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PHOSPHORUS CYCLING IN HUMID TROPICAL SUCCESSIONAL FORESTS

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Introduction

The purpose of this paper is to review what is known of phosphorus cycling in humid tropical successional forests. In order to understand phosphorus cycling, estimates are needed of the size of various vegetation and soil P pools, of fluxes into and out of the forest ecosystem and among the different pools, and of how controls on these processes operate. Unfortunately, such information is incomplete for even the most well-characterized ecosystem - agroecosystems found on base-rich soils in the temperate zones. The data base for humid tropical forests, especially successional ones, is much less complete.

A further complication is that the concept of successional forests includes the notions of forest disturbance and subsequent regrowth. Disturbances can differ in form, aereal extent, intensity, frequency, and duration. These differences, in turn, can affect the quantity, chemical forms, and availability of P as well as the nature and rate of forest regrowth, and so add complexity to the study of such systems.

Windthrows, fire, lightning strikes, landslides, and insect or disease-induced mortality are examples of disturbances which occur in humid tropical forests, but perhaps the most wide-spread and most studied disturbance, and that currently causing the greatest concern, is land-clearing followed by agricultural production. Consequently, much of the following discussion is devoted to considering how this type of disturbance affects phosphorus pools, transformations, and transfers, although the effects of other types of disturbance are also considered when possible.

Land-clearing

The effects of land-clearing on soil and vegetation phosphorus pools can vary greatly depending on the method of vegetation removal and the extent of soil disturbance. Total and available soil P pools, and important determinants of organic P levels in soil such as soil organic matter contents and soil aggregation, generally decrease as disturbance intensity increases (Uhl et al., 1982; Alegre and Cassel, 1986; Alegre et al., 1988). Mechanical clearing is clearly the most deleterious land-clearing practice since most of the vegetation and topsoil, and the P stored in these compartments (a high proportion of total P in weathered soils) is often removed. In general, the use of other, less intense land-clearing methods, such as manual clearing or manual clearing and burning, result in little immediate change in total or available P levels (Lal and

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Cummings, 1979; Ramakrishnan and Toky, 1981; Uhl et al., 1982; Smyth and Bastos, 1984; Stromgaard, 1984; Alegre et al., 1988), although some researchers have reported losses of Olsen-available P from the top 3 cm of a Dystropept due to forest felling alone (Ewel et al., 1981).

The size of the cleared site affects changes in soil P availability. There is little change in extractable soil P when small (<300 m^2) areas of forest are felled, presumably because there is little change in microclimate, hence in organic matter mineralization and P release. Any P mineralized is rapidly adsorbed onto variable charge soil minerals, or taken up by roots of standing vegetation (Vitousek and Denslow, 1987). These generalizations, however, may not hold for larger clearings (Denslow, 1987). Further studies of P availability and loss from a range of different-sized clearings, including those representative of shifting agriculture, are needed.

In cases where felled vegetation is burned on-site, available P levels in soil usually increase after burning (Zinke et al., 1978; Ramakrishnan and Toky, 1981; Kyuma and Pairintra, 1983; Sanchez et al., 1983; Smyth and Bastos, 1984; Stromgarrd, 1984; Werner, 1984; Lambert and Arnason, 1986; Alegre et al., 1988; however, see Ewel et al., 1981). The magnitude and timing of the peak in P availability vary greatly among studies, probably due to differences in the quantity of biomass burned and the amount of P contained in the ashes, interactions of organic and inorganic forms of P with inorganic soil constituents, fluctuations in soil microclimate, rates of mineralization of organic P, and microbial immobilization processes. Fassbender (1975) and Sertsu and Sanchez (1978) have noted changes in P availability in soil due to heating.

It is unclear whether "losses" of P associated with forest felling and burning, such as those reported by Ewel et al. (1981), actually occur as a result of aeolian transport of ashes and particulate matter or increased erosion, runoff, and leaching, or whether phosphorus is simply converted to other forms that are not extractable by the methods used. There have been few studies which have attempted to investigate the forms in which P is lost and the routes by which these losses occur. The loss of P in ash, especially, is not well quantified. Erosion and runoff are likely to be the main routes of loss of P in organic or particulate form from exposed soil in high rainfall regions (Vitousek, 1983). Relatively large quantities of soil and P may be lost during relatively short periods of time when the soil is exposed (Kyuma and Pairintra, 1983).

