

**A Cautionary Note about the Applicability of the CENTURY Soil-Organic-Matter Model
to Ecosystems on Highly-Weathered Tropical Soils**

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ABSTRACT

The CENTURY soil-organic-matter model and its phosphorus submodel have successfully described C and P transformations in many temperate soils. When this model is to be applied to highly weathered, P-deficient soils where P rather than N is the growth-limiting element, an accurate representation of the organic- and inorganic-P pools and transfer kinetics appropriate to such soils is crucial. We here examine which of the - largely empirical - relationships between CENTURY's conceptual P pools and the transformations of C and P in soils will have to be reformulated to make the model successful on P-limited weathered soils of the tropics.

Partitioning of incoming litter into slowly and rapidly cycling P, which is based on C:P ratios (≈ 500), will have to consider the different limits and much wider ranges (300-3000) observed in nutrient-poor tropical soils. Similar arguments apply to the use of N:lignin and C:N ratios. Rapid turnover of all organic matter fractions (mean residence time as low as 3-5y), recently reported for several tropical soils, will require the revision of "slow" and "fast" pools in such a partitioning.

A central problem in the usefulness and validation of a model is the congruence between nutrient fractions measurable in the soil and conceptual pools (state variables) representing such fractions in the model. Recent work on P in the tropics indicates that the parametrization of the model may need to be based on different P fractions than the original temperate version. State

variables thus will change.

Transformations of P, i.e. transfers between state variables, in CENTURY are based on empirical relationships, largely obtained on the North American Great Plains and verified on a number of temperate soils, rather than on mechanistic mathematical models of such P transformations as sorption, desorption, diffusion or enzyme kinetics. Extending the model to soils with very different reactivity to P and with different organic matter turnover characteristics requires the reformulation of the original empirical relationships or the use of mechanistic components to supply the transfer functions between different state variables.

CENTURY's implicit assumption that organic P and organic C are stabilized and mineralized together in a kinetically identical manner may not hold true in severely P-limited soils. Phosphorus fractionation data from contrasting systems in a long-term experiment on a Colombian Oxisol support the concept of independent P mineralization, which would need to be built into the model. It is concluded that great care should be exercised in using the CENTURY model for tropical low-P soils. Recommendations for improvement of the P submodel are given.

ORGANIC MATTER TURNOVER AND SOIL FERTILITY

Agricultural land use on organic-matter-rich soils generally leads to a reduction in soil organic matter (SOM) content and changes in its quality. During the process of mineralization, essential plant nutrients are lost, primarily N (leached) and P (sorbed or leached). The levels and rates of that nutrient loss have determined agricultural productivity on the North American Great Plains and other grassland areas. In these soils, 50 to 90 y of cultivation have resulted in decreases in organic nutrient availability that are sufficient to make fertilization necessary for

acceptable crop production.

Experimentation on the nutrient-furnishing ability of these soils, together with organic matter turnover studies, have been synthesized into computer simulation models such as the CENTURY model (Parton *et al.*, 1987). The model consists of various pools of organic matter with different residence times, receiving litter and organic transformation products as inputs and giving outputs from mineralization in the form of nutrients (N, P and S) available to plants or lost from the system.

The CENTURY model was originally developed for the natural grasslands of the North American Great Plains (Parton *et al.*, 1987, 1988), but it has recently been revised and extended (Metherell *et al.*, 1993b; Parton *et al.*, in press), and now offers options to include a number of agronomic practices, such as crop rotation, tillage, fertilization and irrigation, for use on a wide range of agricultural systems. The model has been used to simulate SOM dynamics in temperate grasslands in New Zealand (Metherell *et al.*, 1993a) and in the grassland biome worldwide (Parton *et al.*, 1993), in long-term wheat and pasture rotations in the south-Australian drylands (Carter *et al.*, 1993), and in studies on the effect of organic matter or fertilizer additions in Sweden (Paustian *et al.*, 1992). It has also been used to study plant litter decomposition under controlled conditions (Seastedt *et al.*, 1992) or across an environmental (altitude) gradient in Hawaii (Vitousek *et al.*, 1994). In combining CENTURY with geographic information systems and climate data, it has been possible to accurately predict levels of soil organic matter across the Great Plains on soils of different texture and under different management (Cole *et al.*, 1989; Parton *et al.*, 1989). That kind of predictability is required for the evaluation of sustainable farming systems which ideally should maintain organic matter levels at a steady state.

On tropical soils, increased population pressures and a quest for increased production have reduced or eliminated shifting cultivation regimes which relied on natural mechanisms of fertility regeneration. More sedentary agricultural practices have been introduced which frequently have reduced soil organic matter and fertility levels severely. The understanding of nutrient transformation processes in such soils would be aided if a model such as CENTURY could be applied to relate organic matter and fertility levels to soil types, and to actual and future management. However, with the exception of parts of the study by Parton *et al.* (1993), CENTURY has only been applied to decomposition processes under conditions of the temperate zone. Investigations concerning the applicability of CENTURY to tropical ecosystems are only just beginning (Parton *et al.*, 1994; Woomer, 1993).

