Dynamics of soil organic phosphorus*

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Abstract. The transformations of soil organic phosphorus are described and organized in a conceptual model. Microbial uptake of P and its subsequent release and redistribution play a central role in the soil organic P cycle. Interactions with soil minerals and stabilization of organic matter and associated P in organo-mineral complexes determine the persistence and buildup of organic P through soil development, in different ecosystems and under varying management. An understanding of organic P turnover in soils will greatly aid assessment of P fertility in many agricultural and native systems.

Compartments of the soil phosphorus cycle

The dynamic nature of soil organic phosphorus (P_o) is masked by the fact that only a small portion of the total soil organic matter may be biologically active. Although this active portion can turn over rapidly and seasonal changes in certain P_o fractions have been demonstrated (Halm et al., 1972; Dormaar, 1972; Chater and Mattingly, 1980; Sharpley, 1985), little net change will be noticed in the total P_o since both immobilization and mineralization occur simultaneously in the soil (Halstead and Mckercher, 1975; Dalal, 1977). Thus, for an adequate description of the dynamics of P_o in soils, it is important to understand the interactions of microbes, fauna and plants upon which the processes involved in the rapid cycling of P-compounds depend (Cosgrove, 1977; Coleman et al., 1983; Tate, 1984).

Any discussion of P_o dynamics must also consider the complete P cycle because the immobilization, mineralization and redistribution of P in soil depends on physical-chemical properties, such as P sorption by colloidal surfaces, as much as it depends on microbial, mycorrhizal or plant uptake of P. This is illustrated in a conceptual P cycle (Figure 1) in which the following processes are described.

Primary P minerals are slowly dissolved providing phosphate ions that enter into the labile or solution P_i pool. A portion of the solution P_i will be precipitated as secondary P minerals and eventually converted to
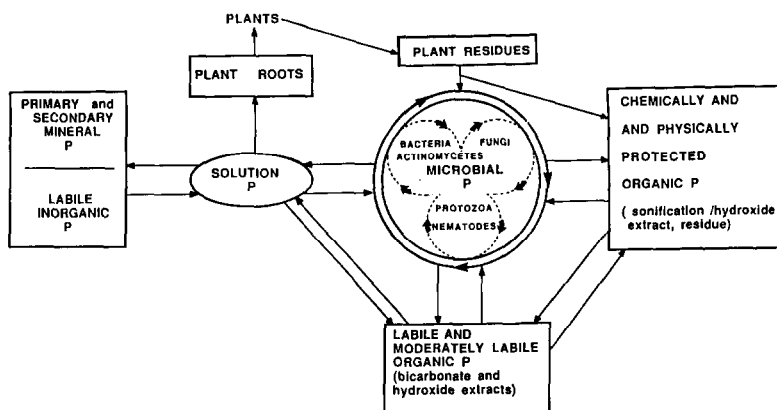
Figure 1. Schematic illustration of the measurable components in the phosphorus cycle (adapted from Tiessen and Stewart, 1983).

occluded (unavailable) forms in more weathered soils (Smeck, 1985). The central component of the active soil P_o cycle is biomass P. Biomass P can be taken up directly by predators or by saprophytes and incorporated into new consumer biomass (Coleman et al., 1983). This process constitutes the most rapid cycling of P_o and is accompanied by rapid rates of C and N transformations. Organic P released by secretion or cell lysis into the soil environment can be taken up by soil organisms or, after hydrolysis, by plants. Alternatively, it can be stabilized as part of the soil organic matter through its organic moiety, or by interactions of the phosphate group with mineral components. The presence of highly charged phosphate groups will prevent most P_o from entering into strongly humified materials, and soil P_o is usually found in reactive sidechain parts of the soil organic matter (Jaquin and Fares, 1974; Batsula and Krivonosova, 1973). Phosphodiesters in particular may enter into associations mediated by their organic moiety whereas monoesters are more likely to bind through the reactive $-OPO_3^{2-}$ to positively charged sites on organic matter, clays, sesquioxides, or to free cations present in the soil solution. Stable P_o accumulates in both chemically resistant and aggregate protected forms (Hedley et at., 1982a). The long-term accumulation of P_o in soils has been well documented but only a few attempts have been made to measure the dynamics of short-term processes that cause the long-term changes in soil P (Cole et al., 1978; Chauhan et al., 1979, 1981).

