

Factors controlling humification and mineralization of soil organic matter in the tropics

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Abstract

The first part of this review focuses on the chemical composition and morphological features that characterize primary and secondary organic resources for humification. The chemical pathways of decomposition and humification of SOM in tropical soils are discussed referring mainly to the chemical structural changes identified by using both solid-state ¹³C nuclear magnetic resonance spectroscopy (¹³C NMR) of bulk soil samples and liquid-state ¹³C NMR of chemically isolated SOM fractions. The stabilization effects and mechanisms exerted on SOM by clay minerals and sesquioxides in tropical soils are also reviewed. Successively, relevant aspects of organic matter mobilization and dissolved organic matter dynamics in temperate versus tropical ecosystems are examined. In the second part of the review, general and specific aspects of mineralization processes in relation to the chemistry of main SOM pools (labile versus stable SOM components) in the tropics are discussed. Amounts, distribution, and forms of nutrients in SOM, nutrient release from organic versus inorganic sources, nutrient cycling in natural and cultivated soils, and the contribution of SOM to cationic nutrition in tropical soils are reviewed. The final part of the review focuses on the main chemical factors that control CO₂ evolution and denitrification processes during SOM mineralization in tropical areas. © 1997 Elsevier Science B.V.

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1. Introduction

Soil organic matter (SOM) represents a major pool (1600×10^{15} g C) of the terrestrial carbon reserves (about 2200×10^{15} g). It exceeds drastically the amount of carbon stored in the living vegetation (about 600×10^{15} g C) which fixes about 120×10^{15} g C per year by photosynthesis (Bouwman, 1990). About half of the fixed carbon arrives at the pedosphere, mainly as litter and root residues, and only 0.7% of the annual terrestrial net primary production is transformed into refractory humic substances (Schlesinger, 1990). In mature undisturbed soils, a balance exists between carbon input (above- and below-ground plant residues) and output due to mineralization and leaching of dissolved organic matter (DOM). But this balance is not in a steady state. During the Quaternary, for instance, climatic fluctuations have influenced the SOM levels seriously. In the higher latitudes, glacial erosion and solifluction destroyed the SOM pools. The humic horizons also disappeared in many tropical regions due to intensive sheet erosion as documented by stone lines (Zech and Mühle, 1989). Since the Neolithic period, human activities (deforestation, burning, livestock rearing, and soil cultivation) started to disturb the SOM balance. These disturbances had only local effects at the beginning. For many centuries, the subtropical and temperate zones of the Northern Hemisphere were mainly concerned, whereas the large areas under tropical rain forests remained more or less unaffected. During the last decades of this century, however, tropical environments have become increasingly disturbed by forest destruction for grazing, cropping, and industrial purposes.

In strongly weathered soils of the tropics, SOM plays a major role in soil productivity because it represents the dominant reservoir and source of plant nutrients (e.g. N, P, S); it also influences pH, cation exchange capacity (CEC), anion exchange capacity (AEC), and soil structure. The profound benefits of SOM to soil fertility and its significance in global warming phenomena forces us to intensify research activities on SOM dynamics of tropical soils. In the following presentation, we focus on factors which control humification and mineralization in tropical ecosystems.

2. Soil organic matter pools and soil organic matter dynamics

In this paper, the term SOM is used in a broad sense, including the above- and belowground macromorphologically identifiable plant residues (primary resources), residues of soil animals and microorganisms (secondary resources), dissolved organic matter (DOM), root exudates, and morphologically unstructured, macromolecular humic compounds. These pools are not stable but characterized by transformations because SOM is in a dynamic state.

Decomposition is closely related to humification, mineralization, DOM dynamics, and SOM stabilization. During the first phase of decomposition, rapid

mineralization of labile components is the dominant process. In the second phase of decomposition, mineralization still occurs but is slowed down due to the accumulation of refractory molecules (Fig. 1).

