

INTRODUCTION

The cultivation of peas, like that of wheat and barley dates from before Greek and Roman times (Mahoney, 1991). In Australia, peas were grown as early as 1827 in Tasmania, and they are the main cool season legume in south eastern Australia (Lovett and Lazenby, 1979). Peas grow well on alkaline heavier clay soils whilst lupins are grown on the neutral/ slightly acidic soils. Currently the main pea growing areas in Australia are South Australia and Victoria although their production in New South Wales and Western Australia is rapidly increasing (Munroe, 1989; Lamb and Poddar, 1992 and 1994).

Field peas have long been of great value in human and livestock nutrition. Their grain provides a good source of protein for human consumption, while the haulm makes good quality hay (Munroe, 1989). The quality of field peas for either human consumption or stockfeed is determined by their genotypic characteristics (Munroe, 1989; Lamb and Poddar, 1992 and 1994). They are grown in crop rotations to reduce weeds, root and foot rot disease cycles in cereals, and to conserve soil nitrogen. When incorporated in crop rotation systems, peas fix atmospheric nitrogen for their own requirements and may allow winter cereal crops to be grown with little or no need to apply nitrogen fertiliser (Lamb and Poddar, 1992 and 1994).

A large number of field pea varieties has been produced but the major groups which are commonly grown in Australia are the Dun types (which are used mainly for stockfeed); white types (which are used mainly for human consumption); maple types (which have speckled seed) and the blue boiler types (which are usually grown under contract for the canning trade). The differences among the varieties include the colour of flowers, seeds and

cotyledons which accounts for the quality of the seed and hence the end use; internode length which affects the height of the plant; morphological characteristics of the leaflets, time of flowering and maturity, and the number of pods per node which often determines seed yield (Munroe, 1989; Lamb and Poddar, 1992 and 1994).

Peas are adapted to a wide range of soils but best yields can be expected from heavy textured soils, soils not susceptible to surface sealing or waterlogging and from the non-saline soils (Lovett and Lazenby, 1979; Munroe, 1989; Lamb and Poddar, 1992). The soils of the Mallee and Wimmera regions of Victoria contain *Rhizobium leguminosarum* (Mahoney, 1986) which nodulate field peas; in soils such as hard-setting duplex soils where *Rhizobium leguminosarum* do not survive, inoculation of pea seeds or the soil with the suitable rhizobium is recommended.

In many Australian soils phosphorus deficiency is one of the major limitations to crop production. Likewise, zinc deficiencies are widespread particularly on alkaline soils throughout all states of Australia. Applications of these nutrients are therefore necessary to maintain or increase crop yields. The two nutrients are similarly active in soil such that their concentration are always low. It has been observed that the application of Zn fertiliser alone on the Wimmera black soils did not alleviate Zn deficiency or improve crop production but when Zn was applied in conjunction with superphosphate marked responses to Zn were visible (Millkan, 1940). Similarly, increasing the level of available P in the soil with low Zn status does not improve plant growth and yields but may result in P toxicity in the plant (Sims and Rooney, 1956; Bingham and Garber, 1960; Wagar *et al.*, 1986; Verma and Minhas, 1987).

Many of the experiments conducted under Australian conditions on the response of crops to P and Zn fertilisation have utilised crops like wheat or maize; there is relatively little research

on pea response to nutrient fertilisation under Australian conditions. For these reasons it was decided to conduct a series of experiments on peas alone and on peas compared to another crop which has been thoroughly studied to compare and contrast the responses to P and Zn fertilisers and also to review the factors which influence absorption and utilisation of both P and Zn by grain crops.

PART ONE: A REVIEW OF LITERATURE

CHAPTER ONE

INTRODUCTION

Phosphorus and zinc are two important elements in the nutrition of many crops; their additive interactions are also important (Bingham and Garber, 1960; Olsen, 1972; Webb and Loneragan, 1988; Wang *et al.*, 1990; Biswas and Prasad, 1991; Jahiruddin and Cresser, 1991). The concentrations of phosphorus (P) and zinc (Zn) in the soil solution are normally low due to their high activities in the soil. The reactions which influence their concentrations in solution are: (i) adsorption by oxides and hydrous oxides of iron (Fe) and aluminium (Al), carbonate minerals and organic matter complexes; (ii) precipitation by Al, Fe and calcium (Ca) ions, and precipitation of Zn by phosphate ions; (iii) sorption by clay minerals; and (iv) complexation with organic compounds.

During plant growth, the concentrations of P and Zn in the soil solution depend on replenishment of each nutrient from its labile source to supplement the amount taken up by plants (Fried *et al.*, 1957). The uptake rates of P and Zn by plants depend on the concentrations of these nutrients in the soil solution and on the ease of diffusion of each nutrient to the absorbing root surfaces. Total uptake depends on the ability of the soil to replenish the soil solution concentrations, the plant requirement for the nutrients and on the ability of roots to absorb the nutrients.

The rate of replenishment of the soil solution concentrations is determined by the content of the nutrient in the soil (the quantity factor) and by those soil factors which directly or indirectly affect the activity of P and Zn in soil. Plant requirements for P and Zn are

determined by the functions of these nutrients in plants, their remobilisation in the plant, the P and Zn interaction effect, the cultivar type and the level of production desired. Factors which control the ability of the roots to absorb these nutrients are the plant root system and other factors related to the roots, the rhizosphere and, for some plants, mycorrhizal associations.

This review discusses how these factors, singly and together, influence the removal of P and Zn from the soil system by grain crops. Where appropriate, differences in absorption of either nutrient between different crops will be discussed. Particular attention will be paid to differences in the absorption of P and Zn between cereals and grain legumes, two groups of crops which constitute the major components of crop rotations in many countries.

CHAPTER TWO

SOIL FACTORS

The most important chemical soil factors which determine P and Zn concentrations are clay mineralogy, iron and aluminium oxides and hydrous oxides, soil pH, organic matter content and rhizosphere micro-organisms. The major physical soil factors are soil texture, structure, moisture content and temperature.

2.1. Forms of Phosphorus and Zinc Present in Soil

2.1.1. Phosphorus

Various forms of P occur in soil but from the viewpoint of plant nutrition and crop production they can be classified into the soil solution P, labile P and the non-labile P. Soil solution P consists of orthophosphate anions in soil solution, and is the fraction of soil P which is directly accessible for absorption by plant roots. The labile P is the pool of readily available P which replenishes P in the soil solution following the uptake of P by plant roots. This is made up of adsorbed and organic P, and of sparingly soluble P minerals. Non-labile P is the fraction of soil P present in effectively insoluble minerals and which is, if at all, very slowly available.

Soil solution P

Soil solution P occurs as orthophosphate ions, H_2PO_4^- and HPO_4^{2-} . The concentration of these anions is dependent on soil solution pH, as shown in Fig. 2.2 (Page 14). H_2PO_4^- is predominant at pH values below 7 and HPO_4^{2-} at pH values above 7. In addition to

inorganic phosphate ions about half the soil solution P may be present as soluble organic phosphate compounds, particularly in soils with appreciable content of organic matter. In soil where most of the organic P present is in the form of monophosphates and lower esters of inositol polyphosphates, the proportion of soil solution P which is organic P may exceed that of the inorganic P present (Wild and Oke, 1966). Reviews of the availability of organic P have been undertaken by Martin and Cartwright (1971), Anderson *et al.* (1974) and Probert (1983).

Adsorbed P

P is adsorbed on the surfaces of the oxides and hydrous oxides of iron (haematite and goethite) and aluminium (gibbsite), various clay minerals, carbonates and organic matter complexes. The availability of the adsorbed P is controlled by adsorption/desorption processes and the soil factors affecting those processes such as soil pH, soil type and age. For instance, in acid soils, orthophosphate ions are predominantly adsorbed onto the surfaces of haematite or goethite or gibbsite (depending on which one predominates), clay minerals such as illite, kaolinite and smectite, and Al and Fe organic matter complexes. However in neutral to alkaline soils, P is predominantly adsorbed onto the surfaces of Ca and Mg carbonates and Ca organic matter complexes.

The quantity of the adsorbed P depends on the content of the adsorbing materials in the soil. Thus a number of Australian great soil groups such as prairie soils, black earths and red and brown podzolic soils show highly significant correlations between the levels of phosphate ions and iron oxides; in chernozem and alpine humus soil from Tasmania adsorbed P is well correlated with both iron oxides and sulfur associated with organic matter (Norrish and Rosser, 1983). In soils which contain considerable amounts of CaCO_3 or Ca from fertilisers orthophosphate anions are adsorbed on to the surface of the carbonates or react with Ca to form a calcium phosphate precipitate (Criffin and Jurinak, 1973).

Generally, in Australian soils more P is adsorbed by Fe oxides than Al oxides due to the larger surface area of Fe oxides (Norrish and Rosser, 1983). In soils with a long cropping and fertiliser history and in which most of the surface area of iron oxide is already saturated, aluminium oxides largely account for remaining P adsorption capacity (Norrish and Rosser, 1983).

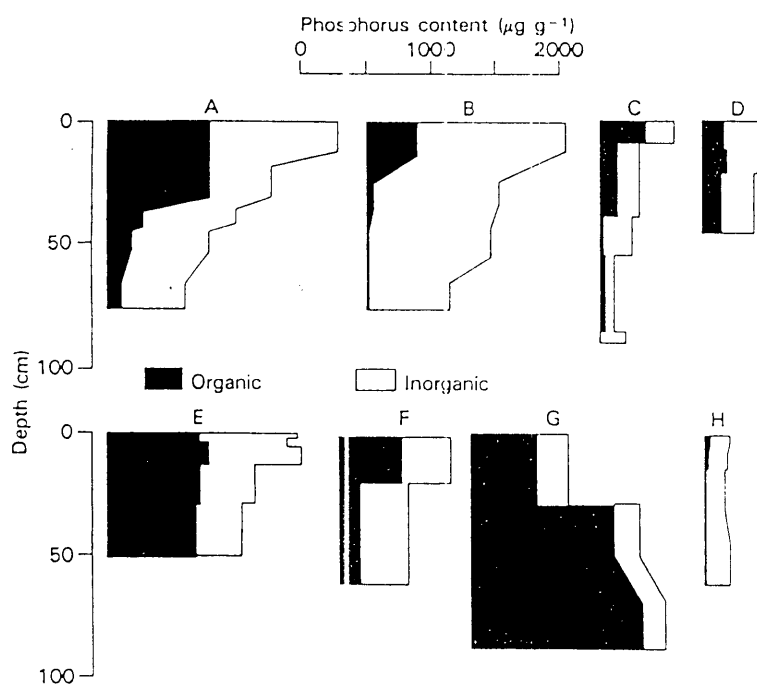


Fig. 2.1. Distribution of phosphorus in various soil profiles. *Source:* Anderson (1980, cited by Wild, 1988).

A & B Freely and poorly drained cultivated clay loams of the Inch Association, Scotland.

C Uncultivated Koputaroa soil developed on windblown sand, New Zealand.

D Uncultivated Dawes silt loam, Nebraska.

E Uncultivated Pima calcareous clay loam, Arizona.

F Cultivated Orthic Deep Black, Melfort, Saskatchewan.

G Uncultivated *Carex globularis* pine bog, northern Finland.

H Leached forest soil, Ibadan, Nigeria.

