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Phosphorus control of soil organic matter accumulation and cycling

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Abstract. The present level of understanding of P controls on organic matter accumulation and cycling in a pedological context owes much to soil sequence studies, and the hypotheses that emerged from them to explain the variation of P compounds with soil type and development. It is now widely accepted that nutrient transformations in soil are closely linked through a more dynamic biological cycle in which microorganisms have a central role. Concepts developed to account for the effects of P on N cycling, and for interpreting inter-relationships of C, N, P and S in both a pedological and biological context have yet to be tested adequately across different ecosystems. These concepts are discussed, in relation to some recent supporting evidence.

Introduction

The close relationship between C, N, organic P (P_0) and S contents in mature soils, and the special role that P has in controlling soil organic matter through its effect on nitrogen fixation, are both well established tenets of soil science (Walker & Syers 1976). However, predictions of nutrient transformations based on an assumed stoichiometry of the major nutrient elements in soil organic matter (Cole & Heil 1981) or plants (Till et al. 1982) can be misleading, because different nutrients cycle at characteristically different rates in the same system.

The processes involved in nutrient transformations in soil are generally well understood, but comparatively little is known yet about the mechanisms controlling these transformations (Paul 1984). This is especially true where the interaction of two or more nutrients is involved. For example, despite strong evidence to indicate the close linkages between P and N (Cole & Heil 1981) more research is still needed to resolve cause and effect relationships, particularly across different ecosystems.

The purpose of this brief overview of P controls on organic matter accumulation and cycling is to indicate some of the supporting evidence, and to draw attention to several recent reviews relevant to this topic. Among these, Cole & Heil's (1981) excellent review of P effects on N cycling is essential reading. Other recent reviews have discussed progress towards a better understanding of soil P dynamics in soils and landscapes (Smeck 1985), compared the P cycle between some different temperate ecosystems (Harrison 1985) and discussed the soil P cycle, emphasising the rates and pathways of P through soil organic matter (Tate 1984, 1985). Many aspects of the C, N, P, S, and micronutrient cycles have also recently been discussed by Stevenson (1985).

Discussion

P transformations and availability

The complete transformation of P from primary mineral forms to sparingly soluble Al and Fe phosphates (occluded P) occurs through the formation of a number of intermediate forms, over a geological timescale. These forms vary in their availability to plants and soil microorganisms, principally because their solubilities in the soil environment differ.

Pedological P transformations are mainly driven by leaching and varying acidity, whereas the biological P cycle is controlled by the need for P in the energy transport processes of living cells. In reviewing P transformations along both pedological and biological pathways, Smeck (1985) considered that the long-term evolution of P forms in soil ecosystems is controlled by the less dynamic pedological pathway, ultimately resulting in the accumulation of P in mainly occluded forms.

In the short term, the pathways by which P becomes more or less available to plants and soil microorganisms can be summarised by the following equilibria:

$$\text{soil solution P} \underset{\text{fast}}{\rightleftharpoons} \text{labile P}_i \underset{\text{slow}}{\rightleftharpoons} \text{non-labile P}$$

The labile P_i (inorganic P) per unit soil volume, soil solution P concentration, the ability of the soil to replenish solution P, and the rate of replenishment, all interact to control the overall P supply. The non-labile P includes the P in primary (apatite) and secondary minerals (P_i and P_o sorbed to Fe and Al on clay minerals), insoluble Ca salts, and the P in organic forms. The rate of P release from these non-labile forms is controlled by the soil mineral composition and reaction, as well as the size, composition, and activity of the soil microbial population. The possible ecological significance of rapid transfer of P from dying roots to living plants should also not be overlooked when considering pathways by which P is made available to perennial plants (Ritz & Newman 1985).

The stabilisation of organic matter by clay minerals has a considerable influence on the short- to medium-term cycling of P (Tiessen et al. 1984b, Van Veen et al. 1985). An extreme example is the limitation of P availability by clay minerals of short-range order (e.g. allophane) in Andisols, where P_i, and organic matter -TP_i complexes, linked through Al bridges, effectively remove P from active cycling (Borie & Zunino 1983). The amounts of the different P compounds present also influence P availability. In moderately weathered soils, for example, secondary P_i minerals are an important source of available P, whereas in strongly weathered acid soils (e.g. some tropical soils), available P is increasingly supplied by mineralisation of labile P_o (Tiessen et al. 1984a).

Soil microorganisms are also an important reservoir of potentially available nutrients, including P, as well as being the main agents of decomposition. It is, however, the size of the P flux through the microbial biomass, rather than the biomass itself, that determines P availability from this source (Brookes et al. 1984). Indeed, sustained P cycling through an active decomposer population, regulated by microbial/faunal interactions (Ingham et al. 1985, Lee 1985), is considered essential for maintaining soil fertility (Harrison 1985).

The factors controlling the population dynamics and activities of these soil organisms, such as temperature, moisture, aeration and the soil reaction (Tate 1985), also determine the rates and pathways of P through soil organic matter, and consequently the supply of available P and other nutrients from this source. The mechanisms involved are not well understood, however, compared to dissolution–desorption processes in relation to P availability.