Research on the organic matter depletion and nutrient turnover of tropical soils has shown much greater rates of mineralization than were observed in temperate zones. While the soils of the Great Plains in North America showed a loss of about 50% of their C content over some 80 y of cultivation, similar losses were observed in semiarid tropical soils after only 6 to 10 y of cultivation, and in some extremely humid rain-forest soils after 1 to 3 y (Tiessen *et al.* 1994a). The organic matter in the soils of the Great Plains has an average radiocarbon age of some 700 to 800 y, and some fractions have considerably shorter mean residence times near 100 to 300 years (Paul and Martell, 19..). A collection of radiocarbon dates for soils across different climatic zones (Trumbore, 1993) showed much lower average radiocarbon ages for tropical soil organic matter, and Tiessen *et al.* (1994a) reported very low average radiocarbon ages well below 100 y under both cultivated and native conditions in tropical soils. After a loss of 30% of the native soil C, the residual organic matter showed no evidence of greater radiocarbon age indicating that

there was no measurable residual pool of long residence time in a soil from northeastern Brazil.

This suggests that a model for tropical soils requires pools of organic matter of very short residence time with little long-term stabilization.

Heavy leaching regimes during the growing season, common in many tropical regions including the semiarids, may remove inorganic soil nutrient reserves (esp. nitrogen) very quickly, so nutrient supply by mineralization becomes critical for the plants. Strongly-leached highly-weathered tropical soils are generally deficient in phosphorus (P) (Sanchez and Logan, 1992) and the small amounts of inorganic P (P_i) present are strongly stabilized by iron- and aluminum-containing minerals. Only a small fraction of the total P_i is available to plants. The P_i released by mineralization of organic P (P_o) may also become sorbed by the mineral soil. Mineralization rates, therefore, must be matched closely by plant uptake or there is a strong chance that sorption will remove P from the short-term-available P pool.

Given these very different conditions compared to the temperate zone, is it possible to adapt a successful temperate SOM model such as CENTURY to tropical conditions and what might be the required adaptations? Adapting the model requires a detailed knowledge about the size and transformations of the various organic and inorganic nutrient pools, and the flows between them. In particular, understanding P dynamics is crucial for modelling nutrient cycling in many tropical soils. However, most information on P is obtained from soils of the temperate zone which are not as strongly P sorbing. Recently the amount of detailed tropical data has increased (Salcedo *et al.*, 1991, Tiessen *et al.*, 1992, 1994b; Beck and Sanchez, 1994; Oberson *et al.*, in prep.). Attempts to apply CENTURY to the highly-weathered Oxisols of the Colombian Llanos have met with limited success (Gijssman, *unpublished*), as the model proved very sensitive

to small changes in input parameters, and calculated equilibrium SOM levels were not realistic. We here explore the potential reasons for this limited success, and examine how CENTURY or similar models might be adapted to the conditions of highly-weathered tropical soils.

THE P CYCLE AND PLANT-AVAILABLE P

Both P_i and P_o cycle among soil, plants, microorganisms and animals (Figure 1, adapted from Tiessen *et al.*, 1994c). Plants apparently take up P exclusively in inorganic form from the soil solution (Barber, 1984; Morel and Plenchette, 1994), where the concentration of P_i is usually less than 1 mg l^{-1} . Even in soils with ample P supply, this satisfies the demand of the plants during periods of intensive growth for only a few hours. In tropical soils, solution concentrations are even lower ($<0.05 \text{ mg l}^{-1}$), often near the detection limit. The depleted solution therefore has to be replenished constantly from labile and moderately labile P_i and P_o . Both P_i present in the soil solution and easily-exchangeable P_i can therefore be considered as plant available.

Defining P availability by a separation of soil P_i into extractable and non-extractable (unavailable) P is a simplification (Fardeau and Frossard, 1992), but the wide range of interactions between soils and extractants has made it until now impossible to find a universally applicable method for defining available P (Fardeau *et al.*, 1988). The interpretation of data from chemical extracts is based on calibration against field experiments. However, since the utilization of soil P_i by the plant strongly varies with factors such as root length and distribution (Van Noordwijk and De Willigen, 1979), presence or absence of mycorrhiza (Sieverding, 1991; Morel and Plenchette, 1994), rhizosphere effects (Armstrong and Helyar, 1992; Jungk *et al.*, 1993), and spatial and temporal distribution of water in the soil (Marschner, 1986; Fardeau *et al.*, 1991),

information from such a correlative approach can only be applied to the crops and soil types included in the calibration. Moreover, soil P tests have been less successful when applied to highly-weathered tropical soils (Tiessen *et al.*, 1994c).