Organic P

The amount of organically held phosphorus varies between soils and within the soil profile as shown in Fig. 2.1. The content of organic P is related to the organic matter content of the soil. However, the C:P ratio is more variable than the C:N ratio, possibly because, unlike N which chemically bonds within the humic acid structure, P is bonded to structures peripheral to humic acid (Wild, 1988), where it is exposed to reactions which may lead to the replenishment of soil solution P.

The forms of organic P that occur in soil are inositol phosphate esters (60 % of organic P), nucleic acids (about 5 %), phospholipids (about 1 % of organic P), phosphate sugars, phosphoproteins, glycerol phosphates and some forms which have not yet been characterised (Probert, 1983; Mengel and Kirkby, 1987; Wild, 1988).

Of the inositol phosphate esters, myo-inositol is a plant constituent and others are probably synthesised by unknown micro-organisms. Nucleic acids and phospholipids are mainly contributed by plant and animal remains and by *in situ* microbial synthesis. In most Australian and New Zealand soils organic P occurs mainly as inositol polyphosphates and a class of higher molecular weight components which still need to be characterised (Martin, 1970; Stewart and Tate, 1971). The release of organic P into soil solution depends on the net difference between mineralisation and immobilisation; since the two processes often tend to occur at comparable rates, the net mineralisation is often relatively small compared with total soil organic P content.

P-containing minerals

A number of minerals containing phosphorus occur in soils. Some of these are residues from the parent materials while others are pedogenic minerals which had formed during weathering and soil formation or have formed when phosphorus fertilisers are added to the soil. The minerals are mainly P combined with Fe, Al and Ca. The persistence of residual and pedogenic minerals indicates their low solubilities and hence poor ability for supplying P for plant growth.

Residual minerals

Apatite is the commonest P mineral in soil; different forms of which occur in different kinds of rocks. Fluorapatite, $\text{Ca}_5(\text{PO}_4)_3\text{F}$ occurs in igneous and metamorphic rock. In sedimentary rocks it occurs as carbonate-apatite in which some of the phosphate is replaced by carbonate. There are two groups of carbonate-apatite, one in which the fluorine is replaced by chlorine (chlorapatite) and another in which the fluorine is replaced by hydroxy group (hydroxyapatite). It is very slowly soluble and hence its persistence in the soil. Residual apatite has large particles, sometimes occurring in the sand fractions. It is most abundant in soils originating from granite parent material such as red earth and non-calcic brown soils, and its content increases with depth of the soil profile (Norrish and Rosser, 1983). Carbonate-apatite is exceptionally fine grained and it is the most soluble of all the apatite minerals hence it can contribute to the supply of available P. It occurs mainly in calcareous soils and in less weathered soils although its contribution to total soil P in the latter soils is not significant (Norrish and Rosser, 1983).

Other residual P-containing minerals are the plumbogummite minerals of the sedimentary origin, monazite, xenotime and some silicate minerals (Norrish and Rosser, 1983). Their solubility is low and hence so is their contribution to the supply of P.

Pedogenic minerals

Apatite also occurs as a pedogenic mineral. Pedogenic apatite minerals are fine-grained ($<1 \mu\text{m}$). They have been shown to be derived from plant ashes although it has not yet been

resolved whether they are formed in plants prior to ashing or whether they are crystallised in the organic debris after burning (McManus *et al.*, 1979 cited by Norrish and Rosser, 1983). They have been observed in chernozems within organic matter fragments (Norrish and Rosser, 1983). Lindsay and Vlek (1977) postulated that pedogenic apatite minerals form at very low temperatures and probably in alkaline soils according to their solubility data. However, the extent to which apatite has formed in alkaline soils in Australia has not been well researched.

Other pedogenic minerals are plumbogummite minerals and vivianite. Plumbogummites of this group are fine-grained (0.5 - 5 μm). They are a product of quaternary weathering, being formed when P from apatite and other minerals reacts with clay minerals (Altschuler, 1973). The P in these minerals occupies the tetrahedral position alternatively with S and As, while Al and Fe occupy the octahedral coordination. Minerals of this group have been identified in various Australian soils that have developed from different parent materials, such as terra rossa, rendzina, krasnozems and lateritic podzolic soils (Norrish, 1957 and 1968). In some Australian soils plumbogummite minerals contribute from 12 to 60 % to the total soil P (Norrish, 1968).

Vivianite ($\text{Fe}_3(\text{PO}_4)_2 \cdot 8\text{H}_2\text{O}$) is formed by reduction of Fe in the presence of organic matter (Palache *et al.*, 1951). It has been identified in alluvial soils in New South Wales (Koch, 1956) and in waterlogged soils and peat (Wild, 1988).

Reactions of applied phosphate

When P is added to the soil as a phosphate fertiliser, it is initially adsorbed onto the soil colloids and some of it may precipitate with the cations present in the soil to form phosphate compounds of variable solubilities. As the P adsorbing materials age the adsorbed P may penetrate into the solid phase. This process is referred to as sorption and retained P as

absorbed, chemisorbed or sorbed P (Tisdale *et al.*, 1985). Adsorption of fertiliser P is favoured at low concentrations of soil solution P whereas precipitation and sorption are favoured at high soil solution P concentrations (Cole *et al.*, 1953; Griffin and Jurinak, 1973; Tisdale *et al.*, 1985).

In calcareous soils and soils high in exchangeable Ca^{2+} , P in fertiliser precipitates with Ca^{2+} to form di-calcium phosphate, $\text{CaHPO}_4 \cdot 2\text{H}_2\text{O}$, which slowly converts to hydroxyapatite. Di-calcium phosphate is itself soluble enough to provide appreciable amount of P for plant growth but its conversion to apatite results in P being retained unavailable to plants. Many of calcium-phosphate compounds which form under high phosphate concentration and at pH values near neutrality are relatively soluble and produce a good source of P for plant growth for a short period, that is before they revert to less soluble forms, compared to those which form at alkaline pH values (Tisdale *et al.*, 1985).

In mineral soils, P fertiliser reacts with hydroxy-aluminium species bound to organic matter and clays. Al on organic matter is more active and hence retains more P fertiliser than Al on clays as the latter is mostly fixed between crystal layers and thus has a reduced reactive surface area. The high phosphate retention capacity of complexes of Al-organic matter has been confirmed by many authors for a range of soils with low pH conditions (Williams *et al.*, 1958; Williams, 1960; Bromfield, 1965; Saunders, 1965; Norrish and Rosser, 1983).

Hydrous oxides of Fe naturally have a high adsorption capacity for P due to their large surface area. Thus in virgin soils, native P is retained on the surfaces of the hydrous oxides of Fe such that the largest portion of the exposed sites of the clay minerals for P adsorption is on the surfaces of the Al oxides (Norrish and Rosser, 1983). When P fertilisers are applied to the soil and the level of P in the soil solution rises, Al oxides exhibit high adsorption capacities compared to hydrous oxides of Fe as the surfaces of the latter would

by then be highly or completely saturated with P (Norrish and Rosser, 1983). Increasing concentration of P in the soil solution in the presence of clays minerals results in the formation of aluminium phosphate precipitates.

2.1.2. Zinc

Zinc occurs in soils in soluble and adsorbed forms and as a constituent of minerals of varying solubilities. Soluble and insoluble Zn organic complexes also occur. Adsorbed Zn and soluble Zn organic complexes and Zn minerals form the fraction of Zn similar to the labile P pool, while the insoluble Zn forms correspond to the non-labile phosphate pool.

Soil solution Zn

Components of soil solution zinc are the divalent cation, Zn^{2+} , and soluble Zn compounds. The dominant form present in solution is very much dependent on soil solution pH. In acid soils the largest proportion of Zn (71-76 %) present in soil solution is Zn^{2+} with the rest occurring as $ZnSO_4$. In alkaline soils, hydrolysis species, $Zn(OH)^+$ and $ZnHCO_3^+$, dominate while Zn^{2+} , $ZnSO_4$ and $ZnCO_3$ occur in smaller concentrations (Davies and Jones, 1988). Some of the soil solution Zn occurs as soluble Zn organic complexes of amino and organic acids (Stevenson and Arcahani, 1972). On average, the soluble Zn organic complexes constitute 60 % of the soluble Zn in soils (Hodgson *et al.*, 1966).

Adsorbed Zinc

Zinc can be adsorbed by hydrous oxides of Fe where it is held as a bridging ligand between two neutral sites. It can also be adsorbed non-specifically by either Al or Fe hydroxides where Zn^{2+} is retained at low energy and is susceptible to replacement by Ca^{2+} , Mg^{2+} or Ba^{2+} (Quirk and Posner, 1975; Tisdale *et al.*, 1985). Zinc is also adsorbed by clay minerals, carbonates and soil organic matter (Tisdale *et al.*, 1985).

Organic Zinc

Soil organic Zn occurs as soluble and insoluble Zn organic matter complexes and immobilised Zn (Stevenson and Ardakani, 1972). The solid soil organic Zn comprises the insoluble humic- and fulvic-Zn complexes and Zn immobilised by high-molecular-weight organic substances such as lignin.

Mineral Zinc

There are not as many zinc minerals as P minerals because Zn^{2+} occurs in minerals in trace amounts. Zn occurs in ferromagnesian minerals, such as augite, biotite and hornblende which form when applied Zn^{2+} replaces Mg^{2+} and Fe^{2+} in the crystal lattice by isomorphous substitution (Tisdale *et al.*, 1985). Resistant minerals such as ilmenite and magnetite, can have a high content of Zn (Tiller, 1988). The minerals franklinite ($ZnFe_2O_4$) and sphalerite (ZnS), form in flooded calcareous soils following solubilisation of Zn from readily soluble compounds. These two minerals exhibit low solubility, especially at high pH and in anaerobic conditions, and hence reduce the availability of Zn^{2+} . Complexes of Zn with chloride, nitrate and phosphate also form in soil; these are poor suppliers of Zn with the exception of Zn-phosphates (Tisdale *et al.*, 1985).

2.2. Occurrence of Phosphorus and Zinc in Soil

2.2.1. Sources of P and Zn

The main sources of P and Zn in soils are parent material, fertilisers and organic materials returned to the soil. The amounts of P and Zn present in a soil vary according to the type of parent material, the fertiliser history of the soil and its organic matter content. Soils derived from basic igneous rocks such as basalt are usually rich in P and Zn compared to soils developed on siliceous parent materials (Mengel and Kirkby, 1987). An example occurs in Nile Valleys soils, which receive annual depositions of P-rich alluvium derived from the basic rocks of Ethiopian plateau (Wild, 1988). Soils derived from weathered rocks, in which apatite, the main phosphate containing mineral in rocks, is dissolved by acid leaching water before the formation of sufficient Fe and Al oxides and clay minerals onto which the orthophosphate ions are adsorbed, are usually low in P (Wild, 1988).

Soils rich in organic matter usually contain appreciable amounts of P (Wild, 1988) and Zn (Follett and Lindsay, 1970; Lindsay, 1974). The release of P and Zn into the soil solution depends on immobilisation/mineralisation processes. Loss of surface soil through soil erosion and runoff results in the reduction of P and Zn especially when the largest proportions of these nutrients occur as organic forms in the topsoil (Mengel and Kirkby, 1987; Wild, 1988). Cropping soils are usually higher than virgin soil in P due to prolonged P fertiliser application (Williams and Raupach, 1983).