In addition to climatic and physical factors, chemical factors like pH, C/N ratio, and resource quality (e.g. lignin and polyphenol contents), control the

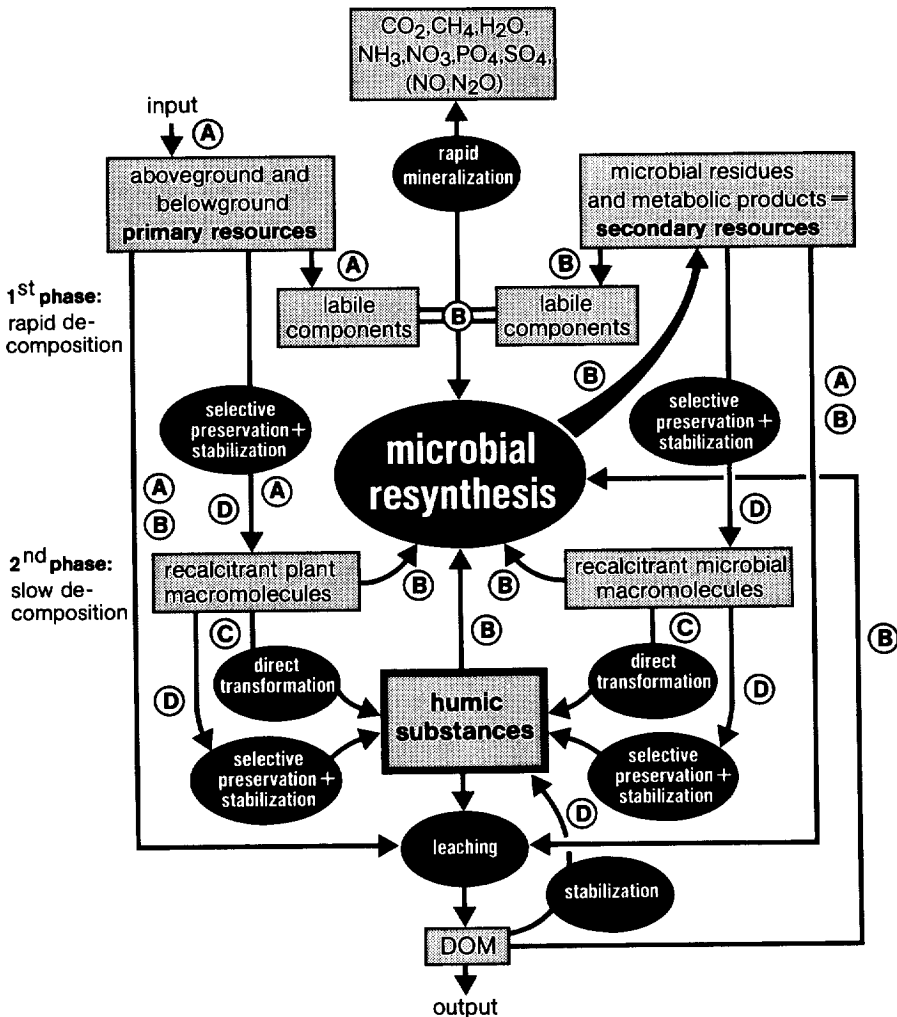


Fig. 1. SOM pools and SOM dynamics with special reference to litter decomposition and humification (including microbial resynthesis, selective preservation, and direct transformation), mineralization, leaching of dissolved organic matter (DOM), and stabilization by interactions with inorganic compounds. These processes are controlled by different factors: (A) control of the quality and quantity of the primary resources; (B) control of the microbial activities; (C) possible catalytic effects on direct transformation; and (D) control by stabilization with inorganic compounds.

