absorption and Utilization of Phosphate by Young Barley Plants: IV. The Initial Stages of Phosphate Metabolism in Roots." J. Expt. Bot. 8:280-293. 1957.

104. Lundegardh, H. "Salts and Respiration." Nature (London) 185: 70-74. 1960.

105. Lundegardh, H., and Stenlid, G. "On the Exudation of Nucleotides and Flavanone from Living Roots." Ark.f.Botanik 31A, No. 10. 1944.

106. Mattingly, G. E. G., and Widdowson, F. V. "The Use of P32-Labelled Fertilizers to Measure 'superphosphate equivalents' of Fertilizers in Field and Pot Experiments." Trans. 6th Int. Congr. Soil Sci. Paris. B 461-470. 1956.

107. McAuliffe, C. D., Hall, N. S., Dean, L. A., and Hendricks, S. B. "Exchange Reactions between Phosphates and Soils:Hydroxylic Surfaces of Soil Minerals." Soil Sci. Soc. Amer. Proc. 12: 119-123. 1948.

108. Medappa, K. C., and Dana, M. N. "Influence of pH, Calcium, Iron, and Aluminum on the Uptake of Radiophosphorus by Cranberry Plants." Soil Sci. Soc. Amer. Proc. 32:381-383. 1968.

109. Mellado, L., Puerta, J., and Caballero, F. "Absorption of Phosphorus by the Bean; Influence of Nitrogen Supply and Placement of Dose on Phosphorus Availability to Bean Plants, Radioisotopes in Soil-Plant Nutrition Studies. Intern. Atomic Energy Agency, Vienna. 491-426. 1962.

110. Michaelis, L., and Menten, M. L. "Die Kinetic der Invertinwirkung." Biochem. Zeits. 449:333-369. 1913.

111. Mitchell, J., Kristjanson, A. M., Dion, H. G., and Spinks, J. W. T. "Availability of Fertilizer and Soil Phosphorus to Grain Crops, and the Effect of Placement and Rate of Application on Phosphorus Uptake." Sci. Agr. 32:511-525. 1952.

112. Moreno, E. C., Brown, W. E., and Osborn, G. "Solubility of Dicalcium Phosphate Dihydrate in Aqueous Solutions." Soil Sci. Soc. Amer. Proc. 24:94-98. 1960.

113. Moreno, E. C., Brown, W. E., and Osborn, G. "Stability of Dicalcium Phosphate Dihydrate in Aqueous Solutions and Solubility of Octacalcium Phosphate." Soil Sci. Soc. Amer. Proc. 24:99-102. 1960.

114. Nassery, H., and Harley, J. L. "Phosphate Absorption by Plants from Habitats of Different Phosphorus Status: I.Absorption and Incorporation of Phosphorus by Excised Roots." New Phytol. 68:13-20. 1969.

115. Noggle, J. C., and Fried, M. "A Kinetic Analysis of Phosphate Absorption by Excised Roots of Millet, Barley, and Alfalfa." Soil Sci. Soc. Amer. Proc. 24:276-280. 1960.

116. Nye, P. H. "The Effect of the Nutrient Intensity and Buffering Power of a Soil, and the Absorbing Power, Size and Root Hairs of a Root, on Nutrient Absorption by Diffusion." Plant and Soil 25:81-105. 1966.

117. Nye, P. H. "Processes in the Root Environment." J. Soil Sci. 19:205-215. 1968.

118. Nye, P.H., and Foster, W. N. M. "A Study of the Mechanism of Soil-Phosphate Uptake in Relation to Plant Species." Plant and Soil 9:338-352. 1958.

119. Olsen, R. A., and Drier, A. F. "Nitrogen, a Key Factor in Fertilizer Phosphorus Efficiency." Soil Sci. Soc. Amer. Proc. 20:509-514. 1956.

120. Olsen, S. R., and Kemper, W. D. "Movement of Nutrients to Plant Roots." Adv. in Agron. 20:91-152. 1968.

121. Olsen, S. R., Kemper, W. D. and Jackson, R. D. "Phosphate Diffusion to Plant Roots." Soil Sci. Soc. Amer. Proc. 26: 222-227. 1962.