2.2.2. Soil Contents and Concentrations

Australian soils in particular, are low in P. Their average content is $350 \mu\text{g P g}^{-1}$ compared with $700 \mu\text{g P g}^{-1}$ for the UK and $420 \mu\text{g P g}^{-1}$ for the USA (Cooke, 1958; Wild, 1958; Shacklette *et al.*, 1971, cited by Wild, 1988). This is mainly due to the long history of P-

depleting weathering cycles that have affected Australian soils and parent materials. The concentration of P in soil solution is also lower in Australian soils than other soils. For example, an average soil solution P in Australian soils is 0.03 % whereas those of English and US soils are 0.045 and 0.04 – 0.09 %, respectively (Piper and Prescott, 1951; Leeper, 1964).

A wide range of total Zn content is found in soils ($1.5 - 2000 \mu\text{g g}^{-1}$) but values from 50 to $300 \mu\text{g g}^{-1}$ with a typical mean of $60 \mu\text{g g}^{-1}$ are most common in agricultural soils (Davies and Jones, 1988). The concentration of Zn in soil solution ranges from 2 to $200 \mu\text{g/l Zn}^{2+}$ (Hodgson *et al.*, 1966). These figures are very low compared with the concentrations of P and Zn in plants (Asher and Lonergan, 1967; Tisdale *et al.*, 1985; Mengel and Kirkby, 1987).

Soil deficiencies of P have been reported from Australia, South America and South Africa (Wild, 1988) and those of Zn from USA and Australia (Berger, 1961; Mengel and Kirkby, 1987). Thus the capacity of the soil to replenish P and Zn into the soil solution during the plant growth is the most important factor controlling their supply to plant roots. Similarly, applications of P and Zn fertilisers are essential for successful cropping.

2.3. Factors Affecting the Availability of Phosphorus and Zinc

2.3.1. Soil Chemical Properties

Clay content and type

Clay soils have high P buffering capacity compared with silty soils and hence retain greater amounts of P and only small amounts are present in soil solution at equilibrium (Olsen and Watanabe, 1970). The high P buffering capacity of clay minerals is due to their

large surface area exposed for sorption (Tisdale *et al.*, 1985). Ionic phosphate can also be adsorbed on the edges of the clay micelles by the ligand exchange, whereby an OH^- or $(\text{OH})_2^+$ group from the co-ordination shell of exposed Al or Fe is displaced by an oxygen atom from H_2PO_4^- or HPO_4^{2-} (White, 1979).

Clay minerals with a low silica : alumina ratio such as the 1:1 kaolinitic clays have very strong P adsorption capacities compared with clays with a high ratio such as the 2:1 clays, illite and montmorillonite (Mengel and Kirkby, 1987). The high P adsorption capacity of kaolinitic clays and allophanes is attributed to their relatively high content of Al which is associated with a large number of exposed hydroxyl groups, their non-specific cation adsorption sites and to their high content of associated hydrated oxides of Fe and Al (Mengel and Kirkby, 1987). Other minerals with high P retention are gibbsite, goethite and hematite (Sanchez and Uehara, 1980).

Strongly buffered soils require large amounts of P fertiliser to support plant growth compared with the poorly buffered soils with relatively low labile P (Tisdale *et al.*, 1985). The latter soils depend heavily on P fertilisation for adequate P supply while the former require P fertiliser for replenishment of the soil solution. Thus, phosphate buffering capacity is important in controlling P concentration of the soil solution and hence P uptake by growing plants.

Zn is adsorbed by clay minerals such as kaolinite, montmorillonite and illite (Tisdale *et al.*, 1985; Jahiruddin and Cresser, 1991). The presence of Al and Fe oxides influences Zn adsorption by clays (Tisdale *et al.*, 1985). The increase in Zn adsorption and the decrease in its retention by these clay minerals at low Fe content (Tisdale *et al.*, 1985) indicate that adsorption is favoured more by Al whereas retention is favoured by Fe. Adsorption of Zn occurs on the surfaces of clay minerals due to their negative charge; it is usually directly

related to CEC of clays (Tisdale *et al.*, 1985). Zinc adsorbed on clay minerals occurs as the exchangeable cation, Zn^{2+} , which is readily available to plants. Retention of Zn^{2+} by ferric clay minerals occurs through isomorphous replacement of original Fe^{2+} at octahedral sites within the crystal structure, resulting in low Zn availability.

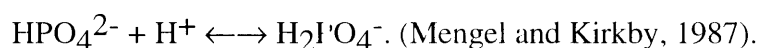
Other minerals

Zinc is also strongly retained by magnesite ($MgCO_3$) and intermediately by dolomite [$CaMg(CO_3)_2$]; in both situations Zn exchanges with Mg for the lattice sites into the crystal surfaces (Lindsay, 1972; Tisdale *et al.* 1985). This occurs typically in calcareous soils. At high concentrations in solution, Zn^{2+} can precipitate to $Zn(OH)_2$ and $ZnCO_3$. However, due to its high solubility in soil solution, $ZnCO_3$ does not persist in soils (Udo *et al.*, 1970), and hence can help maintain soil solution Zn^{2+} during plant growth.

Soil pH

Phosphorus

The primary effect of soil pH on the availability of P is in the control of the levels of orthophosphate ions ($H_2PO_4^-$ and HPO_4^{2-}) in the soil solution (Fig. 2.2). At acidic pH, the monovalent ion is more abundant than the divalent ion and the two are nearly at equal proportions at pH 7. Under acidic conditions the occurrence of $H_2PO_4^-$ at relatively higher levels than HPO_4^{2-} is the result of protonation of the latter due to high concentration of H^+ thus:



Soil pH also has a profound influence on the activity of P in soil, and hence on its concentration in soil solution. In acid soils (pH 5.5-6.5) P is adsorbed onto the surfaces of hydrous oxides of Fe and Al, and Al-organic matter complexes and forms part of the labile pool. When soil pH is less than pH 5 the amount of exchangeable Al on mineral surfaces

increases, resulting in precipitation and/or adsorption of P by Al (Coleman *et al.*, 1960; Tisdale *et al.*, 1985; Wild, 1988).

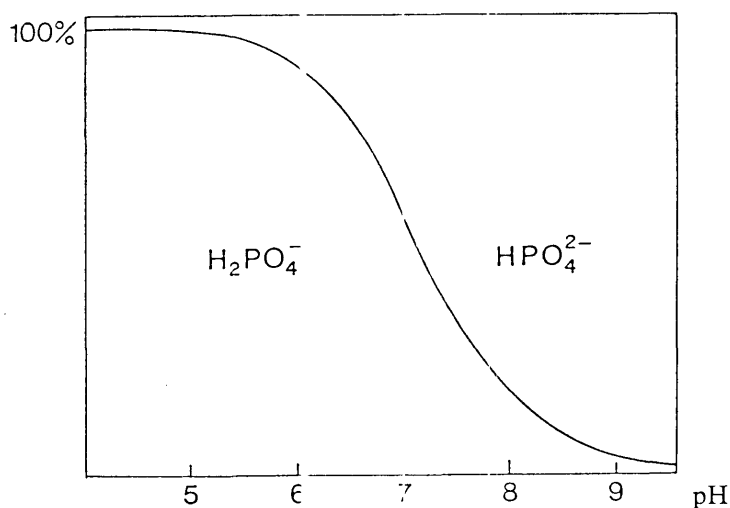


Fig. 2.2. Effect of solution pH on ionic forms of dissolved phosphate. *Source:* Mengel and Kirkby (1987).

In alkaline soils the solubility of Al is depressed and P is adsorbed mainly by Ca and Mg carbonates and Ca-organic matter complexes (Tisdale *et al.*, 1985; Wild, 1988). Adsorption by Ca and Mg carbonates occurs mainly in calcareous soils and adsorbed P is slowly converted into apatite (Harrison and Das, 1921; Parfitt, 1978) which dissolves very slowly under high pH (Wild, 1988).

There is a difference in the effect on P availability between naturally occurring high pH and high pH induced by liming. Liming acid soil increases desorption of P by ligand exchange from Fe and Al oxides surfaces, and hence increases its availability (Wild, 1988). However, there is evidence that availability of P immediately after liming is reduced (Clarkson, 1967; Haynes, 1984). This is attributed to fresh precipitates of Al-hydroxyl polymers that are produced during liming, which have relatively high P adsorption capacity (Wild, 1988). The

adsorption capacity of these polymers decreases with time or may be reduced by the effect of drying following liming (Haynes, 1984). Thus, the effect of liming on increasing availability of P in acid soils with high P adsorption capacity can be enhanced by leaving the soil for some time to dry before applying P fertiliser.

In acid soils following the application of lime the availability may decrease as a combined result of increased phosphate ions and excessive donation of Ca ions from overliming (Parfitt, 1978). When HPO_4^{2-} and Ca^{2+} are present in soil solution they precipitate to form di-calcium phosphate, which dissolves slowly at high pH. The availability of P in most soils is greatest in the pH range 6.0 to 6.5 (Tisdale *et al.*, 1985) or 6.0 to 7.0 in alkaline calcareous soils (White, 1979).

Zinc

Like P, the activity of Zn in soils and its availability are pH dependent. Zinc occurs in soil solution predominantly as the Zn^{2+} ion, especially in acid soils (Davies and Jones, 1988). Above pH 5.7, the most dominant forms of zinc are $\text{Zn}(\text{OH})^+$, $\text{Zn}(\text{HCO}_3)^+$ and ZnCO_3 . Since Zn is exclusively absorbed by plants as the divalent ion (Zn^{2+}) and this form is dominant in acidic conditions, Zn is more available at low than at high pH.

Soil solution pH affects Zn^{2+} concentration through its effects on chelation and precipitation (White, 1979) and adsorption/desorption reactions in dilute soil solutions (Davies and Jones, 1988). At low pH, Zn^{2+} is adsorbed by Fe and Al oxides, clay minerals and organic matter forming a labile pool that releases Zn^{2+} during plant growth. As pH increases, adsorption by goethite intensifies, reducing the availability of Zn (Mengel and Kirkby, 1987). Jeffery and Uren (1983) reported that Zn solubility decreased by 100-fold as pH of the soil increased from 4.4 to 7.5.

In basic calcareous soils the effect of high pH on the availability of Zn is enhanced by the presence of CaCO₃, resulting in the precipitation of Zn(OH)₂ and ZnCO₃. However, the effect of precipitation of ZnCO₃ on the availability of Zn is small (see Section 2.3.2).

Organic matter and rhizosphere micro-organisms.

Organic matter (O.M.) affects the availability of P and Zn (i) through its effect on acidification, (ii) by blocking the adsorption sites for P and Zn on sesquioxide particles and (iii) through complexation of P and Zn by organic substances.

Soil acidification

When O.M. decomposes CO₂ is produced which reacts with H₂O as follows:



Under alkaline conditions this process proceeds to release two protons for each molecule of CO₂. The production of H⁺ ions and the decrease in pH in alkaline soils increases the solubility of the sparingly soluble minerals and hence the availability of P and Zn as described in Section 2.3.1. The CO₃²⁻ produced can react with Zn²⁺ to form ZnCO₃, which is fairly soluble. The carbonic acid from the decomposition of organic matter is capable of dissolving some P containing soil minerals, and hence increasing P availability. The importance of increased soil O.M. for the availability of P and Zn through the effect of CO₂ on lowering pH has been described by Sinclair (1992).