Complete identification of individual P compounds and their modes of association with soil organic and mineral components has so far not been accomplished. Several specific phosphate esters such as phospholipids (Kowalenko and Mckercher, 1970), glycerol phosphates, phosphatidyl choline (Hance and Anderson, 1963) and nucleic acids (Anderson, 1970), have been identified, though usually in quantities amounting to less than

1 or 2 percent of the total soil P_o, and possibly accounted for by P_o contained in the microbial biomass (Torsvik and Goksør, 1978). Inositol P in various combinations with humic and fulvic acids or as metal complexes has been found to account for up to one third of the soil P_o (Grindel and Zyrin, 1965; McKercher and Anderson, 1968; Veinot and Thomas, 1972; Baker, 1977). In addition, some phosphonates (C—P bond) have been identified in organic matter of soils developed under moist conditions in New Zealand and Norway (Newman and Tate, 1980, Tate and Newman, 1982; Ogner, 1983), and polyphosphate (Anderson and Russell, 1969; Ghonsikar and Miller, 1973; Pepper et al., 1976) and other non-orthophosphate P_i (Beever and Burns, 1980) occur in soil and microbial tissue.

Unidentified soil P_o may consist of orthophosphate that is loosely absorbed to soil organic matter (Carloni and Garcia Lopez de Sa, 1978) or bound through metal bridges rather than by direct covalent bonding (Dormaar, 1963; Grindel and Zyrin, 1965; Fares et al., 1974; Harter, 1969). In some cases though, the methods of organic matter extraction and purification may artificially have produced such orthophosphate by P_o hydrolysis. Condron et al., (1985) have been able to extract about 80% of soil P_o from a New Zealand pasture and found more than 90% of this P_o to be orthophosphate monoester by NMR. Higher resolution NMR and solid state MAS-NMR, which are currently available for some elements such as carbon (Wilson, 1981), will further improve the identification of P-compounds in the future.

An alternative to the identification of individual P compounds is the use of extraction procedures which fractionate P_o according to its stability with respect to specific reactants and attempting to relate these fractions to bioavailable P pools. For instance, bicarbonate extractable P_o has been found to be highly labile and related to plant available P (Bowman and Cole, 1978a). In soils with low labile P_i content, NaOH extractable P_o was found to be a source for microbial uptake (Chauhan et al., 1981). Fulvic acid associated P, which constitutes a large fraction of the P_o in most soils (Krivonosova and Basevich, 1980), may in part be derived from recent organic materials and plant litter (Grindel and Zyrin, 1965), and is considered to be relatively labile (Bowman and Cole, 1978b). Humic acid associated P turns over more slowly and is less affected by short-term perturbations (Grindel and Zyrin, 1965; Batsula and Krivonosova, 1973; Bowman and Cole, 1978b). Such extraction methods, in conjunction with experiments aimed at understanding the biological availability of the fractions extracted, have been used to investigate the processes involved in the redistribution of soil P (Stewart and McKercher, 1982). Hedley and coworkers developed a more complex extraction procedure utilizing sequentially an anion exchange resin, sodium bicarbonate, sodium hydroxide, mild sonification followed by a second sodium hydroxide extract,

acid, and a final complete wet digestion of the residue (Hedley et al., 1982a). Application of this method to soils that showed substantial P_o turnover in laboratory incubations (Hedley et al., 1982a), in the vicinity of plant roots (Hedley et al., 1982b) or under long-term cultivation (Tiessen et al., 1983) and soils of differing weathering stages (Tiessen et al., 1984; Roberts et al., 1985) has aided the development of the conceptual P-cycle presented in Figure 1.