Solution P_i can also be replenished by the mineralization of P_o . This requires the presence of phosphatase enzymes, which are produced by soil microorganisms, plant roots and also earthworms (Herbien and Neal, 1990). The biological and biochemical reactions responsible for the mineralization of P_o are well understood *in vitro* and in experiments involving controlled microcosms (Helal and Sauerbeck, 1984; Tarafdar and Jungk, 1987; Tarafdar and Claassen, 1988). However, for soils, where P_o undergoes a multitude of stabilizing reactions, no direct measurements on mechanisms, rates and extent of P_o mineralization exist. Instead, data are obtained by interpreting net changes in soil- P_o content e.g. upon cultivation (Hedley *et al.*, 1982a; Tiessen *et al.*, 1983; Sharpley, 1985). Moreover, even the measurement of total- P_o content is indirect (Tiessen *et al.*, 1994c).

In the temperate zone the contribution of P_o mineralization to plant-available P_i is considered of minor importance within a single growing season (Fardeau, 1993). However, the need to look at P cycling (including P_o) rather than available- P_i pool size has been recognized for perennial plants and natural ecosystems (Tiessen and Moir, 1993). Under tropical conditions, P_o was shown to contribute significantly to crop P uptake (Adepetu and Corey, 1976; Agboola and Oko, 1976), and several studies indicate that P_o might play a major role in the short-term P fertility of tropical soils (Tiessen *et al.*, 1992; Ball-Coelho *et al.*, 1993).

ASSESSMENT OF P_i AND P_o BY SEQUENTIAL EXTRACTION

Hedley *et al.* (1982a) developed a sequential extraction method for temperate soils, which, to some extent, permits the determination of the type of chemical P bonds and/or the nature of P compounds in a soil. Tiessen and Moir (1994) adapted the method, omitting the microbial-P and sonication steps and introducing a further extractant to fractionate P left in the final soil residue. Its present version (Figure 2) aims at quantifying the labile (plant-available) as well as the more stable forms of P_i and P_o using the following extractants: H_2O with resin, $0.5M NaHCO_3$, $0.1M NaOH$, $1M HCl$ and hot concentrated HCl . The forms of P associated with each fraction are thought to be the following:

- (i) Labile forms of P_i adsorbed on surfaces of crystalline P compounds, sesquioxides or carbonates (Mattingly, 1975) are extracted with resin and bicarbonate. This P_i is assumed to be easily available for plant uptake (Cooperband and Logan, 1994; Fardeau *et al.*, 1988).
- (ii) Organic P extracted with bicarbonate has been shown to be easily mineralizable (Bowman and Cole, 1978) and, therefore, is likely to contribute also to short-term plant-available P.
- (iii) $NaOH$ -extractable P_i has lower plant availability (Barekzai and Mengel, 1985) and represents Fe- and Al-associated P (Williams *et al.*, 1980).
- (iv) The organic forms of phosphorus extracted with $NaOH$ are rather stable and are considered to be involved in long-term transformations of P in soils (Batsula and Krivonosova, 1973), but in tropical soils also undergo seasonal transformations (Ball-Coelho *et al.*, 1993).
- (v) Dilute HCl extracts mainly Ca-bound P_i , which includes most primary-mineral P (Williams *et al.*, 1971). In natural non-calcareous or highly-weathered soils which have not received phosphate rock or lime applications, its amount may be very small, so that this

step could be omitted.

- (vi) The original fractionation scheme left between 20 and 60% of soil's P unextracted. This residue often contained significant amounts of P_o which may participate in short term transformations (Tiessen, 1991; Oberson *et al.*, 1994). Therefore a hot HCl step (Mehta *et al.*, 1954) was introduced which extracts an important part of the residual P.

This rather empirical sequential extraction method is currently the only approach that can be used with moderate success for the evaluation of available P_i as well as P_o , although the nature of different extractable P_o pools is even less well defined than that of the P_i pools (Tiessen *et al.*, 1994c). Organic P turnover and availability often depends on the mineralization of C during which P is released as a by-product, although soluble P_o is also rapidly mineralized by soil enzymes. Due to the reactivity of P_i with the soil mineral phase, determination of a potentially mineralizable P_o pool, analogous to the mineralizable N or S pools measured by incubation and leaching techniques (Ellert and Bettany 1988), is not feasible.

THE STRUCTURE OF THE P SUBMODEL OF CENTURY

The P submodel of CENTURY (Figure 3) consists of a P_o and an P_i section (respectively, the left and right parts of the figure), the two being linked when P_i enters the organic cycle via P uptake by roots or microbes, or adsorption onto organic matter.