Reduction of adsorption capacity

O.M. can also increase the availability of P by producing substances which react with P adsorbing materials and hence reduce their P adsorption capacity. Organic anions, such as citrate, humate and malate, and other organic colloids can form complexes with Al and to some extent with Fe, and decrease their P adsorption capacity increasing the concentration of P in the soil solution (Nagarajah *et al.*, 1970). Also, the organic anions mentioned above can specifically replace P adsorbed by hydrous oxides of Fe and Al, thus rendering it more available (Tisdale *et al.*, 1985). In addition, P adsorption and buffering capacities of these

colloids can be reduced by the formation of a thin film of humus on their surfaces (Tisdale *et al.*, 1985).

Complexation

Depending on the concentration of P in soil solution, P may be adsorbed onto the complexes of organic substances in a labile form. Examples of P organic matter compounds are phosphates of Ca/Mg–organic complexes and the phosphohumic complexes. There is evidence that the latter compounds are easily assimilated by plants (Tisdale *et al.*, 1985). Research has shown that soluble organic phosphate compounds have relatively higher mobility than dissolved inorganic P (Lewis and Racz, 1969; Fox and Kamprath, 1971); this increase mobility should increase P availability.

O.M. increases availability of Zn through production of organic compounds which form complexes of varying solubilities with Zn. The proportion of Zn organic complexes in solution in relation to inorganic Zn increases as soil pH increases (Hodgson *et al.*, 1966). This factor tends to offset the reduction of mobility of inorganic Zn as soil pH increases.

The term chelation is normally used to refer to the formation of soluble organic substances which shield micronutrients from fixation reactions, and hence increase their availability to plants. Amino and organic acids are known to form soluble complexes with Zn (Stevenson and Ardakani, 1972). The organic acids can also increase the availability of Zn by increasing its movement to roots and causing the weathering of rocks and dissolution of minerals with the release of Zn into the soil solution (Stevenson and Ardakani, 1972; Sharma *et al.*, 1992). Tisdale *et al.* (1985) reported that substances present in or derived from freshly applied organic supplements have a high capacity to chelate Zn²⁺.

Zn can be strongly adsorbed by some organic compounds, such as humic acids, and Zn adsorbed can gradually become unavailable as these organic substances are converted into

insoluble salts (Stevenson and Ardakani, 1972; Tisdale *et al.*, 1985). However, because humic acids are produced later in the process of O.M. decomposition than the chelating agents, the formation of stable Zn organic complexes is normally inhibited by chelation of Zn.

The organic substances that form complexes with Zn and P are produced through the activities of micro-organisms and the concentrations of these organic compounds are greatest in zones of high microbial activity, such as in the rhizosphere and near decomposing plant residues (Stevenson and Ardakani, 1972). The management of environmental conditions in these zones to maintain microbial populations and their activity (Warcup, 1967; FitzPatrick, 1983) should increase the availability of P and Zn.

Most cropping soils in Australia have relatively low levels of O.M. (Bauer and Black, 1981; Geiger *et al.*, 1992). In view of the proven benefits of organic matter for P and Zn availability to plants, management practices to raise organic matter levels in soil, such as stubble retention and conservational tillage, should be adopted. Returning crop residues to the soil increases nutrient levels through nutrient cycling. According to Wild (1988), the proportions of organic P and Zn are larger in pasture soils than in cropping soils and they increase with the length of pasture phase up to an equilibrium value. Organic forms also vary with the pasture species grown and pH of the soil (Wild, 1988).

2.3.2. Soil Physical Properties.

Soil texture

The effect of soil texture on availability of P and Zn and the respective uptakes has already been described under the effect of clay content of the soil in Section 2.3.1.

Soil structure

The availability of P and Zn are very much dependent on factors such as the ease of movement of water in the soil, oxygen diffusion and root penetration which are in turn determined by structure of the soil. In soils with degraded structure these processes are impaired. Soil compaction is a form of soil structural degradation caused by trafficking when the soil is in a deformable state, resulting in a reduction of the number of large soil pores and an increased number of smaller pores and hence high soil moisture tensions (McAfee *et al.*, 1989; Ankeny *et al.*, 1990). The subsequent result of this process is the reduction of the diffusion rates of P and Zn and their increased deficiencies (Ankeny *et al.*, 1990; Dolan *et al.*, 1992; Kirkegaard *et al.*, 1992).

Deficiencies of P and Zn in compacted soil can also be the result of increased mechanical resistance of soil to penetration, and hence less accessibility of roots to P and Zn which diffuse poorly in soils (McAfee *et al.*, 1989; Voorhees, 1989; Veen and Boone, 1990; Iijima and Kono, 1992). Reduction in the availability of P as affected by increased soil compaction and subsequent poor soil structure have extensively been reported (Parish, 1971; Dolan *et al.*, 1992).

The reduction of pore size in compacted soils also decreases oxygen diffusion and induces poor aeration conditions, most significantly at root surfaces (Tisdale *et al.*, 1985; McAfee *et al.*, 1989; Wolkowski, 1990). This reduces root respiration and consequently inhibits metabolic activities of the roots and production of energy essential for uptake of P and Zn. Deficiencies of P and Zn as a result of poor root functioning in compacted soils has frequently been reported (Schmid *et al.*, 1965; Bowen, 1969; Lindsay, 1972; Moore, 1972 and Giordano *et al.*, 1974). Compaction usually occurs in the top 30 cm of the soil profile,

which is the depth containing of the largest proportion of plant roots and accumulated available nutrients accumulate (Voorhees, 1989 and Dolan *et al.*, 1992).

Soil moisture

Diffusion is a dominant mode of transportation for both P and Zn to the absorbing root surfaces. However, due to their activities in soils, P and Zn diffuse very poorly necessitating the growth of roots towards the nutrient pools rather than nutrients in solution moving to the roots. Thus any factor limiting diffusion will reduce the availabilities of P and Zn.

Diffusion is defined as ion transport from zones of high to low concentration by the random thermal motion of particles. It is described by Fick's Law:

$$F = -D (dc /dx)$$

where F is the amount of diffused nutrient per unit cross section and per unit time (diffusion rate), D is the diffusion coefficient (ability of nutrient to diffuse), x is the distance that the nutrient moves to reach the root, c is the nutrient concentration in the bulk soil (mol/m³) and dc/dx is the nutrient concentration gradient. Diffusion is directly influenced by the diffusion coefficient and nutrient concentration both of which have strong correlations with soil moisture (Mengel and Kirkby, 1987).

The diffusion coefficient directly depends on soil moisture so that limitations of the latter result in a decreased cross section for diffusion subsequently causing the pathways to the roots to become tortuous and thus longer. As a consequence of the inverse relationship between diffusion and the distance moved by nutrients to the roots, as shown by Fick's Law, the long diffusion pathways caused by decreased soil moisture result in reduced diffusion rates.

Furthermore, a decrease in soil moisture in the rhizosphere results in a local increase in nutrient concentration, causing a decrease in concentration gradient and thus a decrease in diffusion rate. Diffusion and nutrient availability are increased by the development of a nutrient concentration gradient between the soil solution of the rhizosphere and the bulk soil due to a lower nutrient concentration around the roots than in the bulk soil (Olsen and Watanabe, 1970). Low soil moisture in the rhizosphere can result in low diffusion coefficients and reduced diffusion rates of P and Zn. Since the availability of nutrients or rather their uptake rate largely depends on diffusion rate (Barrow, 1982), the slow diffusion rates of P and Zn cause depletion zones around the roots to extend outwards, thus promoting the deficiencies. A reduction in availability of P and Zn due to decreased diffusion commonly occurs in compacted soils (Section 2.4.2)

Under waterlogging conditions, reduction of Fe(III) phosphate to the more soluble Fe(II) phosphate may release occluded P and increase the availability in the soil solution. However, the availability of P released by reduction of Fe(III) depends on the pH of the soil solution. At pH values near 7.0, P released by reduction can be precipitated by the Fe(II) oxides which have greater surface area and affinity for P than the Fe(III) oxides (Willett and Higgins, 1978a, b; Holford and Patrick, 1979 cited by Willett, 1983). At pH 5, Fe(II) does not precipitate and hence P released by reduction of Fe(III) oxides to Fe(II) oxides can be released into the soil solution to increase the availability (Holford and Patrick, 1979 cited by Willett, 1983). However, since most reduced soils have pH around 7.0 availability of P in flooded soils is low.

The availability of Zn in flooded soils is decreased by precipitation of Zn^{2+} with reduced ferrous iron and sulfide forming franklinite ($ZnFe_2O_4$) and sphalerite (ZnS), respectively (Tisdale *et al.*, 1985). These two minerals have low solubilities, and hence are a poor supply of Zn for plant growth. Deficiency of Zn in flooded soils is also attributed to low availability

of oxygen and hence retardation of root respiration which results in reduced ability of roots to absorb nutrients. The crop may be severely or completely damaged or killed by the singular or combined effect of oxygen and Zn deficiencies or either of these acting singly, depending on the sensitivity to each condition (Tisdale *et al.*, 1985).

The effects of moisture deficit can be overcome by irrigation. Ensuring sufficient soil moisture is also important for the dissolution of the fertiliser granules or particles and hence fertiliser efficiency (Tisdale *et al.*, 1985). The installation of drainage systems reduces the effects of waterlogging and oxygen deficiency and may increase availability of P and Zn, but it is a costly operation. Fe(III) oxides formed by oxidation of Fe(II) species are less crystalline and have greater sorption capacity for P than the Fe(III) oxides which have not undergone reduction and oxidation cycles; hence the drainage of flooded soils may reduce the availability of P (Willett and Higgins, 1978a, b; Kuo and Mikkelsen, 1979; Willett, 1979 cited by Willett, 1983).

Temperature

Temperature has a large effect on the rate of chemical, biological and physical processes associated with nutrient availability. It accelerates processes related to retention and release of nutrients alike (Barrow, 1979). Which direction of reaction is accelerated by temperature depends on the equilibrium between soil solution P or Zn and the quantity of the labile pool.

When the concentration of a nutrient in the soil solution is below the equilibrium for the particular soil, high temperature increases the solubilisation of minerals and thus the release of that nutrient into the solution. In a factorial experiment with P and Zn fertiliser applications to a soil deficient in both nutrients, Martin *et al.* (1965) observed that P-induced Zn deficiency, associated with high availability of P and low availability of Zn, was more significant at lower temperatures (10 and 15.6° C) than at higher temperatures (21 and

26.7° C). These observations were in agreement with later reports that deficiencies of Zn are more pronounced under wet and cold soil conditions and that responses to Zn fertilisation are greater under cold than warm temperatures, due to greater availability of Zn under warmer conditions (Tisdale *et al.* 1985).

Higher temperatures also accelerate the release of P and Zn from organic matter by increased microbial activity whilst also enhancing their diffusion rate, and hence their availability (Martin *et al.*, 1965; Tisdale *et al.*, 1985; Fitzpatrick, 1983). Since warm temperatures also increase plant growth and their requirements for P and Zn, there should be a complementary increase in solubilisation of P and Zn minerals and mineralisation of organic P and Zn to meet demand.