Quantities and forms of microbial P

Following the approach used for estimating microbial carbon and nitrogen after a chloroform treatment (Anderson and Domsch, 1978a, b; Domsch et al., 1979; Jenkinson and Ladd, 1981), a method to estimate microbial P has been developed. Microbial P is determined from the change in the quantity of P_o and P_i removed by specific extraction agents following chloroform treatment (Brookes et al., 1982; Hedley and Stewart, 1982). Since P compounds from microbial cells react with varying intensity with soil colloidal material when the cell membrane is lysed by chloroform, a variable proportion of the released P is recovered in a mild extraction reagent, depending on the reactivity of soil colloidal surfaces (Hedley and Stewart, 1982). Therefore, methods of direct measurement of microbial P have to be calibrated from soil to soil and at best will remain estimates. Spatial and temporal variations in soil microbial populations which are well known from viable counts and direct microscopic observations (Alexander, 1977; Söderström, 1977) further complicate microbial P estimates. Residue management and cultivation practices are also known to influence microbial numbers and distribution of microbes in the soil (Doran, 1980a,b). An average of 83 kg ha^{-1} of microbial P was reported by Anderson and Domsch (1980) for several European soils based on C determination and average C/P ratios. Incubation of P-deficient and P-sufficient soils with energy sources (cellulose), though, has been shown to result in a soil biomass of widely differing C to P ratio (15:1 to 45:1) and in great differences in the extractability of soil P_i and P_o fractions (Chauhan et al., 1979, 1981).

The composition of microbes with respect to P compounds has only been studied in cultures. Over 60% of microbial intracellular P is usually in the form of nucleic acids, 20% in acid soluble P-esters and 5% in phospholipids (Webley and Jones, 1971). Quantities of all metabolically active P-forms can fluctuate greatly in cells. Nucleotide content may vary by 5 to 10 times, depending on growth stage and activity of cells, Surplus P from growth media may reversibly accumulate as polyphosphates inside bacterial (Harold, 1966) and fungal cells (Beever and Burns, 1980).

Phospholipids are concentrated in the cell membranes and occur in relatively constant quantities. The most common phosphatide in bacteria is phosphatidyl ethanolamine ($> 50\%$), followed by phosphoglycerol,

phosphatidic acid and phosphoinositols (< 10%). Phosphatidyl choline, which is abundant in plants, is largely absent in bacteria (Ikawa, 1967).

Extracellular structures (walls, capsules etc.) can account for over 80% of the bacterial biomass (Harris and Mitchell, 1973) and the P content of these materials is highly variable, depending on P availability in the growth medium. Bacterial walls for instance are known to be assembled from P-free teichuronic acid units instead of the P-containing teichoic acids if P supply is limited.

The uptake, release and redistribution of P through microbial and faunal activity

Transport of P_i into microbial cells is energy dependent, obeys Michaelis-Menton kinetics, and is affected by such factors as pH, cation concentrations and inhibition by pollutants such as arsenate and short chain fatty acids (Beever and Burns, 1980). Much of the information on P uptake has been obtained from research performed in nutrient media, and few papers deal with the uptake of P_i ions by microorganisms in a soil environment (eg. Mayaudon and Simonart, 1964). A possible exception to this is the research done on the P dynamics of vesicular-arbuscular (V.A.) mycorrhizae (Stribley et al., 1980), which aid the P uptake of their host plants by exploring a greater soil volume than is accessible to noninfected roots (c.f. reviews Sanders, Mosse and Tinker, 1975; Hartley, 1978; Rhodes and Gerdemann, 1980). Experimental work using isotopic labelling of the resin extractable P_i and measurement of the specific activity of plant phosphate has indicated that the V.A. mycorrhizal plants and non-V.A. mycorrhizal plants are utilizing the same P sources, although some contradictory results have also been reported (Bolan et al., 1984). Similar results have been obtained with ectomycorrhiza (Thomas et al., 1982).

Although the uptake of P_i by active microbial populations has been examined in some detail, the release of P from the microbial cell is less well understood. Cole et al. (1977) designed a simulation model that included abiotic and environmental factors such as freezing and thawing and heating and drying of the soil in order to decrease the size of the microbial population and provide a return of P to the soil solution. The effect of low soil temperature on the viability of microorganisms and the particular effectiveness of repeated freeze thaw cycles have been reported by Biederbeck and Campbell (1971). Apart from temperature, other natural events which have a negative effect on microbial biomass and activity in the soil include changes in available soil moisture, soil atmosphere or energy supply (Lynch, 1982; Domsch, 1984; Paul and Voroney, 1984).