SOM dynamics. As one approach, the influence of these controlling factors on total SOM can be identified and quantified by relating the soil carbon stocks with selected parameters. For the Liberian rain forests, for instance, W. Zech (unpubl. data) found positive correlations between C stocks and total soil phosphorus stocks (P_t) ($R = 0.434^*$), effective cation exchange capacity ($R = 0.776^{***}$) and clay stocks ($R = 0.613^{***}$). On a basis of 26 experimental plots, multiple correlation analyses identified only clay stocks and total soil P stocks to significantly control C stocks according to the following equation:

$$\text{C stocks} = 1140.4 + 16.92 \text{ clay stocks} + 3.28 P_t \text{ stocks} \\ (R^2 = 0.380^{**}; \text{stocks in } 10^6 \text{ g ha}^{-1} \text{ in 1 m soil depth})$$

In semiarid Africa (Senegal, $n = 18$), simple correlation analysis identified close relationships between soil C stocks and N reserves ($R = 0.929^{***}$), P reserves ($R = 0.625^{***}$), fine earth fraction ($R = 0.505^*$), potential CEC ($R = 0.797^{***}$), and again clay stocks ($R = 0.786^{***}$). Eliminating intercorrelations by multiple regression analysis, it could be shown that only clay stocks significantly control soil carbon stocks:

$$\text{C stocks} = 15.86 + 0.0167 \text{ clay stocks} \\ (R^2 = 0.620^{***}; \text{C and clay in } 10^6 \text{ g ha}^{-1} \text{ in 1 m soil depth})$$

Including data from 30 experimental plots in arid Somalia (< 250 mm mean annual precipitation) into the statistical evaluation on the controlling factors for soil carbon reserves in humid, semiarid, and arid Africa, pH of the A horizons was also significantly correlated with C stocks. The negative correlation coefficient $R = -0.710^{***}$ is due to more acidic soils in humid Liberia which show higher C stocks than soils in semiarid to arid Africa. Multiple regression analyses found the following factors to be correlated significantly with soil carbon stocks:

$$\text{C stocks} = 11857.2 + 10.31 \text{ clay stocks} + 29.68 \text{ mean annual precipitation} + 137.59 \text{ altitude} \\ (n = 74, R^2 = 0.670^{***}, \text{stocks in } 10^6 \text{ g ha}^{-1} \text{ in 1 m soil depth})$$

Similar studies have been previously carried out by Jenny (1941) for other soils and locations.

The objective of this paper is to focus on processes which contribute significantly to SOM dynamics and thus to the terrestrial carbon cycle including:

- humification, defined as the transformation of macromorphologically identifiable resources into amorphous humic compounds;
- SOM stabilization by interactions with inorganic compounds;
- DOM production and translocation; and
- mineralization, defined as the transformation of organically bound elements (C, N, S, P) into inorganic compounds (CO_2 , CH_4 , NH_4^+ , NO_3^- , SO_4^{2-} , HPO_4^{2-}).

3. Humification: an important process in the terrestrial carbon cycle

3.1. Chemical composition of the starting materials of humification: primary and secondary resources

Besides temperature and water regime, the amount and chemical composition of the primary and secondary resources control SOM dynamics and, especially, humification (Swift et al., 1979). In some ecosystems, belowground inputs from fine root turnover may be higher than aboveground inputs from litterfall (Raich and Nadelhoffer, 1989). The root residue input is estimated to be 20–50% of the total C input in temperate forest soils (Vogt et al., 1986). The belowground inputs of tropical soils may be of great importance for maintaining the SOM level because litter, in general, is rapidly mineralized to CO₂, whereas the root residues, which are in close contact with the mineral soil, have more chances to be stabilized by clay particles or sesquioxides (Oades, 1988). In addition to leaf and root residues, woody debris contribute 24–39% to the total organic matter input in forest ecosystems (Harmon et al., 1986).

CPMAS ¹³C NMR analysis shows that there is considerable variability in the overall chemical composition of the various plant tissues of tropical forest trees (Fig. 2). Carboxyl carbon accounts for about 5–10% of total carbon, with bark showing the weakest signal. The aromatic carbon contents are low and vary between 10 and 15%. Leaf litter contains less O-alkyl carbon (about 50%) than do wood, bark, or roots (about 75%). Correspondingly, the contribution of alkyl C is higher in the leaf litter (20–25%).