In summary, these complex physico-chemical and biochemical mechanisms together govern the equilibrium concentration of P in the soil solution, and the capacity of the soil to maintain this concentration against uptake by plants and microorganisms. A better appreciation of these mechanisms will certainly assist in unravelling the cause and effect relationships between P and other nutrients, with ensuing benefits for improved management of terrestrial ecosystems.

P controls on organic matter transformations

Present knowledge of the influence P has on organic matter owes much to early studies of pedogenesis involving soil sequences (Walker & Syers 1976). In a wind-blown sand chronosequence, for example, the continued accumulation after 10,000 years of C, N and S depended on the recycling of P through organic forms (Syers et al. 1970), at a rate sufficient to satisfy the high energy demands of the nitrogen-fixing organisms. These rapidly recycling forms of P_0 include orthophosphate diesters of mainly microbial origin, identified recently in a climosequence of increasingly acid New Zealand soils (Tate 1984).

The P and Fe chemistry of these climosequence soils confirmed they also represented a development sequence (Molloy & Blakemore 1974), with C/P_0, N/P_0 and P_0/P_i ratios all increasing across the sequence (Table 1). The changes in these ratios with soil development mainly resulted from an increased loss of P with weathering intensity, causing P_0 accumulation to decrease relative to C and N. Organic matter accumulation was also favoured in this sequence by increases in both clay content and secondary clay minerals with soil development (Churchman 1978), making differentiation of the effects of clay and P on C and N accumulation difficult (Schimel et al. 1985). Other evidence however supports the hypothesis that organic matter accumulation and cycling in these soils is largely controlled by P, as proposed by McGill & Cole (1981). Appreciable increases in N mineralisation rates, yields of dry matter, and plant N contents resulted from the addition of P, K and S (Ross & Bridger 1978) (Fig. 1) suggesting that P was controlling N cycling. Similar soils have required very high P applications, as well as S, when developed for agricultural use (McIntosh et al. 1985). Air-drying, with or without P, K and S additions, had a similar effect on N

Table 1. Organic C, N, total P, and $C:P_0$, $N:P_0$ and $P_0:P_i$ ratios of topsoils from a climosequence under tussock grassland, South Island, New Zealand. The soils are listed in order of increasing weathering.[1]

Soil classification	C (%)	N (%)	P_t ($\mu g\, g^{-1}$ soil)	$C:P_0$	$N:P_0$	$P_0:P_i$
Xeralfic Haplargid	3.5	0.21	1060	106	6	0.5
Typic Ustochrept	2.1	0.18	940	46	4	1.0
Udic Haplustalf	2.3	0.19	890	61	5	0.8
Haplic Cryohumod	9.3	0.52	1040	107	6	5.1
Typic Cryorthod	4.9	0.32	880	75	5	2.8
Dystric Cryochrept	4.8	0.30	840	80	5	2.5
Typic Placaquept	7.3	0.33	520	170	8	4.8
Typic Dystrochrept	7.5	0.49	510	160	10	11.8
Typic Placaquod	18.7	0.44	430	468	11	13.3

[1] Molloy & Blakemore 1974.

mineralisation rates (Fig. 1), due in part to the release of P (Sparling et al. 1985) and other nutrients from killed microbial cells.

Increases in N mineralisation rates (Cornish & Raison 1977) and mineral-N uptake (Cole & Heil 1981) can occur in response to P through more effective root growth and soil exploitation. Furthermore, biochemical effects, such as increased assimilation of NO_3–N into proteins may result from correcting P deficiency in plants (Schjorring 1986). Although P supply might also control nitrification in some soils, in others NH_4–N supply, moisture, or pH seem to be more important. Pastor et al. (1984) have found across a series of edaphic climax forests for example that differences in nitrification