In addition to environmental factors, the interactive effects of bacteria, fungi and microbial grazers such as amoeba and nematodes are important. Recent studies of microbial-faunal interactions (Coleman et al., 1983) in

microcosms examined only some of the processes involved, rather than all the interactions in a complete soil population. In microcosm studies, it has been shown that soil micro and mesofauna affect substrate decomposition and concurrent P mineralization (Coleman et al., 1977; Cole et al., 1978; Coleman et al., 1978). Bacterial grazers, such as protozoa and nematodes, increased system activity as measured by CO_2 output and P mineralization, possibly by returning nutrients to the soil solution. When the complexity of the system was increased by interactions between omnivorous nematodes and amoebae, respiration was further increased in spite of the decreased bacterial numbers in the grazed system (Coleman et al., 1978). Elliott et al. (1980) and Elliott (1986) showed that microbial trophic structure, as influenced by the effect of soil texture and habitable pore space on different size classes of organisms, has important effects on energy and nutrient flows in terrestrial ecosystems. Their work indicated that protoza make food more available to nematodes by entering soil pores inaccessible to nematodes.

Several further trophic interactions have been studied by other workers. It has been shown that earthworms can enrich surface soils with P (Barley, 1961) and increase the amount of readily exchangeable P_i as well as the rates of mineralization of easily extractable P_o (Sharpley and Syers, 1976; Mackay et al., 1982). Sharpley and Syers (1977) estimated that 9 and 13 $kg\,ha^{-1}\,yr^{-1}$ of P_i and P_o respectively accumulated in surface casts, which represented a significant amount of P cycling in a New Zealand pasture soil. Short-term plant availability of P derived from plant litter was increasd two to three-fold upon digestion by surface casting earthworms (Mansell et al., 1981).

McKercher et al. (1979) examined the biomass, numbers and P content of three soil invertebrate taxa (Enchytraeidae, Dorylaimidae and Elateridae) in a native grassland ecosystem, and found that the soil invertebrates accounted for a small fraction of the total soil biomass, but that their role in P transformation may be relatively more important.

Termites are also important agents in soil organic matter decomposition and nutrient cycling in tropical regions (Leprun and Roy-Noel, 1977; Brian, 1978; Arshad, 1982). Similarly, the grazing of plant materials and subsequent recycling of P and other nutrients to soil by large herbivores is important in pastures (Batzli, 1978; Till, 1980; Floate, 1981). The presence of growing plant roots has been shown to increase the release of P from plant litter compared to purely microbial turnover (Sekhon and Black, 1969; Blair and Boland, 1978). Uptake, storage and transformation of P by plants have been reviewed by Bieleski (1973).

Mineralization and redistribution processes, biochemical and biological mineralization

The typical compositions of biomass P_o and free soil P_o are greatly dif-

ferent. This difference is the result of preferential stabilization of specific P_o compounds in the soil environment. For instance, the percentage of P_o that is in the form of inositols is much higher in soils ($> 30\%$) than in microbes ($< 10\%$). Soil inositols are frequently in isomeric forms that appear not to be plant derived (Anderson and Malcolm, 1974) but may be epimerized from plant forms by microbes (L'Annunziata et al., 1977). The high charge density of inositol phosphates allows rapid adsorption on soil minerals, and extensive interaction with sesquioxides that protect free inositols from degradation. Phosphodiesters have lower charge densities and their phosphate groups are considerably shielded from ionic interactions. This leaves them accessible to microbial or enzyme attack in the soil environment; and explains the small proportions present in the soil system (Tate, 1984). Association of lipids or other diesters with polysaccharides, that envelop most microbial cells in soils, renders the P-esters much more stable. The presence of free Fe^{3+} further retards ester degradation and at the same time reduces its chemical extractability (Moucawi et al., 1981). Co-adsorption of Fe or other metal ions and phosphates to microbial polysaccharide flocs is recognized as an important part of waste treatment by activated sludge processes (Brown and Lester, 1979). Similar reactions are likely to occur in the soil environment. Differences in strength of complex formation and subsequent extractability of P_o complexes will determine the real and apparent composition of the soil P_o pool.