The P_o section has the same basic structure as the carbon section of the SOM submodel. Plant and animal residues are partitioned between metabolic and structural pools; the former contains easily-decomposable material such as sugars and proteins, the latter more resistant

material such as lignified cellulose. This split between metabolic and structural material is calculated as a linear function of the lignin:nitrogen ratio, independent of the residue's P content. The structural material is defined as having a fixed C:P ratio (generally 500, but this can be modified), leaving the remaining residue P to be partitioned into the metabolic pool. Actual decomposition starts only after this partitioning when the organic matter flows into the aboveground or belowground microbial pools (respectively, surface microbes and active SOM), the slow SOM pool and, finally, the passive SOM pool. The amounts of P_o present in the various organic pools and the P_o flows between them are linked to the carbon pools and flows via C:P ratios. As nutrient contents of organic pools are confined by minimum and maximum allowable carbon:nutrient ratios (*i.e.* C:N, and, optionally, C:P and C:S), the availability of organic and inorganic nutrients controls the size of organic C as well as organic nutrient pools and flows. Nutrient flows between organic pools are thus not calculated by simply dividing the carbon flow by the carbon:nutrient ratio of the receiving pool, but carbon and nutrient flows are mutually dependent.

The section on inorganic P includes pools of, respectively, labile, sorbed, strongly-sorbed (or secondary), occluded and parent P_i . The labile- P_i pool represents the P_i in the soil solution plus the easily-exchangeable P_i which is in direct and immediate equilibrium with it. The labile- P_i pool is in equilibrium with a pool of less-easily-exchangeable P_i (sorbed- P_i), which in turn is in equilibrium with an even more-strongly-sorbed P_i pool (secondary P_i). Part of this latter pool can become totally unavailable (at least within a non-geological time frame), thus entering the occluded- P_i pool. Phosphorus can enter the P cycle by weathering of parent-material P, mostly apatites, and by fertilization. After any addition to or removal of P_i from the soil solution the

equilibrium between the labile- and the sorbed- P_i pools is recalculated, the relationship being based on sorption affinity and sorption maximum parameters.

LIMITATIONS TO THE APPLICATION OF THE P SUBMODEL

P_i pools vs. P_i fractions:

The P_i section of the CENTURY model includes five P_i pools: labile, sorbed, strongly-sorbed, occluded and parent P_i , which must be estimated to parameterize the model. It would be ideal if one could simply assign different P_i fractions from a sequential fractionation to the different P_i pools. However, a "functional pool" should be "homogenous" with all phosphate ions showing similar kinetics of transport and transformation (Fardeau, 1993). The extractability of a P_i fraction has little relation to the P_i kinetics in the soil, and P_i present in a certain extract usually represents a cross section of several different P_i pools (Fardeau *et al.*, 1988) with different transfer kinetics and plant availability.

As it is thus not possible to directly relate pools to fractions, indirect approaches have been followed in which phosphorus pool sizes were estimated from empirical relationships between P fractions and P transformations as seen in field observations or experimentation. The P status of a soil can then be characterized relative to a conceptual model of P pools and their transformations (Figure 2), as was done by Stewart and Tiessen (1987) and Stewart and Sharpley (1987). For the dominant soil types of the temperate zone, sufficient data exist on P fractionation in relation to P availability to allow such estimates of P_i pool sizes. These data include P transformations under incubation (Hedley *et al.*, 1982a), near plant roots (Hedley *et al.*, 1982b), with cultivation (Tiessen *et al.*, 1983) or during soil development (Tiessen *et al.*, 1984; Roberts *et al.*, 1989). For

the highly-weathered low-P soils commonly found in the tropics such a database is only beginning to develop (Tiessen *et al.*, 1992; Ball-Coelho *et al.*, 1993; Beck and Sanchez, 1994; Oberson *et al.*, in prep.) and the correlation of conceptual P_i pools and analytical fractions remains tenuous. Improving the congruity between measurable fractions and functional pools is consequently a central task in the improvement of the CENTURY model and its application to tropical low-P soils.

Presently, the P_i -pools of CENTURY reflect a compromise between the needs of the model and the fractionation data available for the North-American prairie soils for which the model was developed. In the original formulation of the P submodel (Parton *et al.*, 1988), labile P_i was defined as orthophosphate which is either isotopically exchangeable or resin extractable. In the user manual of the most recent model version (Metherell *et al.*, 1993b), labile P_i has been defined as resin-extractable P_i although elsewhere one of the authors uses bicarbonate-extractable P_i to quantify this pool (Metherell, 1992). A study by Fardeau *et al.* (1988) with ^{32}P -labelled phosphate supports this definition, showing that from 50% to 100% of the P extracted with 0.5 M NaHCO_3 may be plant available.