About 50–65% of the total carbon signal intensity of the NMR spectra of the primary resources can be identified by wet-chemical methods. For example, about 50% of the alkyl carbon is accounted for by extractable lipids (Ziegler and Zech, 1989), and about 60–75% of the O-alkyl carbon is accounted for by hydrolysable polysaccharides (cellulose and hemicellulose; Kögel-Knabner, 1993). Lignin and tannins contribute to the aromatic signal intensity. The alkyl carbon unaccounted for by extractable lipids is attributed to the polyesters cutin and suberin as well as to highly aliphatic biomacromolecules recently discovered in plant cuticles (Tegelaar et al., 1989; Kögel-Knabner et al., 1992). Some of the litter constituents, such as polysaccharides and proteins, are easily decomposable, but lignin, polyphenols, and some aliphatic biomacromolecules are relatively resistant to microbial breakdown.

As mentioned above, soil microbes and soil animals contribute to the secondary resources, but are of less quantitative importance (Swift et al., 1979). According to Kassim et al. (1981) the microbial standing biomass contributes 1–4% of the soil organic carbon, and the total edaphon about 10%.

The chemical composition of the secondary resources is even more complex than that of the primary resources. Rogers et al. (1980), for instance, found that the fungal cell walls contain chitin, chitosan, cellulose, and different non-crystal-

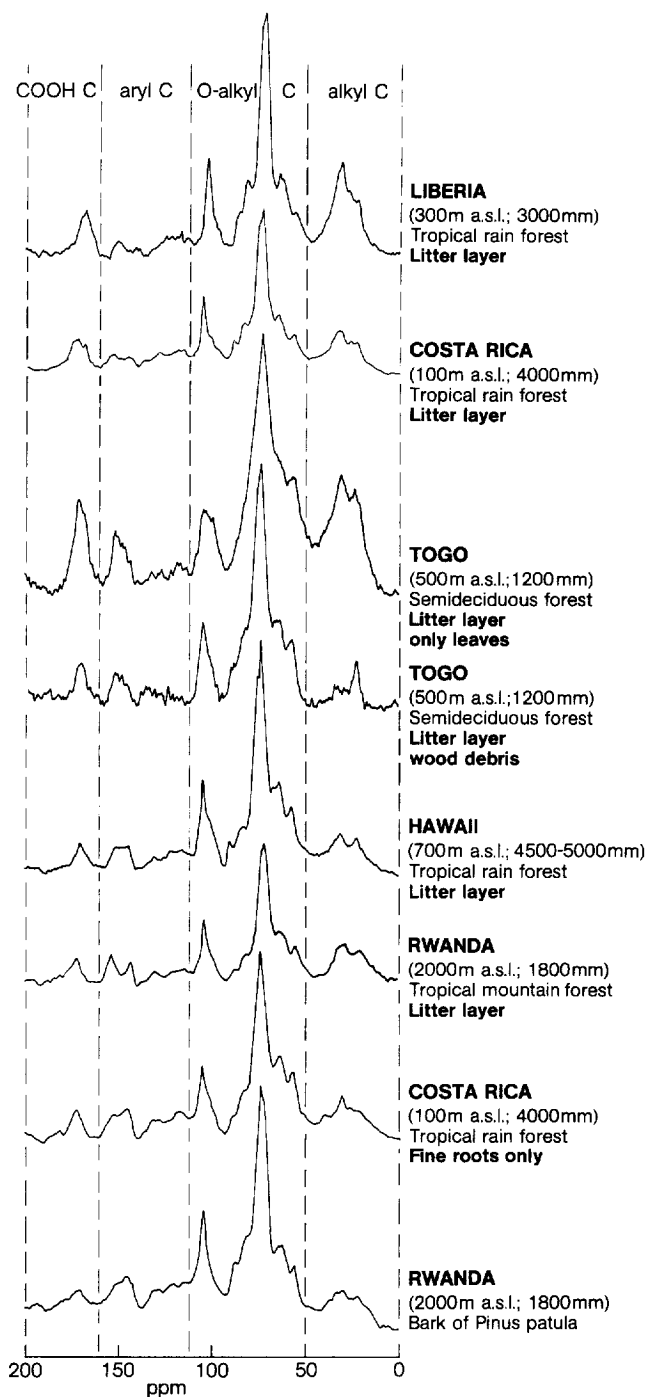


Fig. 2. Carbon distribution of some primary resources of tropical forests according to CPMAS ^{13}C NMR spectroscopy.