Stabilized soil P_o can re-enter the cycle of P transformations during the biological mineralization of soil organic matter (McGill and Christie, 1983). Due to the energy requirements of the organisms involved in this process, C will be lost from the soil as respired CO_2. Alternatively, extracellular enzymes present in the soil or released in response to low P_i availability can hydrolyze P esters independent of C turnover in a purely biochemical mineralization (McGill and Cole, 1981). The relative accessibility to hydrolases of the $R-OPO_3^{2-}$ groups on the surface of soil organic matter associations may explain the wide range of C to P_o ratios in soils through which P_o mineralization has been observed (Blair and Boland, 1978). Strong phosphate interactions with sesquioxides or organic matter will prevent enzymatic hydrolysis, since phosphatases bind directly to this terminal group, possibly involving divalent metal cofactors (Nath, 1969).

Phosphatase activity is common in soils (Kiss et al., 1975; Skujins, 1976). Phosphateses may be stabilized by association with soil organic matter, or they may be of a more transient nature being excreted by microbes or plants as a response to low P_i availability (McGill and Cole, 1981; Burns, 1982). Phosphatase activity is usually greater in the rhizosphere than in the surrounding soil (Tarafdar and Chhonkar, 1978). Phosphatase added to soil, though, is quickly metabolized by the microbial population (Nielsen and Eiland, 1980) and the persistence of abiontic phosphatases in soil remains largely unexplained. The activity of enzymes is affected by their environment, possibly due to interference with the
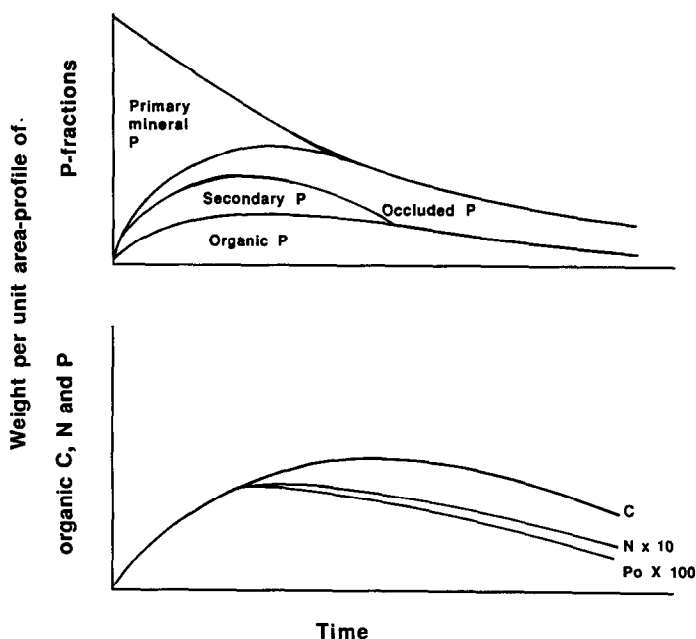
Figure 2. Changes in form and amounts of soil P and soil organic constituents with time (adapted from Floate, 1971 and Walker and Syers, 1976).

substrate or substrate binding. The activity of an enzyme (K_m) in soils is usually smaller than in aqueous media (Cervelli et al., 1973), particularly in the presence of large amounts of soil organic matter. It has also been reported that phosphatase activity in soil is decreased when energy substrate such as labile organic matter is limited (Spiers and McGill, 1979). The presence of a P sink such as a plant root in the soil system lowers P_i concentrations in the soil solution, promotes biochemical mineralization and minimizes the residence time of free P_i and thus the fixation of the hydrolyzed P by inorganic soil components, thus increasing P turnover (Saunders and Metson, 1971; Blair and Bowland, 1978).