While it may also be acceptable to equate the resin P_i fraction with the labile P_i pool (Sen Tran *et al.*, 1992), it is not clear which fractions should be equated with the sorbed, strongly-sorbed and occluded P_i pools. Metherell (1992) further suggested equating (i) the sorbed- P_i pool with the NaOH-extractable P_i fraction; (ii) the occluded P_i with the difference between total P_i and 1 N H_2SO_4 -extractable P; (iii) the parent P_i with HCl-extractable P according to Condron and Goh (1989); and (iv) the unextractable residue of the above fractionation with the strongly-sorbed P_i . However, sorbed P_i ([i] above), which is considered plant available, is also extracted

with NaHCO_3 . Furthermore, in a Typic Cryoboralf, NaOH-extractable P_i (Metherell's sorbed P_i) was found to be related to a P_i pool with slow isotopic exchange characteristics (Morel *et al.*, 1994), thus corresponding to strongly-sorbed P_i . The poor definition of these pools and fractions indicates that bicarbonate- P_i and NaOH-extractable P_i cannot be considered separate pools, particularly in acid soils, but instead represent a continuum of Fe- and Al-associated P extractable with solutions of increasing alkalinity (Tiessen and Moir, 1993). Thus, for some soils, bicarbonate-extractable P_i may be an estimate of sorbed- P_i while for others (esp. acid tropical low-P soils), the sum of NaHCO_3 - and NaOH-extractable P_i may be more appropriate.

For the strongly-sorbed and occluded- P_i pools, similar problems exist (see Figure 2). Thus, the difference between total and 1 N H_2SO_4 -extractable P (Metherell's occluded P_i [ii]) will overlap with several sequential fractions including the NaOH-extractable P_i fraction which, depending on soil type, may include both sorbed- and strongly-sorbed P_i (see above). Although cold acid P_i in the sequential extraction (Metherell's [iii] above) probably corresponds quite closely to primary Ca-associated P (and thus, parent P_i in most soils), the assignment (in [iv] above) of strongly sorbed P to a fraction which is resistant to all previously applied chemical attack seems unreasonable; one would rather perceive this fraction as occluded P. In summary, much of the exercise of assignment of fractions to pools remains highly conjectural and requires a substantially improved database before it can be done with confidence.

Flows between P_i pools:

In the CENTURY model, the flows between the P_i pools are formulated as first-order reactions of the type:

*Flow = rate constant * pool size * abiotic reduction factor.*

[1]

Defining the P_i pools already poses considerable problems, but estimating the rate constants for the transfers between these pools is even more difficult (Metherell, 1992). This difficulty is due to the numerous competing reactions, inorganic and organic, which occur both concurrently and consecutively in soil systems. Some of these reactions have been studied in isolation in model systems and have been described by various kinetic equations (Olsen and Khasawneh, 1980; Barrow, 1983). The chemical reactions at the liquid-solid interface are usually measured in stirred laboratory systems and provide an understanding of surface reactions only, because the reaction kinetics of phosphate with soil inorganic phases *in situ* are generally controlled by diffusion and transport (Aharoni and Sparks, 1991). Since diffusion processes follow pseudo-first-order kinetics, the CENTURY flow formulation may adequately represent the reaction rates.

Reactions in which P moves from the solid phase or from organic pools to dissolved inorganic P may follow different kinetics. Phosphate release from soils and phosphate rock dissolution, for example, were described by an Elovich-type equation (Chien and Clayton, 1980; Chien *et al.*, 1980). Enzyme mediated dephosphorylation is likely to follow higher-order kinetics. Besides these limitations, the greatest difficulty remains in estimating kinetic parameters of individual processes in the complex environment of the soil. Use of ^{32}P and ^{33}P tracers may provide useful information when coupled with time series fractionation studies.

Parameter-optimization methods can be used in systems such as these which can be described by multireaction rate functions, if sufficient data are available (Amacher, 1991). However, due to the short half-life of both P radionuclides, these studies are still limited largely to the more

rapidly cycling pools in soil, virtually excluding studies on long-term "sustainability" which are a central purpose of the use of this type of model.

The abiotic reduction factor (range: 0-1) in equation [1] consists of a temperature- and a moisture-related component, and is the same factor used as multiplier on the organic-matter decomposition rate. However, the effect of temperature and moisture on the rates of physico-chemical processes driving phosphate-ion transfer between inorganic pools is very different from the effect on biological and biochemical processes which involve the decomposition or transformation of organic P compounds or the assimilation of inorganic P into organic pools. In Barrow's (1983) studies the Arrhenius equation explained the temperature dependence of the slow reactions of P_i with soils. Rates of biological/biochemical processes governed by microorganisms, on the other hand, often double for each 10°C rise in temperature. However, there exists no verification that similar rules apply for such processes in soil systems. Rates of P_i uptake by plants may be expected to exhibit a Michaelis-Menten dependence modified by moisture and temperature, although factors controlling supply of P to the root surface (diffusion, water flow, P solution concentration, etc.) may be more important in controlling uptake than influx kinetics (Barber and Silberbush, 1984).

A final point concerning the flows between P pools is that the P_i section of the P submodel has a linear structure, implying that P_i has to go through a whole sequence of P_i pools (labile - sorbed - strongly sorbed - occluded) to reach one of the more strongly-sorbed pools. In contrast, Fardeau (1993) proposed a conceptual P model, based on the kinetics of ^{32}P transformations, in which all the P_i pools branch off from one central plant-available P_i pool ("modèle mamellaire"). Reality lies somewhere between these two concepts, as suggested in the P cycle described by

Stewart and Sharpley (1987). Thus, while P_i may flow directly between soil solution and several P_i pools, it may also move directly (in either direction) between more and less labile pools, and to stable and essentially inert pools.