It has been suggested that P leaching, at least in temperate forest ecosystems, may occur via production of low molecular weight, narrow C/P ratio organic acids (fulvic acids) which are more mobile than inorganic phosphate anions and may be transported downwards through the soil profile or in surface run-off (Rolston et al., 1975; Schoenau and Bettany, 1987; Frossard et al., 1989). Some data suggest that leaching may also occur in areas clearead of tropical forest (Stromgaard, 1984). While it is clear that high soil temperature, greater fluctuations in soil moisture, and the destruction of soil aggregates as a result of clearing of tropical forest may result in rapid rates of decomposition and the production of such organic P complexes, other factors such as the pattern of water movement through the soil profile and the interaction of these complexes with

charged soil minerals are likely to determine the importance of leaching as a mechanism of P loss. Given that these processes are complex and are likely to differ among permanent and variable charge soils (Oades, et al., 1989) much work remains to be done in order to assess the importance of leaching for P loss from disturbed tropical sites.

Crop production

Crop production following land-clearing decreases total P levels in soil due to P removal in harvested products. Reductions in the size of the soil organic P pool also occur as a result of increased mineralization (Agboola and Oko, 1976; Adepetu and Corey, 1977; Mueller-Harvey et al., 1985; Mueller-Harvey and Wild, 1986). Limited data show that the relative amounts of organic P mineralized can vary widely even on similar soil types (Nye and Bertheux, 1957; Acquaye, 1963; Brams, 1971; Igue et al., 1971; Adepetu and Corey, 1977; Mueller Harvey et al., 1985). These differences may be due to differences in the quantity and type of soil minerals present, limitation of mineralization by the availability of other nutrients, wetting and drying cycles, soil temperature, and organic matter quality (Duxbury, et al., 1989). During organic matter mineralization, soil C/P ratios often narrow, suggesting that P limits soil microbial populations and is immobilized by them or that interactions of P, especially inositol phosphates, with charged soil minerals result in relatively greater retention of P than C (Acquaye, 1963; Adepetu and Corey, 1976; 1977; Mueller-Harvey et al., 1985; Stewart and Tiessen, 1987). Since it has been suggested that P availability limits forest productivity on weathered tropical soils (Vitousek, 1984) and that organic forms of phosphorus are highly correlated with crop production on such soils (Acquaye, 1963; Adepetu and Corey, 1976; 1977; Agboola and Oko, 1976; Tiessen et al., 1984;), a much more detailed understanding of organic P transformations is needed, including the development of methods for measuring organic P mineralization.

Changes in inorganic soil P pools occur concomitant with changes in organic P. Some organic P mineralized is taken up by crops or remains available to plants, but other portions become associated with less-available inorganic Fe-, Al-, and occluded-P fractions. The amount of P in these fractions usually increases in proportion to their relative amount initially present (Igue et al., 1971; Adepetu and Corey, 1976, 1977; Mueller-Harvey et al., 1985; Mueller-Harvey and Wild, 1986). Quantities of P mineralized may depend on past management. In one study, P mineralization was greater in soil taken from a recently cleared secondary forest compared to soil from a previously cropped field; relative quantities of organic P mineralized, however, were similar (Table 1). With continued cropping, available P levels may be determined by buffering reactions with organic or inorganic soil P pools (Stewart and Tiessen, 1987).

In temperate ecosystems, the absolute and relative sizes of the inorganic (eg. labile $NaHCO_3$-P, Fe- and Al-P, Ca-P, and occluded P) and organic (eg. $NaHCO_3$ and NaOH-P) soil P fractions and interactions between them vary with weathering of parent material, mineralogy, topographic position, soil texture, and management (Smeck, 1973, 1985; Tiessen et al., 1984; Roberts et al., 1985; O'Halloran et al., 1985, 1987a, 1987b).

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Similar studies of the interrelationships among inorganic and organic P fractions are need for tropical soils where mineralogy and microclimate are often different from those in temperate zones.

Table 1. Changes in phosphorus fractions (mg kg^{-1}) after two crops on previously fallowed or cropped sites. (From Adepetu and Corey, 1977).

	Fallowed site				Cropped site			
Fraction	Before Crop	After Crop	Change	%	Before Crop	After Crop	Change	%
Organic	213	158	-55	26	136	98	-38	28
Al-P	64	82	+18	28	45	5	+11	24
Fe-P	103	130	+27	26	82	106	+24	29
Occluded	75	77	+ 2	3	53	50	- 3	6
Ca-P	11	14	+ 3	27	10	11	+ 1	10
TOTAL	466	461	- 5		326	321	- 5	

P dynamics during forest regrowth

Additions and losses. Additions of P in successional humid tropical forests occur via atmospheric deposition and mineral weathering. Data (Vitousek and Sanford, 1986) from undisturbed humid tropical forests can serve as rough estimates for similar processes in successional forests, since data for the latter are lacking. In general, inputs via rainfall and dust are expected to be relatively small in magnitude, around 0.1 to 0.5 kg $ha^{-1}y^{-1}$ and additions of P to the rhizosphere from mineral weathering on deep, highly weathered soils are also apt to be very small. On younger, more calcareous soils, additions from weathering may be greater, but such minerals are lost relatively rapidly due to rapid weathering under humid tropical conditions.