On the other hand, high temperatures will promote sorption and precipitation of soluble P and Zn, particularly at high concentrations, leaving smaller amounts of these nutrients available for uptake by plants. The magnitude of the reactions between the soil and soluble P and Zn is determined by the retention capacity of the soil (Section 2.3.1). Barrow (1982) proposed that, as a general rule, for every 10° C increase in temperature the rate of P sorption is increased by about threefold

Influence of time

When soluble phosphorus fertiliser is added to the soil only a relatively small fraction goes into the soil solution for absorption by plant roots. The larger portion of the applied P reacts with the soil to form the labile pool, consisting of that adsorbed on soil colloids and precipitated by soil cations. The amount of fertiliser P which is taken up by the crop during the first year or season of application depends on the rate of application, the crop requirement, the phosphate buffering capacity of the soil, fertiliser particle size and climatic conditions. The recovery of fertiliser P by the next crop is usually in the order of 20 - 30 %

of the total applied P. Devine *et al.* (1968) found that an average effectiveness of powdered single superphosphate applied to four soils was 58 % in the first year of application. The recovery of the residual fertiliser P was 38 % in the following year (equal to 16 % of the original application) and 20 % two years after (equal to 3 % of the original application). At the end of three years only about 77 % of the initially applied fertiliser P has been used. The amount of available fertiliser P decreased with time whereas the amount of unavailable fertiliser P increased with time.

Applications of Zn fertiliser to the soil can have residual effects which can last for a period of at least five years (Glendinning, 1990). Data show that the recovery of Zn fertiliser applied at the rate of 7.26 kg/ha decreased by 13, 21, 34, 34, 38 and 45 % in six successive years relative to effectiveness during the first year of application (Boawn *et al.*, 1960). Haleem *et al.* (1992) observed that extractable Zn and other micronutrients decreased with duration of incubation. Unlike soil treatments, foliar applications are sufficient only for the current crop and they leave little residual Zn for the succeeding crops. Hence repeated annual applications are needed (Boehle and Lindsay, 1969).

CHAPTER THREE

PLANT REQUIREMENTS FOR PHOSPHORUS AND ZINC

3.1. Phosphorus

The absorption of H_2PO_4^- ion is greatest at low pH values whereas the absorption of the HPO_4^{2-} is greatest at high pH values; the monovalent ion is more abundant over the pH range suitable for most crops, hence it is the principal form absorbed. Tisdale *et al.* (1985) reported that there are about 10 times as many absorption sites on the plant roots for H_2PO_4^- as there are for HPO_4^{2-} .

P is absorbed by plants roots at a high rate even though the P content in the root cells and xylem sap is about 100 to 1000 fold higher than in the soil solution (Mengel and Kirkby, 1987). This shows that plant requirements for P are very high and that plant roots absorb P against a very steep concentration gradient between the roots and the surrounding soil solution (Higinbotham, 1973; Mengel and Kirkby, 1987). Absorbed P remains in the plant as a free ion or is bonded to larger molecules by formation of ester bonds (C – O – P), or by the high energy pyrophosphate bonds (P ~ P) and sometimes by more stable diester bonds (C – P – C). The concentration of P in plants varies from 0.1 to 0.4 % depending plant species, plant age and the part of the plant analysed (Tisdale *et al.*, 1985).

The high requirement for P reflects the essential role that it plays in plants. Some of the functions of P in plants are its involvement in energy storage and transfer, the formation of structural components of biochemical molecules, increased root growth and proliferation, accelerated maturation of grain crops, the maintenance of strong cereal straw and improved disease resistance and tolerance.

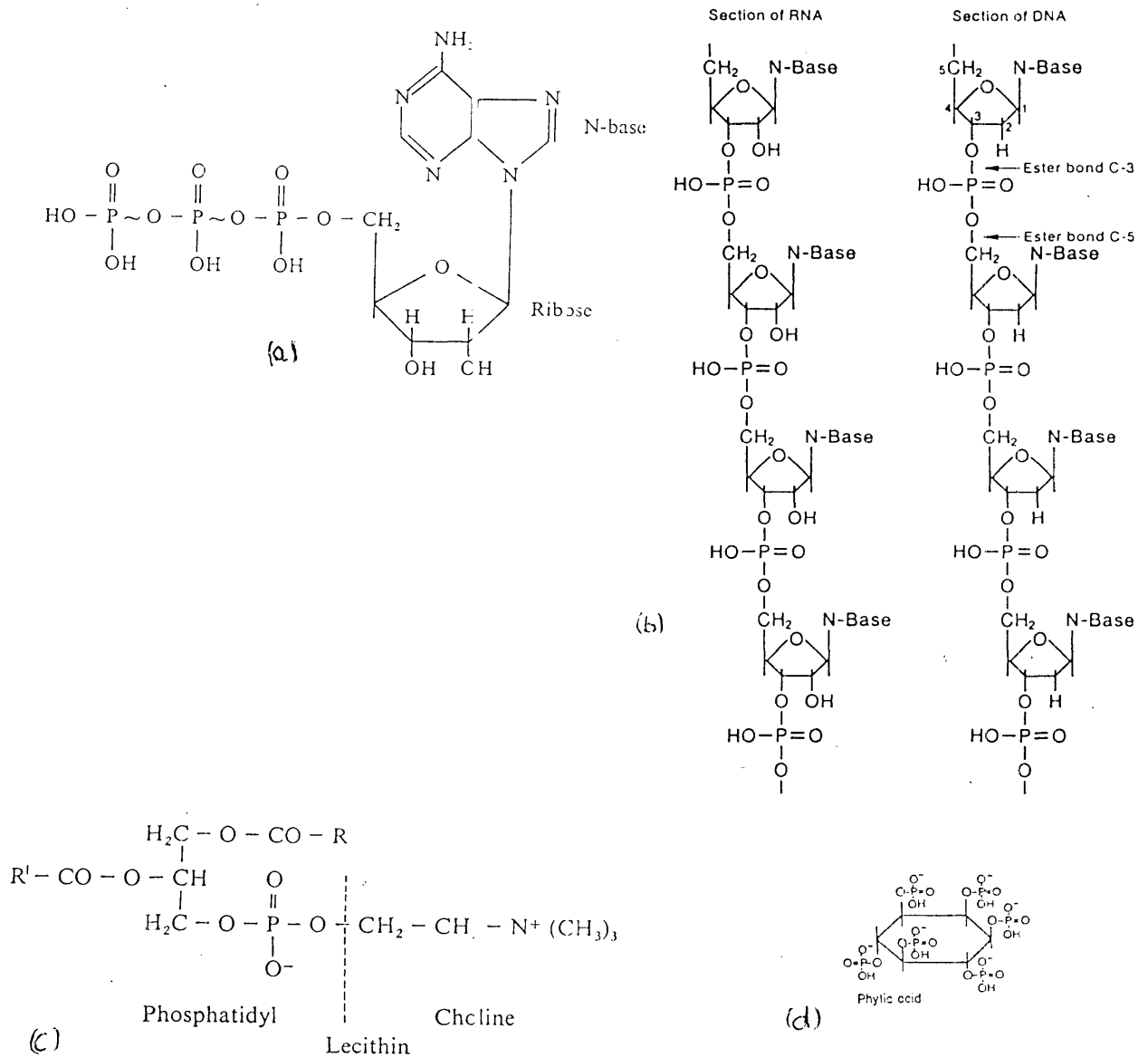


Fig. 3.1. The structures of the two most common phosphate energy currency compounds, ADP and ATP (a) and of the biochemical molecules of which phosphates are a constituent (b-d). *Source:* Mengel and Kirkby (1987).

The energy acquired during photosynthesis and released during metabolic processes such as respiration and glycolysis is stored in phosphate compounds, commonly adenosine di- and

triphosphate (ADP and ATP), and sometimes uridine triphosphate (UTP), cytidine triphosphate (CTP) and guanosine triphosphate (GTP). Energy stored in these forms is used in a number of metabolic processes during plant life (Tisdale *et al.*, 1985; Mengel and Kirkby, 1987). The formation and regeneration of these compounds depends on the presence of sufficient phosphate at the sites of energy production, where the phosphoryl group binds to the sugar or alcohol molecule to form phosphate ester bonds, or to another phosphate group already attached to the carbohydrate molecule to form the high energy pyrophosphate bonds (Fig. 3.1a). When the terminal phosphoryl group from either ATP or ADP, or from any of the analogous compounds of ATP, is split off during the phosphorylation reaction (transfer of the high-energy phosphate group from ATP to energy-requiring substances in the plant), a large amount of energy (12,000 cal/mol) is liberated and the phosphorylated substance is thus activated.

In legumes, ATP is also required for the activity of nitrogenase enzymes associated with nodulation and nitrogen fixation (Jakobsen, 1985). This leads to remobilisation of P from the shoot to the roots to meet the high demands for ATP, especially when P supply is limiting. Thus, a deficiency of P in legumes is marked by the disturbance of shoot metabolism, followed by low supply of photosynthates to the nodules and subsequently retarded nodule growth and reduced N fixation (Rai and Sinha, 1986).

Apart from its participation in energy storage and transfer, P also plays a vital structural role in the synthesis of a wide variety of biochemical molecules such as the nucleic acids deoxyribosenucleic acid (DNA) and ribosenucleic acid (RNA), phospholipids and phytin (Fig.3.1b - d). DNA and RNA are the carriers of the genetic information of plants, hence they control their development and heredity. Thus, an adequate supply of P in the early stages of plant growth for synthesis of DNA and RNA is important for laying down the primordia for the reproductive parts (Tisdale *et al.*, 1985).

In addition, RNA controls the synthesis of plant proteins, so that it is synthesised in larger quantities in protein accumulating plants (legumes) than in carbohydrate accumulating plants (cereals). This accounts for the difference in requirement of P between the two types of crop. The protein content of grain legumes ranges from about 23 % (chickpeas) to 45 % (soybean) compared with 14 % found in prime hard wheat (Lovett and Lazenby, 1979; Knights, 1991; Rose, 1991). It is obvious that legumes require relatively more P than cereals and therefore their potential for P uptake should exceed that of cereals.

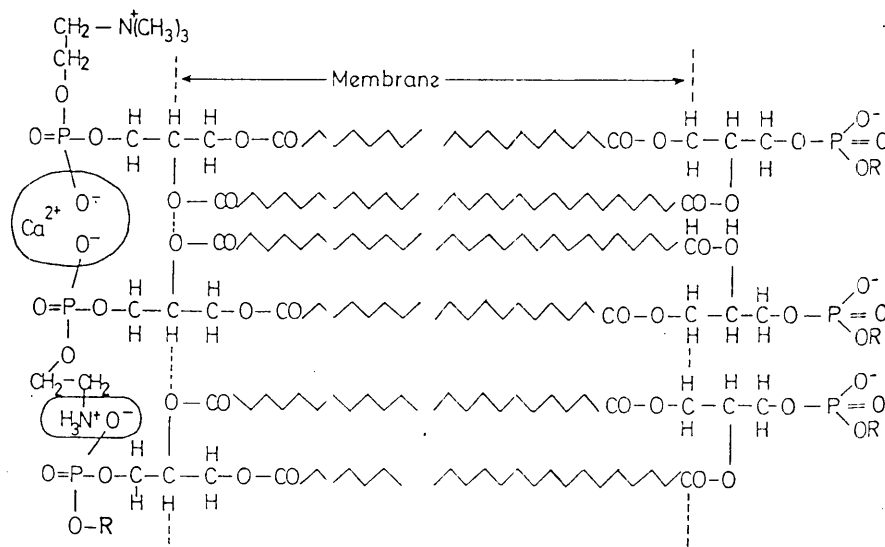


Fig. 3.2. Phospholipids in a protoplasmic membrane. *Source:* Mengel and Kirkby (1987).