Sorption equation:

The equilibrium relationship between labile P_i and sorbed P_i is described in the model in terms of an equation involving coefficients for sorption affinity (*sorpdf*) and sorption maximum (*sorpmx*). Thus, according to the model's source code (version 4.0) the amount of labile P_i is calculated as:

$$c = 0.5 \cdot \text{sorpmx} \cdot (2.0 - \text{sorpdf}) \quad [2]$$

$$b = \text{sorpmx} - (\text{labile } P_i + \text{sorbed } P_i) \cdot c \quad [3]$$

$$\text{labile } P_i = 0.5 \cdot \left(-b + \sqrt{b^2 + 4 \cdot c \cdot (\text{labile } P_i + \text{sorbed } P_i)} \right) \quad [4]$$

This formulation is entirely empirical and bears no relationship with standard equations for ion adsorption such as those of Langmuir or Freundlich (Olsen and Khasawneh, 1980). There is no clear way to apply this relationship to highly-weathered tropical soils where sorption is more important, rapid and less reversible. A theoretical sorption equation such as the Freundlich equation (Barrow, 1983) may have to be incorporated into the model.

Fraction of labile P_i available to the plant:

In the CENTURY model, the fraction of labile P_i that is available for plant uptake has been formulated as a linear function of the mineral N pool size (higher P_i availability at higher mineral-N levels), delimited by a minimum and a maximum available fraction (Metherell *et al.*, 1993b). Since P_i is far less mobile in the soil than inorganic N (nitrate), only a fraction of the plant-available P present in the soil is actually within reach of plant roots, and this fraction is not related to mineral N supply. Calculation of the P uptake potential of the plant is complicated as it is affected by factors such as soil water content, root architecture, soil P sorption capacity, plant P demand, etc. (Van Noordwijk and De Willigen, 1979). The formulation as used in CENTURY ignores this complexity and replaces it by a simple linear dependence on the amount of mineral N. Although such a relationship may reflect increased biological activity of the system, and thus an increasing potential for P uptake, at higher N levels, it is unlikely to be a useful concept in highly weathered soils that have rapid mineral N turnover and strong reactivity competing for plant available P.

Residue partitioning between structural and metabolic pools

The partitioning of plant and animal residues between the metabolic and structural residue pools is formulated in the model as a linear function of the lignin:nitrogen ratio (L:N). This relationship is based on data from a large number of plant residue analyses, separating cellulose and lignin as structural components from water-soluble metabolic components (Parton *et al.*, in press). Recently, this equation was modified so as to also be applicable to residues with very high L:N ratio's, as often found in the tropics (Parton, pers. comm.):

$$\text{Fraction of residues going into metabolic pool} = 0.85 - 0.012 * L:N \quad [5]$$

As Parton *et al.* (in press) have indicated, individual residue types may be partitioned very differently from this general pattern.

According to Fisher *et al.* (1992), plants from the infertile South-American savanna soils have developed nutrient-conserving strategies by rapidly lignifying. With the very low N content of the plant material (esp. grass roots) this leads to L:N ratios up to 65 (Gijsman, unpublished; Thomas, unpublished). In leguminous plants from the same soil, on the contrary, L:N ratios as low as 3 are found. In the model, residue partitioning according to equation [5] is very different for these litter types and, consequently, simulated decomposition rates also. In reality, however, the correlation between L:N ratios and decomposition rates is rather poor for the above-mentioned litter types (Gijsman, unpublished), suggesting that equation [5] may not be adequate for these residues.

In the conceptual model of litter degradation presented by Sinsabaugh *et al.* (1993), the production of lignocellulase by microbes is directly linked to the availability of both N and P. If either of these is in short supply, microbes will expend more metabolic energy in acquiring these nutrients and less in the production of lignin- and cellulose-degrading enzymes. In the CENTURY model, the actual litter decomposition only starts *after* the split into structural and metabolic fractions, and this decomposition is controlled by both N and P. There is, however, a need to also make the initial partitioning in structural and metabolic fractions a function of other factors than the L:N ratio (possibly the litter's P concentration). This holds in particular for systems where N is not the most limiting element, such as natural savanna vegetation on tropical

low-P Oxisols and Ultisols.

Nutrient contents of structural and metabolic pools

When partitioning residues between the metabolic and structural pools, the latter is assigned a fixed C:P ratio of 500, leaving the remaining residue P for the metabolic pool. However, in analyzing freshly deposited leaf litter from 4 grass and 6 legume species on an Oxisol in the Colombian savannas, Thomas and Asakawa (1993) found whole-litter C:P ratios between *ca.* 400 and 2700. Fresh rice leaves from the same location just before harvest had C:P ratios from 380 to 550 (Sanz, unpublished). Fresh *Setaria sphacelata* leaves from a Malaysian Ultisol at three levels of P fertility had C:P ratios from 77 to 704 (Umrit and Friesen, 1994). For roots, ratios ranged from 1000 to 2500 for grasses and legumes (Gijsman, unpublished; Rao, unpublished) and from 800 to 1350 for rice (Sanz, unpublished). Consequently, assigning a C:P ratio of 500 to the structural material would result in negative P concentrations in the metabolic fraction of these plant residues.