Analysis of the relative changes in C, N and P contents of soil organo-mineral size fractions during 4 to 90 years of cultivation (Tiessen and Stewart, 1983b) showed no evidence for preferential P mobilization. Several size fractions of soil organic matter, particularly the more labile ones, showed identical percentage losses of C, N and P_o, indicating a biological, nondifferential mineralization process. Other fractions exhibited greater losses of C and N possibly due to the preferential stabilization of reactive P groups with inorganic soil components, or due to more conservative cycling of P_o. It appears that organic matter mineralization was sufficiently rapid to provide P for crop export avoiding P-limiting conditions. The importance of P_o mineralization in providing plant avail-

able P_i has been well established (Haas et al., 1961; Wild and Oke, 1966; Dormaar, 1972; Halm et al., 1972; Dalal, 1979; Chater and Mattingly, 1980) and is particularly important in highly weathered soils (Adepteu and Corey, 1976; Acquaye, 1973; Tiessen et al., 1984; White and Ayoub, 1983).

Labile P_o appears to be important for the movement of P through soils (Hannapel et al., 1964a; Reddy et al., 1978) and mineralization of labile P_o greatly reduces the P mobility in soils (Campbell and Racz, 1975; Rolston et al., 1975). Hannapel et al. (1964b) found much of the mobile organic P in soils to be colloidal microbial cells and cellular debris. Such colloidal P_o may be deposited in clay skins along soil pores and may therefore form an important store of P that is more accessiblen to plant roots than crystalline inorganic phosphates (Hannapel et al., 1964a).

Organic P turnover during pedogenesis

At the onset of soil development most parent materials contain only P_i, which is subsequently utilized by pioneering organisms and assimilated as P_o. In early stages of soil development, P_i availability controls the accumulation of soil organic matter (Walker and Adams, 1958, 1959; Syers and Walker, 1969; Walker and Syers, 1976; Smeck, 1973, 1985). These authors suggested that the decline in P_i availability during continued soil development and weathering will result in widening C to P_o ratios (Figure 2). The constraints of P availability on N-fixation reviewed by Cole and Heil (1981) and on other N transformations (Purchase, 1974) may similarly result in widening C to N ratios.

In keeping with the concepts of Walker and coworkers, Runge and Riecken (1966) found that low P_i availability was associated with low P_o content and high C to P_o ratios in imperfectly drained soils in Iowa. Westin and Buntley (1967), though, observed higher P contents in organic matter of wetter and warmer soils along an environmental gradient in South Dakota. A similar study in Canada revealed no trend in C to P_o ratios but relatively constant proportions of C, N, S and P in soil organic matter (Dormaar, 1963). Carbon to P_o ratios in Canadian Gley soils were found to be erratic and often quite low, ranging from 51 to 155 (Hinds and Lowe, 1980). Part of the difficulty in following long-term transformations of P and soil organic matter is due to the concomittant development of the soil profile, erosion of the top soil and change in bulk density. For instance, the losses of total P with continuing soil development, described by Walker and Adams in 1959, were frequently only observed when P concentration data (which did not decrease over 10,000 years) were multiplied by variable horizon thickness and bulk densities to give total P contents per unit area (Syers et al., 1969; Syers and Walker, 1969).

At more advanced stages of soil formation the recycling of P_o by the biomass becomes increasingly important for the availability of soil P.

During each cycle there is a possibility of C and N gain or loss by assimilation/fixation or respiration/denitrification processes whereas P is largely conserved in the system in unchanged total quantities. The rates of P cycling at this stage will determine the rates of C and N changes while the direction of such changes and therefore C to N to P_o ratios are governed by the balance of autotrophic/heterotrophic activity, by the organic matter stabilizing potential of the soil (clays, sesquioxides, etc.) and by environmental and physical factors. Some P_o compounds will be withdrawn from the P cycle and stabilized, particularly those with a large number of reactive phosphate groups such as the inositol phosphates. More labile P_o compounds will normally undergo hydrolysis and therefore are present in only small quantities or under extreme environmental conditions which impede their turnover (Tate, 1984).