line polysaccharides. Lipids, lipopolysaccharides, peptidoglycan, and non-crystalline polysaccharides were found in bacterial cell walls. Results of Zeliber et al. (1988) and Tegelaar et al. (1989) indicate that microbial residues also contain stable alkyl macromolecules. Despite the increase of knowledge on the chemical composition of the primary and secondary resources, much more information is required. Quantitative data for tropical soils are almost completely lacking.

3.2. Morphological features characterizing decomposition and humification of the organic starting materials

During litter decomposition and humification, the primary and secondary resources are altered by leaching, comminution, and catabolism (Swift et al., 1979). Catabolism and leaching are heavily accelerated by litter fragmentation by soil animals like earthworms (Gunnarsson et al., 1988; Lavelle and Martin, 1992; Lavelle et al., 1992). In undisturbed soils, various stages of decomposition and humification can be detected, from the fresh litter material (L horizon) and the fermentation layer (Of horizon) to the completely humified horizons (Oh, Ah). In biologically active soils with high earthworm population, the mull humus type develops in L–Ah horizons only. Sometimes the soil surface is completely covered by worm casts. Such morphological features may be accom-

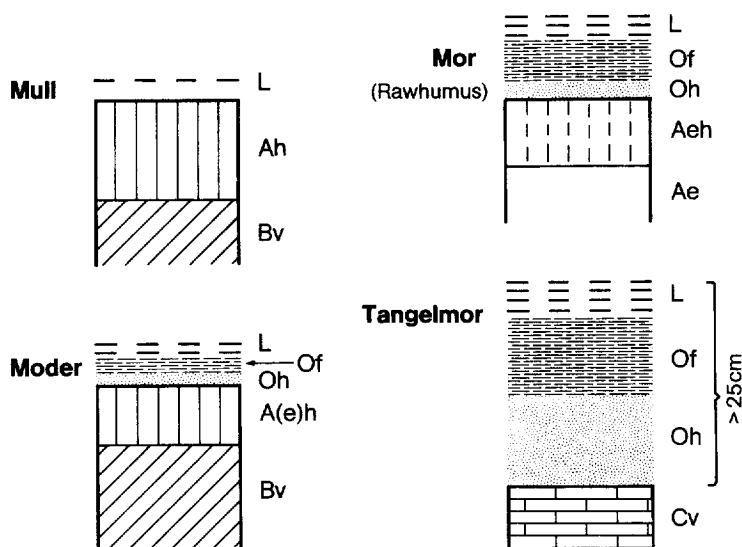


Fig. 3. Morphological features of the main forest humus types typical for rapid (mull), intermediate (moder), and delayed (mor, tangelmor) turnover of the organic starting materials (L, litter; Of, fermentation layer; Oh, completely humified surface layer; Ae, albic horizon; A(e)h and Aeh, transitions between Ae and Ah; Bv, cambic horizon; Cv, weathered parent material).

panied by pronounced chemical changes. Earthworm casts produced in an Oxisol under tropical pasture were richer in primary resources (lignin, carbohydrates) than the adjacent soil (Guggenberger et al., 1995). If less bioturbation occurs, the mor humus type develops, with L–Of–Oh–Aeh horizons. The moder humus type is transitional between mull and mor (Fig. 3).

In the tropical humid lowlands, forest soils generally exhibit the mull humus type and transitions to moder due to the favourable conditions for litter decomposition. Soils in the subhumid and semiarid climates under deciduous forests (e.g. *Tectona grandis* plantations) are often covered by thick L horizons during the dry period. With the onset of the rainy season these litter layers are rapidly mineralized. In tropical mountains at the higher altitudes, thick organic layers can be observed above the mineral soil, indicating low turnover rates due to reduced temperatures and/or high permanent water saturation. Litter accumulation is also observed under some tree species like *Acacia mangium* and *Acacia auriculiformis*, and can play a significant role in soil protection in sloping areas. The strongly weathered, acid tropical forest soils are characterized by a very high root density (especially in the Of, Oh, and Ah horizons), which is necessary for the rapid uptake of nutrients released during litter decomposition. Thus, the morphological features of above- and belowground litter may provide useful information on the degree and intensity of decomposition and humification.