The phospholipids such as phosphatidyl ethanolamine and lecithin form the structural framework of the protoplasm and chloroplasts. Figure 3.2 shows how these two molecules form part of a biological membrane. Phytin, which occurs as the calcium and magnesium salts of phytic acid, is a principal storage form of P in seed plants. Phosphorus stored in phytin in seeds is mobilised from the seed during seed germination to be utilised by young plants before they develop their effective root systems. Other biological P molecules are

phosphoproteins and sugar phosphates, which form the base of the chloroplasts and cytoplasm, respectively.

Other functions of P of agronomic significance include increasing root growth and root proliferation (Drew, 1975; Fig.3.3), enhancing the early maturation of grain crops, and increasing quality of crops, influencing the strength of cereal straw, improved disease resistance and tolerance to root diseases and to adverse conditions such as winter damage (Tisdale *et al.*, 1985; Gregory, 1988; Suklu and Kohli, 1991).



Fig. 3.3. Influence of P on root growth of barley plants grown for 21 days in sand culture continuously irrigated with nutrient solution. The control plants (HHH) received a complete nutrient solution to all parts of the root system. In the LHL treatment, only the middle zone received the complete nutrient solution, the top and bottom being deficient in phosphate.

Source: Drew (1975).

The requirements of P for all these functions means that plants have to take up P in large amounts. The requirement of plants for P for the generation and regeneration of ATP or ADP during photosynthesis, for the synthesis of RNA and DNA and for the formation of phospholipids and the other cell structural components, all of which are in relatively high

demand in the early stages of plant growth, necessitate greater absorption of P by plants in the earlier stages of plant growth than later in the plant's life cycle (Mengel and Kirkby, 1987; Pronina and Lanonin, 1988). P uptake is also high during this period due to the need for adequate root growth and development and for maintenance of strong plant stands.

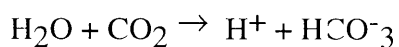
Later in the plant growth cycle the requirement for P is determined more by functions, such as increasing the resistance and tolerance of plants to diseases and/or winter damage, setting and development of grain, synthesis of P reserves (phytin) and maintenance of high quality crops rather than by the functions related to formation of ADP or ATP and the synthesis of biochemical molecular structures as occurs in the early stages of plant growth. At this later stage the requirement for P is satisfied by both absorption and remobilisation of P from older tissues such that the uptake rate is lower than at earlier stages.

At the latest stages of plant growth, that is, after seed formation and the synthesis of P reserves, all the plant processes which require P cease so that total P requirement and hence its uptake rate decline. The uptake rates of P by wheat over the period from sowing to milk stage of grain development, as observed by Smith (1965), were 0.04, 0.17 and 0.08 kg P/ha/day under field conditions for the periods sowing – jointing, jointing – ear emergence and ear emergence – milk stage of grain production, respectively. This trend corresponds well with the different P requirements at different stages of growth as discussed above.

3.2. Zinc.

Zinc is absorbed as a divalent cation (Zn^{2+}), which does not undergo redox reactions in plants but remains as Zn^{2+} . The Zn content of plants is relatively small, normally ranging between 25 and 150 μg Zn per gram dry weight of a plant (Boehle and Lindsay, 1969; Tisdale *et al.*, 1985). It is involved interchangeably with Mn^{2+} and Mg^{2+} in most enzymatic

activities but there is one enzyme which specifically depends on Zn^{2+} for activation. This is carbonic anhydrase, which is localised in the chloroplasts and catalyses the reaction:



which manipulates pH changes caused by H^+ pumps and incorporation of CO_2 into ribulose 1, 5 bisphosphate (Mengel and Kirkby, 1987). Other Zn metalloenzymes in plants are:

(i) superoxide dismutase (Cu - Zn SOD) of the chloroplasts, which catalyses the conversion of the superoxide radical ($O_2^{\cdot-}$) to hydrogen peroxide (H_2O_2) and oxygen (O_2), and hence protects the photosynthetic apparatus from the effect of $O_2^{\cdot-}$, formed during electron transfer in photosynthesis (Jackson *et al.*, 1978; Vaughan *et al.*, 1982).

(ii) Alcohol dehydrogenase, which catalyses reduction of acetaldehyde to ethanol, a reaction that occurs more predominantly in the meristematic tissues in higher plants (Vallee and Wacker, 1970; Price *et al.*, 1972).

(iii) RNA polymerase, which catalyses synthesis of RNA, a nucleotide which controls the synthesis of plant proteins. Zinc is also necessary for the stability of cytoplasmic ribosomes (Praske and Plocke, 1971), and hence protein metabolism (Mengel and Kirkby, 1987).

Zn is also involved in the biosynthesis of an auxin, IAA (indole 3 acetic acid) although it has not yet been established whether it is involved in the synthesis of tryptophan (the precursor of IAA) or in the synthesis of IAA from tryptophan (Mengel and Kirkby, 1987). Nevertheless, a positive correlation between the Zn content of the plant and the rate of stem elongation, which is affected by the auxin IAA, has been demonstrated by Tsui (1940) and Salami and Kenefick (1970) using tomato and maize plants, respectively.

From these functions of Zn in plants, it is clear that the demand for Zn by plants is specifically for the activation of carbonic anhydrase and that for the activation of other enzymes Zn can be replaced by Mn and Mg. This explains why a plant's requirement for Zn

is relatively small. However, the uptake of Zn is relatively greater in young plants when the rate of photosynthesis is faster and Zn is in high demand for its specific role in the activation of carbonic anhydrase.

Furthermore, its necessity for protein metabolism makes it an essential nutrient in legume crops and to some extent in wheat, whose quality, unlike that of other cereals, depends mainly on its protein content (Storrie, 1987). Differences in response to Zn and in Zn uptake between plants are very common. According to Tisdale *et al.* (1985), soybeans, bean, corn and rice are very sensitive to low levels of available Zn, sorghum and wheat show intermediate sensitivity, and oats and peas are not sensitive. Differences in sensitivity to Zn deficiency occur not only between species but also between the cultivars of the same species. This is due to their differences in genotypic characteristics (Clark, 1978; Safaya and Gupta, 1979).

3.3. Phosphorus - Zinc Interaction

The importance of the P and Zn interaction in plant growth and crop production is widely recognised (Bingham and Garber, 1960; Olsen, 1972; Webb and Loneragan, 1988; Wang *et al.* 1990; Biswas and Prasad, 1991 and Iahiruddin and Cresser, 1991). In many experiments, the application of Zn alone did not increase Zn uptake or plant growth or alleviate Zn deficiency symptoms. When Zn was applied together with P, the uptake of Zn increased with the application rate of P and a plant growth response to both Zn and P were observed (Millikan, 1940; Verma and Minhas, 1987). However, high levels of P in soil can induce Zn deficiency, commonly referred to as P-induced Zn deficiency, especially when Zn supply to the growing plants is otherwise sufficient (Olsen, 1972).

There is confusion as to how P induces Zn deficiency. The mechanisms by which P can induce or aggravate Zn deficiency depend on the plant species and prevailing environmental conditions. Proposed mechanisms include: (i) dilution of Zn concentration in plant tissue by increasing plant growth by P fertilisation (Boawn *et al.*, 1954), (ii) reduction of Zn availability by changes in solubility of Zn mineral by pH changes caused by application of some P fertilisers (Giordano *et al.*, 1971), (iii) inhibition of Zn absorption by competitive cations (Ca^{2+} and Mg^{2+}) added with P fertilisers (Chaudhry and Loneragan, 1972), and (iv) reduction of Zn availability through enhancement of Zn bonding by the oxides and hydroxides of Fe and Al as a result of increased P concentration in the soil (Stanton and Burger, 1967; 1970; Bolland *et al.*, 1977).

Some workers like Jahiruddin and Cresser (1991) believe that P induced Zn deficiency is the result of reactions of P and Zn in soil, such as the formation of the $\text{Zn}_3(\text{PO}_4)_2 \cdot 4\text{H}_2\text{O}$ compound, which was thought to be insoluble, and hence reduces the availability of Zn to plants. However, when tested under various conditions (Jurinak and Inouye, 1962), the solubility of this compound even at minimum, was found to be high enough to maintain Zn in the soil solution at a level sufficient for maximum plant growth, as determined by Carroll and Loneragan (1969). Therefore, the possibility that P-induced Zn deficiency is caused by precipitation of Zn by phosphates seems unlikely.

Loneragan *et al.* (1979) suggested that P-induced Zn deficiency depends on soil type and conditions. In soils like siliceous sands, which have a low capacity to react with P and low adsorption surface area for Zn the interaction of P and Zn occurs in the plant system through the dilution of Zn concentration by increasing plant growth through increasing P supply (Loneragan *et al.*, 1979). However, in soil with a high capacity to react with P, such as ferruginous sands, Hillard *et al.* (1991) and Ohno (1992) observed that application of P

fertiliser induces Zn deficiency by enhancing bonding of Zn to oxides and hydroxides of Fe and Al and hence decreases the availability of Zn and its uptake by plant roots.

Christensen and Jackson (1981), Tiscala *et al.* (1985), Sumner and Farina (1986) and Mengel and Kirkby (1987) also attribute the P-induced Zn deficiency to the dilution effect caused by increased P in soils of low Zn fertility. Bingham and Garber (1960) observed that adsorption of Zn onto the surfaces of Al-phosphate compounds in soils high in P is too low to induce Zn deficiency in plants. Thus, as reported by Stanton and Burger, (1967 and 1970) and Bolland *et al.*, (1977), it is unlikely that the deficiency of Zn at high concentrations of P is caused by P enhancement of Zn adsorption by oxides and hydroxides of Fe and Al.

Loneragan *et al.* (1979) and Christensen and Jackson (1981) postulated that when plants are deficient in Zn their ability to regulate P accumulation is either totally destroyed or impaired. P absorbed by roots is then translocated to the shoot in excessive amounts. Webb and Loneragan (1988) also observed that plants deficient in Zn exhibit a high P content, which produces P toxicity symptoms similar to Zn deficiency symptoms. Webb and Loneragan (1988 and 1990) found that Zn deficiency decreases plant shoot DM and therefore increases the ratio of shoot P/shoot DM, causing high P concentrations. Medina and Nicholas (1957), Ambler and Brown (1969) and Safaya and Singh (1977) reported that differential susceptibility of plants to Zn deficiency rarely correlates with Zn content. Carroll and Loneragan, (1969) used the uptake rate of Zn instead of plant Zn content but again this was not well correlated with susceptibility to Zn deficiency. However, P content was always high in Zn deficient plants, and it was negatively correlated with reduced shoot dry matter yield which normally occurs in Zn deficient plants (Olsen, 1972; Safaya, 1976; Safaya and Singh, 1977; Safaya and Gupta, 1979; Verma and Minhas, 1987).