122. Olsen, S. R., and Watanabe, F. S. "Diffusion of Phosphorus as Related to Soil Texture and Plant Uptake." Soil Sci. Soc. Amer. Proc. 27:648-653. 1963.

123. Olsen, S. R., and Watanabe, F. S. "Effective Volume of Soil Around Plant Roots Determined from Phosphorus Diffusion. Soil Sci. Soc. Amer. Proc. 30:598-602. 1966.

124. Olsen, S. R., Watanabe, F. S., Cosper, H. R. Larson, W. E. and Nelson, L. B. "Residual Phosphorus Availability in Long-Time Rotations on Calcareous Soils. Soil Sci. 78:141-151. 1954.

125. Pardee, A. B. "Membrane Transport Proteins." Science 162: 632-637. 1968.

126. Parker, F. W. "Soil Phosphorus Studies: III.Plant Growth and the Absorption of Phosphorus from Culture Solutions of Different Phosphorus Concentrations." Soil Sci. 24:129-146. 1927.

127. Parker, F. W., and Pierre, W. H. "The Relation between the Concentration of Mineral Elements in a Culture Medium and the Absorption and Utilization of those Elements by Plants." Soil Sci. 25:337-343. 1928.

128. Peterson, W. H., and Peterson, C. B. "The Water Soluble Content of Calcium and Phosphorus in Cabbage." J. Agr. Res. 33:695-699. 1926.

129. Phillip, R. E., Place, G. A., and Brown, D. A. "Self-Diffusion in Clays and Soils: I.The Effect of Phosphorus Rate." Soil Sci. Soc. Amer. Proc. 32:41-44. 1968.

130. Pierre, W. H., and Parker, F. W. "Soil Phosphorus Studies: II. The Concentration of Organic and Inorganic Phosphorus in the Soil Solution and Soil Extracts and the Availability of the Organic Phosphorus to Plants." Soil Sci. 24:119-128. 1927.

131. Ragland, J. L., and Colemen, N. T. "Influence of Aluminum on Phosphorus Uptake by Snap-Bean Roots." Soil Sci. Soc. Amer. Proc. 26:88-90. 1962.

132. Randall, P. J., and Vose, P. B. "Effect of Aluminum on Uptake and Translocation of P^{32} by Perennial Ryegrass." Plant Physiol. 38:403-409. 1963.

133. Rennie, D. A., and Mitchell, J. "The Effect of Nitrogen Additions on Fertilizer Phosphate Availability." Can. J. Agr. Sci. 34: 353-363. 1954.

134. Rennie, D. A., and Soper, R. J. "The Effect of Nitrogen Additions on Fertilizer Phosphorus Availability." J. Soil Sci. 9:155-167. 1958.

135. Rennie, D. A., and Spratt, E. D. "The Influence of Fertilizer Placement on 'A' Values." 7th Int. Congr. Soil Sci. 3:535-543. Madison, Wisconsin, U.S.A. 1960.

136. Rivière, J. "Contributions à l'Étude de la Rhizosphère du Blé." D. Sc. Thesis. University of Paris. 1959.

137. Robertson, W. K., Smith, P.M., Ohlrogge, A. J., and Kinch, D. M. "Phosphorus Utilization by Corn as Affected by Placement and Nitrogen and Potassium Fertilization." Soil Sci. 77:219-226. 1954.

138. Russell, R. S., and Bishop, O. N. "A Study of the Absorption and Utilization of Phosphate by Young Barley Plants: II.The Effect of Phosphorus Status and Root Metabolism on the Distribution of Absorbed Phosphorus between Roots and Shoots." J. Expt. Bot. 4:136-156. 1953.

139. Russell, R. S., and Martin, R. P. "A Study of the Absorption and Utilization of Phosphate by Young Barley Plants: I.The Effect of External Concentration on the Distribution of Absorbed Phosphorus between Roots and Shoots." J. Expt. Bot. 4:108-127. 1953.

140. Russell, R. S., Rickson, J. B., and Adams, S. N. "Isotopic Equilibria between Phosphorus in Soil and their Significance in the Assessment of Fertility by Tracer Methods." J. Soil Sci. 5:85-105. 1954.