As previously noted, hydrological factors determining leaching, sediment, and runoff losses are complex and methodological difficulties in quantifying such fluxes result in a scarcity of data. It is clear that most losses, if present, will occur early in succession when the vegetation cover is poorly developed, decomposition is rapid, and plant demand for P is low. Despite these conditions, losses of P may nevertheless be slight from soils which have a high P-fixation capacity (Andisols, Oxisols, humic sub-groups of Inceptisols and Ultisols), and/or high rates of water flow through macropores (eg. Psamments, Spodosols, and well-aggregated Andisols and Oxisols). Moreover, P losses from older secondary forests are apt to be similar to those in undisturbed forest, on the order of less than 1 kg $ha^{-1}y^{-1}$ (Vitousek and Sanford, 1986).

P accumulation in organic matter. It has been suggested that P availability may limit biomass and P accumulation in undisturbed tropical forests growing on Ultisols, Oxisols, Andisols, and Psamments (Vitousek, 1984; Vitousek and Sanford, 1986), but not on moderately fertile soils such as Alfisols, some Inceptisols, and Entisols. This pattern also appears to be generally true for tropical secondary forests (Table 2). Secondary vegetation growing on moderately fertile soils appears to accumulate about 2 times more aboveground biomass and P, over similar periods of time, than vegetation found on infertile soils. Departures from this generalization may be due to a number of factors: 1) Available P levels in soil and rates of mineralization of organic P can be relatively high in the period following field abandonment even on relatively P-infertile sites. 2) Differences in rates of biomass and P accumulation on similar soils may be due solely to difference in age of the vegetation. Rates of biomass and P accumulation are usually greater in younger, as compared to older, vegetation, hence only forests of similar age should be compared. 3) Soils may be misclassified (in some cases, the soil classification was not mentioned or appeared to be doubtful based on cited properties). 4) Previous managment can affect P availability and accumulation of P and biomass. For example, the accumulation of biomass and P in a 3-year-old secondary forest on land cleared by bulldozer were 50 to 100 times less than in a secondary forest growing in an area that had been cut but not burned (Uhl et al., 1982).

Belowground biomass production and rates of P accumulation and their relationship to soil type are difficult to evaluate due to lack of data. Limited data suggest that rates of accumulation of P in roots are much lower than those measured aboveground and are lower on infertile compared to fertile soils (Table 2).

P transfer in litter. Rates of foliage production, aboveground litter production, and the quantity of P cycled in litter in young secondary forest increase rapidly up until canopy closure (approximately 10 years), then level off or decline with time (Miller, 1984; 1986). It has been suggested that the quantities of litterfall are higher and litterfall mass/nutrient ratios are lower on more fertile sites (Vitousek, 1984, Cuevas and Medina, this volume). Unfortunately, few data are available to examine this hypothesis for tropical successional forests. There appears to be no consistent pattern with regard to the relationship between soil fertility and litter production; the amounts of phosphorus returned in litterfall, however, appear to be lower on infertile as compared to fertile soils (Table 2). Again, caution is required in interpreting these patterns due to the considerations mentioned above.

Patterns of P cycling via belowground litter production and exudates in successional forests and their relation to soil fertility are unknown. Few data exist for root litter production or the quantities of P contained in root litter, P retranslocation from roots before their death, or whether root P status changes with vegetation age or species composition. Such studies are greatly needed.

Rates of P transfer from litter to soil depend on rates of mineralization from litter. The latter may be affected by organic residue quality, placement, climate, and soil texture. As a result, rates of

litter decomposition in tropical forests are variable (Anderson and Swift, 1983) and difficult to relate to soil type (Vitousek and Sanford, 1986). In tropical succesional forests, rates are also apt to vary with successional stage due to changes in chemical composition of litter as a result of changes in plant species or nutritional status of a given species and changes in nutrient availability. Rates of mineralization might be expected to be more rapid in early as compared to later successional stages due to the production of more nutrient-rich litter, greater nutrient availability, higher soil temperature, and greater fluctuations in moisture contents of soil and litter in early successional ecosystems.

Table 2. Accumulation of aboveground and belowground biomass (Mg ha^{-1}) and phosphorus (kg ha^{-1}), and dry mass (Mg ha^{-1}) and phosphorus (kg ha^{-1}) content of litterfall in humid tropical successional forests.