Parallel to the formation of P_o from primary minerals is the occurrence of secondary aluminium and iron associated P_i forms, which, with continuing soil development, assume an increasingly occluded (unavailable) character (Walker and Syers, 1976). The relative proportion of different P_i fractions is determined by the activities of calcium, aluminum and iron in the soil, which in turn are greatly influenced by the weathering processes (Williams and Walker, 1969). Soil weathering, through available moisture or time of development, thus determines Fe and Al activities as well as the type and amount of P_o accumulation in soils (Williams and Saunders, 1956). These parameters are further interconnected since a large labile P_i pool, supported by surface associations of P and sesquioxides, will aid active P_i and P_o cycling and thus influence organic matter accumulation and C to P_o ratios. Calcareous soils may therefore show different organic matter and P_o accumulation patterns from acid soils (Walker and Adams, 1959). Cole and Heil (1981) reanalyzed data by Westin and Buntley (1967) and found that organic N correlated positively to aluminium and iron bound phosphate and P_o, and negatively to calcium bound P. Organic P concentrations in different soils were not only closely correlated with C and N but were also a negative function of pH and base saturation and were positively correlated with free iron (Thompson et al., 1954; Tiessen et al., 1984). Increased weathering and soil development will lead to a decline in soil organic matter and P_o levels due to increased sesquioxide activity, which withdraws P from the cycle as occluded P, and due to losses of organic matter and P_o by leaching. Ratios of C and N to P_o are unlikely to be unequivocal indicators of the progress of this process.

Organic P transformations during cultivation

In addition to data from chrono- and environmental sequences of soils, information on the controlling parameters of the P_o cycle may be obtained from studies of soil systems that have been disturbed by man's activities.

Organic P has been found to build up in soils as a result of P_i fertilization (Jackman, 1955; Williams and Donald, 1957; Sadler and Stewart, 1975; Dalal, 1977). Losses of P from the North American prairie soils under cultivation were examined by Haas et al. (1961). In general P_o contents of the soils in the Northern Great Plains decreased by an average of 27% while no. P_i losses were observed. Greater P_o losses in southern soils suggested that P_o mineralization was temperature dependent (Eid et al., 1951; Thompson et al., 1954). Barber (1979) found a loss of 12% of the total P in a soil after 25 years of continuous cultivation, and a comparison with fertilizer inputs and crop export showed that the observed concentration changes in the top 15 cm of soil accounted for only 50% of the total P export. This indicates that a portion of the P nutrition of plants may be satisfied from lower layers in the soil and that P may be actively recycled into the top soil by Plants (Dorman, 1933). This process is of prime importance in tropical bush fallow systems for the restoration of soil fertility (Nye and Greenland, 1960).

Thompson et al. (1954), in Iowa, studied the mineralization of P_o by selecting 25 cultivated and associated virgin soils, analysing them and subjecting samples to a laboratory incubation. An average of 33% of the C, 32% of the N and 24% of the P_o were lost from the soils, indicating that P_o is cycled more conservatively than C and N, which are more easily lost by leaching or volatilization. During the laboratory incubation, less substrate was present for mineralization in the cultivated soils compared to the virgin soils, resulting in lower amounts of C, N and P mineralized. At the same time, a smaller portion of the material present in the cultivated samples was mineralized, indicating a greater stability of the residual materials. This is supported by Batsula and Krivonosova (1973) who reported that the percentage of non-hydrolyzable P_o in humic and fulvic acids doubled upon cultivation.

The reduced mineralizability of organic matter after cultivation depends on the chemical nature and accessibility of the organic materials, the nature and activity of the microbial population and the presence and activity of free soil enzymes (Tate, 1984). The reported differences in mineralization of organic matter and organic P may therefore not only be due to changes in the stability of the organic materials but may reflect other conditions in the soil.

Thompson et al. (1954) and Harrison (1982) observed that the mineralization of P_o under field and laboratory conditions correlated positively with pH, while C and N mineralization were not accelerated by high pH. At high pH, hydroxyls will compete with phosphate for organic or metal-organic bonding sites and release P into the soil solution (Hingston et al., 1972, 1974; Mattingly, 1975). A further, indirect effect of pH was observed by Halstead et al., (1963) who reported increased microbial activity and therefore increased P_o mineralization after liming of acid soils.