Similar problems exist for nitrogen. The C:N ratios in above-ground litter (Thomas and Asakawa, 1993) generally are well below the value of 150 assigned in the model to the structural material, although César (1992) reported values up to *ca.* 200 for standing-dead grass in west-African savannas. In grass roots from the Colombian savanna, C:N ratios of 250 were found (Gijsman, unpublished; Rao, unpublished). Applying the approach used in the model, some of these values would also lead to negative N concentrations in the metabolic fraction.

In principle, the option exists in the model to modify the C:P or C:N ratios of the structural material. However, in order to cover the most extreme values reported above, a C:P ratio of

around 3000 would be needed. Limited work done on P modeling in Hawaii and Puerto Rico suggests that the C:P ratio of structural material should be between 3000 and 4000 (Parton, pers. comm.). No experimental data are available to assess how realistic such a value is and how it varies among species, soil conditions, seasons, etc.. Increasing such an important input parameter six-fold requires a more systematic approach based on studies of nutrient distribution among plant fractions in various ecosystems.

The combined effect of an incorrect partitioning of residues between structural and metabolic material and the use of too low a C:P ratio for the structural material results in the vast majority of the residue P (and also most residue C) entering the structural residue pools from where it flows mainly into the slow-organic-matter pool. The cycling of residue P as predicted by CENTURY will thus be rather slow. This is in conflict with data on the rapid turnover of C and associated nutrients in tropical soils (Tiessen *et al.*, 1994a). Results from sequential P fractionations, combined with microbial-P analyses, and evaluation of the long-term P-balance of improved pastures on an Oxisol in the Colombian savannas also suggest that P_o entering the soil from plant residues and animal excreta cycles readily through those systems (Oberson *et al.*, in prep.).

Structure of the organic-P submodel

The pools and flow structure of the organic-matter submodels of CENTURY are the same for organic C, N and P, the three being linked via C:N and C:P ratios. Such a structure implies that organic C, N and P are stabilized and mineralized in the same way, the size of the flows relative to each other depending only on the nutrient content of the decomposing material and the

potential immobilization of inorganic nutrients. While in many ecosystems the concomitant turnover of C, N and P is driven by biological transformations of litter and soil organic matter, McGill and Cole (1981) hypothesized that organic C and N are stabilized together and mineralized through biological processes, whereas P_o may also be stabilized independently of the main organic moiety and mineralized through biochemical processes. Data on P fractionation (Oberson *et al.*, in prep.) and microbial biomass (Gijssman *et al.*, submitted) from Oxisols in Colombia (Table 1) suggest that biochemical processes might be important, but do not rule out the concomitant occurrence of biological processes where the C:P ratio would be important.

The organic matter collected in the water fraction after resin extraction as first step in the sequential P fractionation is likely to be easily decomposable and thus should form part of the active SOM pool. The same may hold for the organic matter in the NaHCO₃ fraction. For the Colombian Oxisol of Table 1, these two fractions together contain *ca.* 2280 µg C and 15 µg P per g soil. Parton *et al.* (1992, 1993) suggested that the active SOM pool equals about two to three times the amount of microbial biomass, so as to also account for microbial metabolites. Using the microbial biomass data of Table 1, this would imply an active SOM pool of 940-1410 µg C and 19-29 µg P per g soil. The two estimation methods for the active SOM pool thus yield different results, especially concerning the C:P ratios of the material (137-358 based on the sequential P fractionation, and 50 according to the microbial biomass estimate). The quantities of C and P estimated on the basis of microbial biomass and of the easily-extractable organic matter from the sequential fractionation can therefore not be considered as one pool with a common turnover rate. A C:P ratio between 30 and 80 is suggested for the active SOM in the model. While the microbial C:P ratio falls within this range, it is far too low for the H₂O- or

NaHCO₃-extractable fractions. It may thus be too restrictive to estimate available P_o pools and calculate P_o flows in the same way as organic-C and -N flows. On the other hand, neither fraction (extractable or microbially-derived) may be an appropriate measure of available P_o when nutrient availability is determined not by solubility but C turnover. Litter turnover during hot and wet tropical growing seasons is very rapid (Thomas and Asakawa, 1993) and the effect of soil fauna in making P available may be significant (Lopez-Hernandez *et al.*, 1993; Guggenberger *et al.*, 1995).