141. Sabet, S. A., Abdel Salem, M. A., and Lagerwerff, J. L. "Growth and Ion Uptake by Maize Seedlings on Solutions Variable in Phosphate and Flow Rate." Plant and Soil 21:94-100. 1964.

142. Schofield, R. K. "Can a Precise Meaning be given to 'Available' Soil Phosphorus?" Soils and Fertilizers Commonwealth Bur. Soil Sci. 18:373-375. 1955.

143. Shapiro, R. E., Armiger, W. H., and Fried, M. "The Effect of Soil Water Movement vs. Phosphate Diffusion on Growth and Phosphorus Content of Corn and Soybeans." Soil Sci. Soc. Amer. Proc. 24:161-164. 1960.

144. Sommer, A. L. "The Relationship of the Phosphate Concentration of Solution Cultures to the Type and Size of Root Systems and the Time of Maturity of Certain Plants." J. Agr. Res. 52: 133-148. 1936.

145. Soper, R. J., Kalra, Y. P. "Effect of Mode of Application and Source of Fertilizer on Phosphorus Utilization by Buckwheat, Rape, Oats and Flax." Can. J. of Soil Sci. 49:319-326. 1969.

146. Speer, R. J., Allen, S. E., Maloney, M., and Roberts, A. "Phosphate Fertilizers for the Texas Blacklands: I.Relative Availability of Various Phosphatic Fertilizers." Soil Sci. 72:459-464. 1951.

147. Starostka, R. W., and Hill, W. L. "Influence of Soluble Salts on the Solubility of and Plant Response to Dicalcium Phosphate." Soil Sci. Soc. Amer. Proc. 19:193-198. 1958.

148. Strong, J. "Reaction Products of Applied Orthophosphates in some Manitoba Soils as Affected by Soil Calcium and Magnesium Content and Time of Incubation. M.Sc. Thesis. University of Manitoba. 1969.

149. Sutcliffe, J. F. "Mineral Salt Absorption in Plants." Pergamon. Books by Wallace, University of California. 1962.

150. Teakle, L. J. H. "The Absorption of Phosphate from Soil and Solution Cultures." Plant Physiol. 4:213-232. 1929.

151. Terman, G. L., Anthony, J. L., Mortensen, W. P., and Lutz, J. A. Jr. "Crop Response to NPK Fertilizers Varying in Granule Size and Water Solubility of the Phosphorus." Soil Sci. Soc. Amer. Proc. 20:551-556. 1956.

152. Thomas, W. "The Feeding Power of Plants." Plant Physiol. 5:443-489. 1930.

153. Tidmore, J. W. "Phosphate Studies in Solution Cultures." Soil Sci. 30:13-31. 1930.

154. Van Stevenick, R. F. M. "The significance of Calcium on the Apparent Permeability of Cell Membranes and the Effects of Substitution with Other Divalent Ions." Physiol. Plantarum 18:54-69. 1965.

155. Vlamis, J., and Davis, R. "Effects of Oxygen Tension on Certain Physiological Responses of Rice, Barley and Tomato." Plant Physiol. 19:33-51. 1944.

156. Welch, C. D., Hall, N. S., and Nelson, W. L. "Utilization of Fertilizer and Soil Phosphorus by Soybeans." Soil Sci. Soc. Amer. Proc. 14:231-235. 1949.

157. Wiklander, L. "Kinetics of Phosphate Exchange in Soils." Ann. Roy. Agric. Coll. Sweden 17:407-424. 1950.

158. Wild, A. "Soluble Phosphates in Soil and Uptake by Plants." Nature (London) 203:326-327. 1964.

159. Williams, R. F. "The Effects of Phosphorus Supply on the Rates of Intake of Phosphorus and Nitrogen and upon Certain Aspects of Phosphorus Metabolism in Gramineous Plants." Aust. J. Sci. Res. B1:333-361. 1948.

160. Woodruff, J. R., and Kamprath, R. J. "Phosphorus Adsorption Maximum as Measured by the Langmuir Isotherm and its Relationship to Phosphorus Availability." Soil Sci. Soc. Amer. Proc. 29:148-150. 1965.