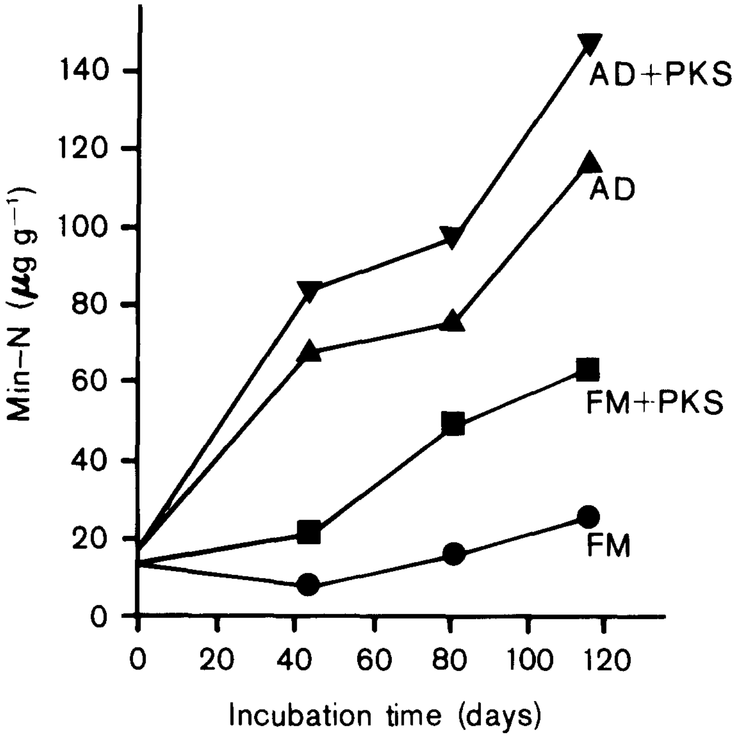

Fig. 1. Mineral-N concentrations in a Udic Haplustalf adjusted to 60% of water-holding capacity and incubated at mainly 15–22 °C. Soil sampled from tussock grassland, South Island, New Zealand. FM, initially field-moist (undried); AD, initially air-dried; +PKS, incubated with P, K, S fertiliser. Modified from Ross & Bridger (1978).

among the soils studied were apparently related to P_i supply in the spring and early summer, but in mid- to late summer, NH_4–N supply was the most influential factor. They suggested that given sufficient time without disturbance, the complex interrelationships among N mineralisation, nitrification, productivity, plant species composition, P supply and site moisture status would eventually approach a steady state. A similar hypothesis was proposed by Cole & Heil (1981) for soil P and N cycling. In both cases, however, although the experimental evidence was suggestive, the hypothesis still awaits adequate testing.

Although soil microbial activity and P_o turnover can be stimulated by increasing the availability of C (Helal & Sauerbeck 1984), the ultimate control on P_o mineralisation appears to be the availability of P_i, rather than a need for energy. Support for this hypothesis (McGill & Cole 1981) was provided from incubation experiments involving additions of C and N to two soils, each with similar microbial biomass, but widely different P status (Hedley et al. 1982). Despite these additions, uptake and accumulation of extractable P_o by microorganisms was still limited in the P deficient soil.

Such incubation experiments illustrate that nutrient transformations in terrestrial ecosystems are closely inter-related through microbial growth processes, (e.g. regulated by microbial/faunal interactions (Ingham et al. 1985; Harrison 1985)), and by larger soil animals like earthworms (Lee 1985). Cole & Heil (1981) have proposed that, given time, N and P supplies become synchronised through these microbial processes, as for aquatic ecosystems. They estimated from experiments using isotopes (^{15}N, ^{32}P) that the amounts of biologically active N and P in a semi-arid grassland were 24 and 3 $g\,m^{-2}$ (240 and 30 $kg\,ha^{-1}$) respectively. A similar close link between C and P cycling, as indicated from correlation of microbial C and P measurements for several UK soils under different management regimes, was recently used (Brookes et al. 1984) to estimate annual P fluxes through the microbial biomass; these ranged between 23 $kg\,ha^{-1}$ for grassland soils, and 7 $kg\,ha^{-1}$ for some arable soils.

The characteristically slower rate of cycling of P compared to C, N and S in temperate ecosystems is also observed in some tropical ecosystems (e.g. Mueller-Harvey et al. 1985). Even here, where soil conditions and climate often favour very large nutrient fluxes through soil organic matter, a dichotomous system, as proposed by McGill & Cole (1981), for stabilising C and N on the one hand, and P on the other, is evident.

McGill & Cole's (1981) conceptual model is also consistent with field observations of changes in C:N:P:S stoichiometry in soil horizons and profiles from a variety of soil sequence studies. On a biological timescale, the model envisages that C, N and C-bonded S are stabilised together, and used by soil microorganisms as a source of energy (biological mineralisation), whereas mineralisation of P_0 and sulphate esters is controlled by the supply of, and need for, P and S (biochemical mineralisation). This latter mechanism operates through adaptive enzymes (e.g. phosphohydrolases) that are produced by plant roots and soil microorganisms at low soil solution P concentrations, but repressed when these concentrations are high. The onset of P deficiency in plants, for example, is accompanied by increases in plant phosphatase activity (e.g. McLachlan 1984). A similar response by soil microorganisms to P stress is likely (Spiers & McGill 1979). In P deficient soils, C:P_0 ratios often exceed 200. Decomposition of substrates with such wide ratios is alone unlikely to satisfy the P needs of a decomposer population with microbial C:P ratios of c. 45 (Chauhan et al. 1981). It must be remembered, however, that the balance point between net mineralisation and immobilisation depends on the C:P ratio of the substrate being decomposed, rather than on the ratio for soil organic matter or plant residues as a whole (White 1981).

The concepts embodied in McGill & Cole's (1981) model provide a rational framework for understanding C, N, P and S inter-relationships over both pedological and biological time scales, with P being the ultimate control on organic matter accumulation and cycling. Rigorous evaluation of this model is however seriously limited by a lack of experimental data. The challenge now is to obtain more quantitative data on the rates and pathways of C, N, P and S through soil organic matter, with particular emphasis on their inter-relationships, and for this, the use of isotopes (e.g. Till et al. 1982) is essential. The ingenuity of experimentalists is also challenged by the incomplete state of knowledge of the relationship between these nutrient cycles and net primary production in different terrestrial ecosystems.

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