Apart from this concern about the P_o-submodel structure, it is not clear what the C:P ratios used for the organic pools in the model are based on. For each pool, a minimum and maximum ratio is defined between which the C:P ratio of the material entering that pool can fluctuate as a function of availability of the labile P_i. For the choice of these ratios, Parton *et al.* (1988) refer to Tiessen *et al.* (1982; 1983), from which C:P_o ratios can be calculated on specific extracts and particle size fractions of cultivated and grassland soils. Whether this is appropriate depends on the congruence of the measured fractions with the conceptual pools of the model, i.e. it is doubtful.

CONCLUSIONS AND RECOMMENDATIONS

In soils from the temperate zone, N is generally the plant-growth-limiting element, whereas many highly-weathered tropical soils are strongly P limited. For modeling SOM dynamics and plant production this implies that accurate representation of the P_i and P_o pools and transfer kinetics is crucial. The structure of the P_o section of CENTURY is based on the hypothesis that organic P and organic C are stabilized and mineralized together, and that the

consequent P availability is determined by the C:P ratios of different pools. While successful on many temperate soils, this hypothesis is questionable in view of the wide range of C:P ratios encountered in organic materials of P limited soils, and the of potential importance of biochemical P mineralization in low-P soils. The basic structure of the model's inorganic-P section is largely in agreement with experimental data, but the various equations are empirical. This makes extrapolation of the model to soils, substantially different from those on which it was developed, difficult.

We conclude, therefore, that the CENTURY model can not easily be transposed to tropical low-P soils, and that attempts to do so (Parton *et al.*, 1994; Woomer, 1993; ASB, 1994), should be carefully justified. Parton *et al.* (1989, 1994) presented a list of research imperatives for improving our ability to simulate SOM dynamics in the tropics. Some of these points have been considered in the most recent model version (Metherell *et al.*, 1993b). In addition, we recommend the following with respect to the P submodel:

1. A data base is needed which improves the congruence between measurable P fractions and theoretical P pools, both organic and inorganic. Besides chemical P fractionation, isotopic-dilution kinetics may be used to obtain information on the intensity, quantity and buffer-capacity factors of available P_i (Fardeau and Jappe, 1976; Fardeau, 1993). Biological parameters related to P dynamics, such as microbial biomass P turnover or phosphatase activity, may be useful in such a data base.
2. Pools are linked by transfer rates whose present model values were estimated using data

from temperate zones. There is a need to determine transfer rates for a range of soil types, both temperate and tropical, to assess whether the use of universal values is appropriate.

As the present values were partly approximated through an empirical trial-and-error approach (Metherell, 1992), their estimations could be improved using P tracer studies.

With appropriate design, and in combination with C tracers, such studies may at the same time give information about organic-P turnover rates.

3. In low-P soils, the hypothesis of McGill and Cole (1981) that P is stabilized and mineralized independently of C and N may be important and require changes in the basic structure of the P submodel. Incubation and field studies assessing C, N and P mineralization in the same samples are needed to test this hypothesis.
4. The extreme flexibility of C:P ratios in plants and microbes of P-limited highly-weathered soils requires a re-examination of C:P ratios for organic matter partitioning. More data on this subject are needed.
5. In strongly-P-sorbing tropical soils, the P_o concentration in the soil solution may be several times higher than the P_i concentration (Oberson *et al.*, in prep.) and movement of P_o in the soil (leaching) may be substantial, particularly under high-rainfall conditions. Although a leaching option exists in the model, very few experimental data are available to quantify the importance of such a P_o flow. We suggest to include the measurement of dissolved- P_o flows in leaching and runoff studies.

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Table 1: Nutrient content of various fractions from a sequential P-fractionation and of microbial biomass in an Oxisol under native savanna (Gijssman *et al.*, submitted; Oberson *et al.*, in prep.)

Soil fraction	P_i^{\S}	P_o^{\S}	C	$C/P_o^{\S\dagger}$	$C/P_i^{\S\dagger}$	C/N^{\dagger}
	===== $\mu\text{g g}^{-1}$ =====					
Water/resin	2.1	1.5	510	358	*	10.5
NaHCO ₃	1.5	13.2	1770	137	*	9.9
NaOH	13.9	53.6	6080	111	*	13.4
HCl	0.7	*	*	*	*	*
HCl-hot	68.0	16.7	2670	219	*	7.4
Residue	45.9		8800	*	191	36.5
Whole soil	86.2	85.0	19830	237	91	17.1
Microbes	9.6		470	*	50	9.3

P_i , P_o and P_t = inorganic, organic and total phosphorus

The ratio averages were calculated as geometric means of treatments, so values may differ from those calculated by dividing the individual-element means.

Figure 1. A conceptual model of the P cycle in an ecosystem (after Stewart and Sharpley, 1987 and Tiessen *et al.*, 1994a).

Figure 2. The P fractions obtained during a sequential P fractionation and an approximation of how to link P fractions to P pools.

Figure 3. The structure of the P submodel of CENTURY (after Metherell *et al.*, 1993b).