As early as the 1940's, attempts were made to explain the mechanics of the P and Zn interaction effect in plants. Reed (1946) report that Zn deficient plants exhibit a higher ratio of inorganic to organic P than plants supplied with sufficient Zn, and postulated that Zn might be involved in a phosphate ester enzyme, which regulates the accumulation of inorganic P in plants. Medina and Nicholas (1957) following Reed's work discovered that Zn plays an important role in processes leading to (i) increasing activity of phosphatase and (ii) impairing the phosphorylation reaction. Both processes can alter the ratio of inorganic to organic P in plants (Nicholas, 1961).

Safaya and Gupta (1979) suggested that the greater absorption of P by Zn deficient plants is probably due to the loss of control over the absorption mechanism. The greater accumulation of P in the shoots of Zn deficient plants was attributed to the reduced esterification of P in roots, which results in increased P translocation to shoots. The higher concentration of P in Zn deficient potato leaves reported by Christensen and Jackson (1981) was attributed to increased P uptake and mobilisation of P from roots to above ground parts which supports the findings of Safaya and Gupta (1979).

The P and Zn interaction creates a number of problems including: (i) reduction of plant growth and yield by induced Zn deficiency and P toxicity, (ii) uncontrolled high P uptake which depletes the supply of available P in the soil, and (iii) high requirement of Zn by plants which is caused by high P absorption, and hence a demand for expensive inefficient Zn fertilisation. The P and Zn interaction may lead to inefficient use of P and Zn fertilisers. What is needed is a fertiliser program that avoids creating imbalances between Zn and P.

3.4. Remobilisation of P and Zn in the Plant.

Nutrient remobilisation within the plant is important in the case of mobile nutrients such as P, N and K but less so for intermediately mobile nutrients like Zn, and the immobile ones like calcium (Ca) and boron (B). During reproductive growth more assimilates are directed to reproductive parts rather than to the roots, thus reducing root metabolic activities and the ability to take up nutrients including P and Zn (Hopkins *et al.*, 1950; Marchner, 1985). Remobilisation of P from older leaves then compensates for the reduced P uptake and can prevent the occurrence of P deficiency (Bouma, 1967). A high proportion of P remobilised from vegetative parts to seed has been observed for pea plants (Marchner, 1985). The capability of P to move from old to young growing tissues does not reduce P absorption but it alleviates the problem of P deficiency in plants growing under low P fertility status or in plants with reduced nutrient absorbing power, as it occurs at flowering or later growth stages.

In contrast, Zn remobilisation from old to new tissues is not great; it depends on plant species or cultivar (Section 3.5) and on the external supply of Zn (Riceman and Jones, 1958; Rinne and Langston, 1960; Loneragan, 1975; Mengel and Kirkby, 1987). In plants with sufficient supply, Zn is remobilised from old leaves to developing inflorescences and grain, but in Zn deficient plants, very little Zn is remobilized from the older leaves to the reproductive organs (Riceman and Jones, 1958; Loneragan *et al.*, 1976). For example, Stepanok and Golonetskii (1990) observed that when Zn was applied to a double cropping system of 30 – 40 % peas and 70 – 60 % oats under field conditions, at the rates of 200 – 300 kg/ha of either $Zn(NO_3)_2$, $ZnSO_4$ or Zn oxides as soil treatments or at 20 – 200 kg/ha $Zn(NO_3)_2$ or $ZnSO_4$ as foliar sprays, higher levels of Zn occurred in stems than in seeds of

peas, and in roots than in grain of oats. In view of low mobility of Zn, an adequate supply of Zn throughout the entire plant life cycle is necessary.

3.5 Cultivar Effects

The species (or cultivar within species) largely determines the optimum concentration of P in the soil solution required to support the growing plants and to produce the potential yield. The newer high yielding cultivars produced through breeding systems may require higher concentrations of nutrients than the older lower yielding cultivars to produce the expected optimum yields.

Table 3.1. Nutrient removal in seed and nutrient concentrations in leaves of various varieties and lines of soybeans.

Soybean variety or PI Line	Yield of Seed (kg/ha)	Nutrient Removal in Seed (kg/ha)			Nutrient concentration in leaves (%)		
		N	P	K	N	P	K
PI92561	2914	195	20	58	4.9	0.38	1.1
Ford	2903	195	17	57	4.7	0.34	0.8
Adams	2882	191	17	59	4.9	0.39	1.0
Seneca	2840	183	16	56	4.3	0.38	1.4
PI80536	1082	75	8	21	4.8	0.39	1.4
PI200479	1024	72	6	19	3.6	0.29	0.8
PI200482	924	67	6	17	3.4	0.34	0.9
PI227212	830	50	5	16	4.6	0.38	1.3

Source: Tisdale *et al.* (1985).

As shown in Table 3.1, the high yielding line of soybean (PI92561) removed 20 kg P/ha in seed in producing the maximum seed yield of 2914 kg/ha, while the low yielding line (PI227212) removed only 5 kg P/ha in seeds to produce a yield of 830 kg/ha. Both lines had the same concentration of P in their leaves (0.38 %), the differences being only in their seed P content and in their yielding capacities. Under high soil fertility conditions, the high

yielding cultivar can initially absorb more P and produce to its full yield capacity. However, the same cultivar can deplete the soil rapidly such that it eventually fails to produce to its maximum yield capacity unless it is supplied with nutrient fertilisers (Tisdale *et al.*, 1985). Other high yielding cultivars, for example, the cultivar F78.1313 of wheat, genetically possess a high nutrient absorption efficiency and high nutrient utilisation (Jones *et al.*, 1992). Such cultivars do not require very high concentrations of P in the soil solution for satisfactory yields, and even for soils with high levels of available P they remove only the optimum P requirement and leave substantial residual P for successive crops (Jones *et al.*, 1992).

Species and cultivar differences in Zn nutrition also occur. Differences in response to Zn application between species and cultivars, usually referred to as differential susceptibility to low Zn, has been reported for cultivars of navy bean (Ambler and Brown, 1969), cowpea (Safaya and Singh, 1977) and different lines of corn (Clark, 1978). Clark (1978) observed that the two lines of maize, A635 and H84, grown in nutrient solutions of varying Zn concentration responded to increases levels of Zn in terms of dry matter yield, Zn concentration and content, but the line H84 produced a higher yield than A635 at the lower levels of Zn (Table 3.2). Thus the former could be called more Zn efficient than the latter. Clark (1978) reported that differential susceptibility in these maize lines is caused by their differences in translocation, requirement and utilisation of Zn, and accumulation of imbalanced amounts of mineral nutrients which interact with Zn, particularly P and Fe. Imbalanced amounts of P and Fe were found to be responsible for differential susceptibility to Zn deficiency in Sanilac and Saginaw cultivars of navy bean (Ambler and Brown, 1969), and to P deficiency in HFC-42-1 and FOS-1 cultivars of cowpea (Safaya and Singh, 1977).

Table 3.2. Dry matter yield, Zn concentration and content, and dry matter production per unit Zn of two maize lines, A635 and H84.

Zn level	Dry matter yields		Zn concentration		Zn content		Dry matter produced Unit Zn	
	A635	H84	A635	H84	A635	H84	A635	H84
μM	g/plant		$\mu\text{g Zn/g dry wt}$		$\mu\text{g Zn/plant}$		mg/ $\mu\text{g Zn}$	
0.0	0.23	0.71*	21	30*	4.9	21.3*	11.1	23.7*
0.017	0.26	0.96*	22	32*	5.8	30.6*	11.9	29.8*
0.17	0.52	1.18*	32	33	16.7	39.1*	16.3	35.9*
1.7	0.84	1.60*	39	48*	32.7	77.0*	21.5	33.4*
16.8	1.39	1.69	49	78*	63.1	132.0	28.3	21.7*
50.5	1.59	1.61	55	142*	87.4	229.1*	28.9	11.4*
168	1.96	2.00	127	167*	249.4	333.5*	15.5	12.0*
505	2.33	1.91*	202	218	470.7	417.2	11.5	8.8
LSD (0.05)	0.24	0.22	7	9	7.2	27.8	2.5	3.0

Source: Clark, R.B. (1978). * Significance between line pairs for a treatment level ($P \leq 0.05$).

The cultivars with high nutrient efficiency (uptake per unit of nutrient applied or available) would normally require less external concentrations of P and Zn than the less efficient ones. Such cultivars gain better positions in cropping enterprises where the aim is to obtain optimal yields from inputs of fertilisers. However, it is important that where the fertility of the soil is low or sub-optimal amounts of fertilisers are applied to avoid exploiting the soil beyond its potential capacity.

3.6. Level of Production Desired

Despite the nutrient efficiency of the cultivars, the maximum uptake of P and its critical concentration are dependent on the level of production desired. Results of the work of Fox (1981 – 1982, cited by Tisdale *et al.*, 1985) showed a positive correlation between the level of production desired and the required P in the soil solution. The critical levels required by soybean were much higher than those for wheat. On the other hand, the concentration

required by wheat to produce 95% maximum yield was three times higher than that for 75% maximum yield compared with an eight fold increase for soybean.

Although the effect of the desired level of production on Zn uptake requirement of plants has not been investigated, it can be inferred from the interaction between P and Zn that since high availability of P increases Zn requirement of plants, the increase in P requirement to meet the desired level of production will increase the requirement and uptake of Zn.

CHAPTER FOUR

NUTRIENT ABSORPTIVE CAPACITY OF ROOTS

Plants differ in their ability to absorb nutrients; the ability of roots to absorb nutrients is determined by root growth and distribution in the soil profile, plant age, root cation exchange capacity, root exudation and mycorrhizal associations.

4.1. Root Growth and Distribution in the Soil Profile

Important root growth parameters in nutrient uptake are rooting density, total root length per surface area, number of root tips and the density and length of root hairs. Rooting density and density of root hairs are important for the absorption of nutrients with large depletion zones such as K^+ and NH_4^+ , where the neighbouring roots compete for available nutrients and uptake depends on the overlap of depletion zones (Costin and Williams, 1982). They have, however, only a minor effect on uptake of P, which has a depletion zone ten times less than that of K^+ and NH_4^+ . This may also apply to Zn whose activity in the soil is similar to that of P. The number of root tips also does not influence the uptake of P greatly because P is absorbed along the whole length of the root (Ferguson and Clarkson, 1975; Clarkson and Sanderson, 1978; Clarkson and Hudson, 1980). However, the importance of this parameter for Zn uptake is uncertain because whether Zn uptake takes place along the entire root length or is localised at root tips is still an open question. Therefore, this leaves root length and the length of root hairs as the major root growth parameters influencing P uptake (Bray, 1954).

Generally, cereals, because they exhibit greater root length than legumes (Costin and Williams, 1982; Gregory, 1988; Hamblin and Hamblin, 1985) have an advantage over the

latter of having greater absorption capacity even under low P fertility status. Root hairs increase P uptake by increasing the surface for P diffusion and by increasing the effective length of the roots (Costin and Williams, 1982). However, root hair production is very low in most grain crops, compared with vegetable plants such as tomato and to some extent lettuce (Itoh and Barber, 1983). Therefore, root length is the main root growth parameter which increases absorption of P and Zn from the soil.