Site	Age (y)	Aboveground Mass	Aboveground P	Belowground Mass	Belowground P	Litterfall Mass	Litterfall P	Ref.
Moderately fertile soils								
Zaire, ferralitic (Alfisol?)	2	17.9	16.9	6.9	4.9	1.9	0.4	1
	5	76.7	21.0	25.7	7.7	9.8	3.2	
	8	121.6	24.9	22.7	9.1	8.0	4.1	
	18	121.1	69.7	31.2	34.2	22.8	4.1	
Colombia, (Inceptisol?)	2	19.0	16.0					2
	5	68.0	22.0					
	16	203.0	55.0					
Panama, (Inceptisol?)	2	15.6	31.0					3
	2	28.5	48.0					
	4	42.5	89.0					
	6	56.5	91.0					
India, (Oxisol?)*	1	5.0	5.0			1.2	1.0	4
	5	23.3	20.0			4.8	2.0	
	10	57.5	25.2			7.1	3.0	
	15	103.7	44.1			7.7	4.0	
	20	147.6	64.1			9.7	5.0	
India, (Oxisol?)*	5	19.8	31.0				17.0	5
	10	50.9	78.0				14.0	
	15	96.8	116.0				26.0	

Table 2. Continued.

Site	Age (y) Ref.	Aboveground Mass	Aboveground P	Belowground Mass	Belowground P	Litterfall Mass	Litterfall P	
Moderately fertile soils (Cont'd)								
India,	1	6.3	7.8			1.1	0.6	6
(Oxisol?)*	2	10.1	13.4			3.3	2.1	
	4	20.1	25.1			5.7	4.7	
	8	50.0	26.7			6.7	5.6	
	12	83.7	46.3			7.3	6.0	
Infertile soils								
Ivory	1.2	8.8	4.6					7
Coast,	2.2	14.1	6.9					
ferralitic	4.0	21.6	10.5					
	6.5	38.4	14.4					
	15.0	77.6	20.2					
Sarawak, Ultisol	12-15	32.1	6.2	6.3	4.0	4.0		8
Venezuela Oxisol	5	40.0	8.4	8.4	2.7	8.2	1.6	9
Venezuela	3	0.8	0.4	(bulldozer cleared)				10
Spodosol	3	12.9	15.7	(cut)				
	3	8.7	17.4	(cut and burned)				
Peru,	3	39.7	18.2		0.6			11
Ultisol*	10	75.0	22.7		5.5			
	25-30	204.0	54.5		15.9			

* Soil classification in doubt based on soil properties.
References: 1 = Bartholomew et al., 1953; 2 = Folster et al., 1976; 3 = Golley et al., 1975; 4 = Toky and Ramakrishnan, 1983; 5 = Rao and Ramakrishnan, 1989; 6 = Swamy and Ramakrishnan, 1987a, b; 7 = Jaffe, 1985; 8 = Andriesse and Schelhaas, 1987; 9 = Uhl and Jordan, 1984; 10 = Uhl et al., 1982; 11 = Scott, 1977.

P transformations in soil. Transformations among various inorganic and organic forms of soil P, differing in availability to plants and soil microorganisms, occur during succession. Although progressively

greater amounts of P are accumulated in vegetation during secondary succession, various studies have noted that available forms of P in soil decrease during the first 4-8 years but increase thereafter (Zinke et al., 1978; Aweto, 1981; Ramakrishnan and Toky, 1981; Szott and Palm, unpublished). These changes in available P are usually associated with similar patterns in soil C, suggesting that soil organic matter plays an important role in buffering available P. The time required for levels of available P to reach levels measured at abandonment vary, perhaps due to differences in soil mineralogy, the quantity and quality of litter added to the soil, and in factors affecting P mineralization/immobilization processes. The importance of these factors deserves further research.

In shifting agriculture fallows, the fallow rotation period, and the number of previous crop cycles, appear to affect the status of available soil P (Table 3). Although there was little difference in organic C in soil among different lengths of fallows, levels of available soil P were much higher with increasing length of the fallow rotation. Presumably, more frequent harvests and greater removal of P in the products harvested in systems with short fallow rotations deplete more rapidly available inorganic P pools and other soil P fractions which buffer this pool. Further work is needed to define the interactions between organic and inorganic soil P pools and their relationship with fallow period.

Table 3. Organic carbon and available phosphorus contents of soil (0-40 cm) prior to clearing. The fields differed in length of the fallow cycle.

Fallow cycle	Organic C	Available P
y	Mg ha^{-1}	kg ha^{-1}
5	8.2	8.3
10	11.7	18.7
30	10.0	24.9

(calculated from Ramakrishnan and Toky, 1981).

Conclusions

The majority of work related to phosphorus cycling in humid tropical successional forest has concentrated on quantifying stocks in aboveground biomass and determining changes of available phosphorus in soil. In order to achieve an understanding of phosphorus cycles, however, much more research having a different focus is needed. Major gaps in knowledge include the dynamic relationships between different inorganic and organic phosphorus pools in soil, controls on organic phosphorus mineralization/immobilization processes, and how these relationships change in response to different types of disturbances. Advances in such research will depend on the development and refinement of appropriate methods.

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