High pH in topsoils is frequently associated with the presence of calcium carbonate and other Ca salts, and a number of researchers have reported the precipitation of Ca—P formed from P_o sources such as manure (Yeun and Pollard, 1951; Campbell and Racz, 1975) or labile soil P_o fractions (Haas et al., 1961; Halstead et al., 1963; Campbell and Racz, 1975). The presence of carbonates (Soper and Elabgouri, 1964) or other calcium salts (McCall et al., 1956; Halstead et al., 1963) have been shown to lead to the mineralization of P_o and cause elevated P_i levels. Variability of soil texture across a field has also been shown to influence the relative amounts of P_i and P_o within one field site (O'Halloran et al., 1985).

There is general agreement that the process of precipitation of phosphate with calcium in carbonate rich soils lowers P solubility (Cole et al., 1953) until the very low levels, determined by the solubility product of hydroxyapatite, are reached (Larsen, 1966). Plant availability of P is determined by labile, surface absorbed or precipitated rather than by crystalline forms of phosphate (Murrman and Peech, 1969), and in calcareous soils the availability of the crystalline phase is further reduced by the low surface area of calcium phosphates, which are mainly present in sand and silt-sized particles (Scheffer et al., 1960; Chu and Chang, 1966).

These reports suggest that the mineral fraction of a calcareous soil competes directly with plants for mobile and potentially available P. Lindsay and Moreno (1960) pointed out that the conversion of labile P to less soluble crystalline forms is slow and that rates of reaction may be important for the balance in soil. The intermittent plant growth of a cropping system, and particularly of crop-fallow rotations (Haas et al., 1961; Lehane et al., 1964) favour the precipitation of P_i and reduction of P availability to a level determined by the solubility product of the P_i species, whereas a native grassland system, in which P is closely recycled in organic forms, maintains a higher level of P availability.

Fares et al. (1974) state that the ability of Chernozemic soils to maintain P in an organic form facilitates the P supply to plants and limits the retrogression of the soil to a state where apatitic P forms predominate. Cultivation disrupts the stability of the soil organic matter and thereby induces a shift in the P balance towards less available phosphates. At the same time total P reserves in the soil are diminished by crop export. The overall effect is a deterioration of the P supplying power of the soil beyond the level expected from crop export alone (Tiessen and Stewart, 1983a).

Low solubility iron and aluminum phosphates similarly act as a P scavenger in more weathered soils. In tropical soils P availability often depends on the amounts and mineralization of organic P (Acquaye, 1963; Adepetu and Corey, 1976; Agboola and Oko, 1976; White and Ayoub, 1983).

In cultivated soils a decline in total organic matter levels will, under temperate regimes, be accompanied by a smaller decline in P_o, since P has

fewer loss mechanisms than C or N and is therefore more conservatively recycled (Tiessen et al., 1982). If organic matter mineralization frees P in excess of crop demands, precipitation as P_i such as apatites may occur (Fares et al., 1974; Tiessen and Stewart, 1983a). Under tropical conditions where organic matter and associated materials are frequently only stabilized in biomass and recent dead materials, breakdown of this organic matter will cause C, N and P losses in equal proportions (Dalal, 1977; Brams, 1973). Use of phosphate fertilizers may lead to an accumulation of P_o if adequate C and N supplies are available, whereas P_i is likely to accumulate in a rapidly degrading system.

Conclusions

The dynamics of soil organic phosphorus are greatly influenced by interactions of the biological, chemical and physical properties of the soil. Conclusions about the type and extent of P_o transformations that were obtained from a narrow range of parent materials, environmental conditions and land uses can therefore rarely be generalized.

Changes in the quantity and nature of P_o, observed in field studies, are the net result of the transformations in a highly dynamic P cycle. The central controlling factors of soil P_o transformations are the solution P concentration and the activities of the soil biomass. Immobilization of P_o therefore depends on the availability of P_i and of organic substrates for the growth and maintenance of the soil biomass. Mineralization of P_o is controlled by the balance of P_i availability and P demand of biomass and crops, and by the mineralization of organic matter which releases P_o as a by-product.

Detailed concepts of the P cycle have been based on numerous short term studies of individual processes. These have been integrated into computer models, which may be able to predict P transformations under field conditions. The extrapolation of such short term processes to long term P transformations during pedogenesis or agricultural use have so far met with limited success.

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