The development and distribution of the roots is much greater in the topsoil than in the subsoil. An increase in root length per unit volume of soil into the subsoil may be enhanced or inhibited by soil physical conditions and localised nutrient accumulation (Drew, 1975; Gregory, 1988). Coincidentally, the occurrence of P is much higher in the topsoil than in the subsoil, in both uncultivated and cultivated soil (Wild, 1988); this is due to its circulation through vegetation and deposition in leaf fall and litter in the former, and in addition, partly due to P fertilisation in the latter. Thus there is a positive correlation between P uptake and root length increase and distribution of roots in the topsoil. Therefore, the more favourable the soil conditions are for root growth and proliferation the greater the uptake of P.

4.2. Plant Age

As a plant matures, and immediately after commencement of reproductive growth, the strongest sink for photosynthates switches from the shoot and root apices to the developing seeds, decreasing the metabolic activity of the roots and their active uptake of P and Zn (Jungk and Barber, 1975). Since the root absorbing power is directly related to root metabolism (Barber, 1979), any factor which offsets the metabolic activity of roots causes a reduction in production of the energy required for the absorption of P and Zn, and hence a decline in their absorption capacity. This effect is particularly true for P and Zn because their

uptake depends strongly on energy expenditure (Schmid *et al.*, 1965; Bowen, 1969; Lindsay, 1972; Moore, 1972; Giordano *et al.*, 1974).

4.3. Root Cation Exchange Capacity

Another important factor influencing species absorbing power is root cation exchange capacity (CEC) which is relatively high for dicotyledonous plants (20.2 to 53.2 meq / 100 grams root dry matter) compared with monocotyledons (5.3 to 23.6 meq / 100 grams root dry matter) (Tisdale *et al.*, 1985). Although there is some controversy as to how root CEC affects ion uptake, the most favoured view is that high root CEC favours uptake of divalent ions, such as Ca^{2+} and Mg^{2+} , at the expense of monovalent ions (Haynes, 1980).

It has been postulated that high root CEC tends to restrict P uptake, especially under low available P conditions (Gregory, 1988). This is thought to occur through the anion repulsion effect caused by greater negative charge on the root surface. This effect may explain why cereals, which are monocots with relatively low root CEC, are able to absorb more P under conditions of low P fertility than legumes, which are dicots with significantly higher root CEC. The literature indicates that cereals growing under low P conditions are able to absorb P and grow better than legumes. The latter require higher soil solution P concentrations in order to achieve the same level of production as the former.

4.4. Root Exudates and the Rhizosphere

Root exudates increase the absorption of P and Zn by increasing their availability. They increase nutrient availability by enhancing root growth and increasing the contact between roots and soil colloids, through chelation and through the improvement of rhizosphere conditions such that they favour increased availability of nutrients. Root exudates are

particularly important for increasing availability and hence absorption of P and Zn, which are less mobile in the soil. They are derived from the photosynthates translocated from the aerial parts of the plant to the roots and excreted by the latter into the rhizosphere. Their origin can easily be investigated by using $^{14}\text{CO}_2$ as a source of CO_2 for photosynthesis to label plant metabolites, and hence trace their movement from the leaves to the roots and into the rhizosphere (Hale and Moore, 1979).

The primary root exudate is the slimy polysaccharide mucilage produced by the Golgi apparatus in the root cap cells in response to resistance of the soil to root growth (Jones and Moore, 1967; Paul and Jones, 1975 *a, b*, 1976; Iijima and Kono, 1992). The mucilage acts as a lubricant and reduces friction and mechanical resistance between the growing root tip and the soil. It also adsorbs to soil particles and brings about a close contact between the root and the soil. Thus the production of mucilage indirectly increases absorption of P and Zn through enhanced root growth and increased contact between root surfaces and soil colloids.

Other root exudates which play an important role in increasing the availability of P and Zn include 2-keto-gluconate and organic acids. The 2-keto-gluconate has the potential to decrease the pH of rhizosphere and increase the solubilisation of P from hydroxyapatite (Moghimi *et al.*, 1978). Organic acids increase the availability of P by desorbing it from the surface of Fe and Al sesquioxides by ion exchange (Gardner *et al.*, 1983). They increase the mobility and availability of Zn through direct chelation (Lindsay, 1974).

Another way in which root exudates can increase the availability of P and Zn is through their supply of energy for rhizosphere micro-organisms (Costin and Williams, 1982; Rovira *et al.*, 1983). The composition of root exudates varies with the age of the roots (Hamlen *et al.*, 1972) but basically it consists of organic acids, amino acids and sugars. Micro-organisms

produce organic compounds like acids and chelates which can increase the availability of P and Zn as the root exudates do (Lindsay, 1974).

When the roots absorb cations they release H^+ in exchange, and lower rhizosphere pH (Tisdale *et al.*, 1985). The decrease in rhizosphere pH may increase nutrient solubility and availability and result in higher uptake of P and Zn, especially if the pH was initially high. On the other hand, when anions are absorbed, HCO_3^- ions are released in exchange and as a result rhizosphere pH is increased. Again, depending on the initial rhizosphere pH, an increase in pH will affect the availability of P and Zn (Section 2.3.1.).

Apart from increasing the uptake of P and Zn, the rhizosphere and root exudates support rhizosphere micro-organisms. These micro-organisms compete with plants for nutrients, and may reduce nutrient uptake by plants. Other micro-organisms can reduce nutrient absorption by plants by causing diseases in plants (eg. *Xanthomas phaseoli* that lives in bean root rhizosphere) and reducing the strength of the plants and their ability to absorb nutrients. The survival of these organisms depends mainly on glutamic acid found in root exudates (Hale and Moore, 1979).

4.5. Vascular Arbuscular Mycorrhizae

Vesicular arbuscular mycorrhizae (VAM) are endomycorrhizal soil fungi that form associations with a wide range of crops, including horticultural and ornamental species (Plenchette *et al.*, 1983; Wellings *et al.*, 1991), and also with some pasture species (Mosse, 1972a, b; Cooper and Tinker, 1978). The name VAM is derived from the occurrence of two types of characteristic structures: the vesicles which form by swelling of hyphae and usually occur within or between the cortical cells; and the arbuscules, the shrub – like structures

similar to haustoria but produced by dichotomous branching of hyphae (Phillips and Hayman, 1970; Harley, 1971).

The association with the host plant is such that the plant supplies the mycorrhizae with organic carbon compounds while the mycorrhizae benefit the plant by increasing the absorption of inorganic nutrients, particularly those with low diffusion rates like P and Zn (Singh *et al.*, 1966; Cooper and Tinker, 1978; Graham *et al.*, 1982; Plenchette *et al.*, 1983; Wellings *et al.*, 1991). Evidence exists that VAM also enhance the uptake of other nutrients such as sulphur (Cooper and Tinker, 1978), copper, magnesium and ammonium – nitrogen (Cooper, 1984; Fairchild and Miller, 1988). Hamilton (1990) observed a high positive correlation between VAM colonisation in the roots of common bean plants and the uptake of P, Zn and Cu.

Mycorrhizae increase diffusion rates and uptake of the nutrients by enlarging the contact area between the soil and the absorption sites. The hyphae of VAM extend from the roots into the soil, to a distance of up to 2 cm from the root surface, forming mycorrhizal systems. These increase the absorptive surface area of the infected roots and the nutrient depletion zone to a distance relatively far from the roots. VA mycorrhizal systems are particularly important for P which has its depletion zone just around the roots. Extension of depletion zones of P and Zn increases the concentration gradients and hence diffusion rates of P and Zn (Fick's Law of diffusion, Section 2.1.2.).

VAM also increase P uptake due to their high affinity for P and to their high absorbing power, which greatly exceeds that of plant roots (Cress *et al.*, 1979; Costin and Williams, 1982). The mycorrhizae absorb P from labile pools in a readily available form (Cox *et al.*, 1980) and from less soluble P forms such as occur in acid soils of the tropics (Tinker, 1984). Thus, plants can benefit from VAM and their ability to survive conditions of P and Zn

deficiency, such as occur in most Australian soils, is enhanced (Williams and Raupach, 1983).

Plants can also benefit from VAM for absorption of P and Zn where soil mechanical strength restricts penetration of roots and root hairs (Singh *et al.*, 1966; Mosse, 1972a; Anderson *et al.*, 1987), and where low soil moisture content limits diffusion of these nutrients (Singh *et al.*, 1966; Mosse, 1972a; Gerdemann, 1975; Menge *et al.*, 1978). In the former situation mycorrhizal hyphae, because of their small diameter (2 – 4µm), have a greater ability to penetrate the minute soil pores and exploit the soil for P and Zn than the root hairs whose diameter is five times larger (Costin and Williams, 1983).

The importance of VAM for nutrient uptake is most pronounced in plants with relatively few root hairs like wheat or with fleshy roots like carrots (Baylis, 1970; Plenchette *et al.*, 1983) and in plants with high requirements for P and Zn, such as most legume crops (Plenchette *et al.*, 1983). Such plants have been classified as being dependent on mycorrhizae for the absorption of these nutrients and for adequate growth. Their ability to absorb these nutrients depends more on the extension of mycorrhizal systems than on the degree of root colonisation. Thus disruption of the systems, for instance by soil disturbance treatments, decreases the benefit that plants get from VAM even with high levels of infection (Sanders and Tinker, 1971; Mosse, 1972a; Graham *et al.*, 1992; Miller *et al.*, 1992).

CHAPTER FIVE

METHODS OF INCREASING THE AVAILABILITY OF PHOSPHORUS AND ZINC

The availability of P to plants can primarily be optimised by modifying soil conditions so that replenishment of P into the soil solution is maintained at a level to satisfy plant uptake. For heavy soils with high pH and high phosphate buffering capacity the introduction of a legume crop or pasture can help to reduce the soil pH. The incorporation of a pasture phase into a crop rotation system or adoption of stubble retention and conservational tillage practices should increase organic matter content of the soil, and hence the availability of P (Section 2.3.1.). Application of lime on acid soils can also increase the availability of P (Section 2.3.1.). Alternatively, efficient use of soil P can be controlled by using highly P efficient cultivars (Section 3.5.).

In naturally low P fertility soils as is the case for most Australian soils, or soils where P fertility has declined due to continuous cropping (Williams and Raupach, 1983), fertiliser P has to be applied. The method and time of application and the selection of the most efficient fertiliser materials need special consideration where high crop production is to be achieved at reasonably low fertiliser costs (Glendinning, 1990). The rate of application should be determined by a combination using test strips, soil testing, plant analyses, nutrient deficiency symptoms and other approaches (Tisdale *et al.*, 1985).

Methods for optimising P supply (modifying soil conditions, use of fertilisers and use of nutrient efficient cultivars) also apply to Zn. Glendinning (1990) has recommended applying Zn fertiliser at 8 to 10 kg Zn/ha for dryland farming and at up to 18-20 kg Zn/ha under

irrigation. These applications should be sufficient for a period of 5 years. Another treatment which is gaining a wide popularity is an initial soil treatment of 5 to 12 kg Zn/ha and then 2-3 kg Zn/ha/yr blended in the planting fertilisers (Glendinning, 1990). Where deficiencies of Zn are evident, Zn can best be applied as foliar sprays at 1 kg Zn/ha/yr, split into 3 or 4 sprays to improve the efficiency of the fertiliser. Rates higher than 1 kg/ha are not encouraged as they result in leaf burn.

For legume crops in Australia however, there is relatively little information on the P and Zn requirements. In particular, plant analysis data which suggests critical values and how these relate to likely P responses are not known in any detail. The following experimental work describes both pot and field experiments which attempt to provide information in these areas.