3.3. The chemical pathways of humification

Humification and decomposition can be studied in the laboratory, using incubations, or in the field, using litter-bag experiments. A third, less frequently practiced approach to humification studies is based on the investigation of the chemical structural changes with soil depth in undisturbed soil profiles. Such profiles provide natural systems that allow to follow the long-term course of humification by following the changes in carbon-species distribution with depth, because the distinct horizons represent organic matter at progressive stages of humification. In this paper we focus on the results of soil profile studies (Zech et al., 1992, 1994) which entail the analysis of: (i) bulk soil samples; and (ii) physical or chemical fractions, like particle-size separates or humic acids.

3.3.1. Identification by chemical structural analyses of bulk soil samples

As described in Section 3.2, the different stages of litter decomposition and humification are morphologically well documented in the forest soil horizons from the L to the Ah layer. Using solid-state ^{13}C NMR spectroscopy, it is possible to identify different carbon types and their changes during decomposition and humification. For example, changes have been shown to occur to the carbon species distribution from the fresh litter (L horizon), via the fermentation

layer (Of) with about 50% of macromorphologically identifiable plant residues, to the completely humified Ah horizon of a Lithic Hapludoll below a moist evergreen to semideciduous rain forest in Liberia (Fig. 4). Dominant tree species were: *Scotelia coronicea*, *Drypetes chevalieri*, *Tetrapleura chevalieri*, *Stenyogetha macrophylla*, *Triplochiton scleroxylon*, *Nesogordonia papaverifera*, *Afroseralisia afzelii*.

During litter decomposition and humification, signal intensities due to carboxyl C (175 ppm) and alkyl C (around 30 ppm) increased (Fig. 4). There was also a slight increase in the aromatic carbon region (110–160 ppm), especially near 150 ppm (phenolic carbon), whereas in the O-alkyl region (50–110 ppm) signal intensities decreased (see signal near 105 ppm, characterizing the anomeric C of polysaccharides). A similar trend was found in the surface soil horizons of humid tropical rain forests in the lowlands of northern Costa Rica (Fig. 5). Compared with results from southern Germany (Zech and Kögel-Knabner,

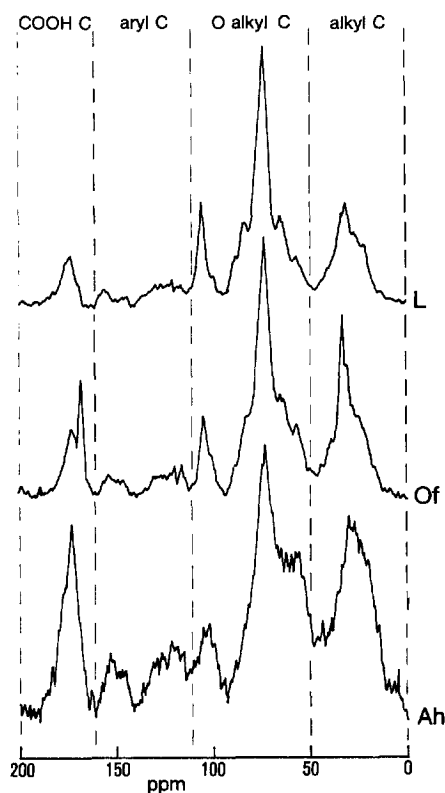


Fig. 4. Changes in carbon-species distribution according to CPMAS ^{13}C NMR spectroscopy of bulk samples during litter decomposition and humification in a moist, evergreen to semideciduous rain forest in Liberia (L, fresh litter; Of, fermentation layer; Ah, completely humified A horizon of a Lithic Hapludoll derived from metamorphic rocks).

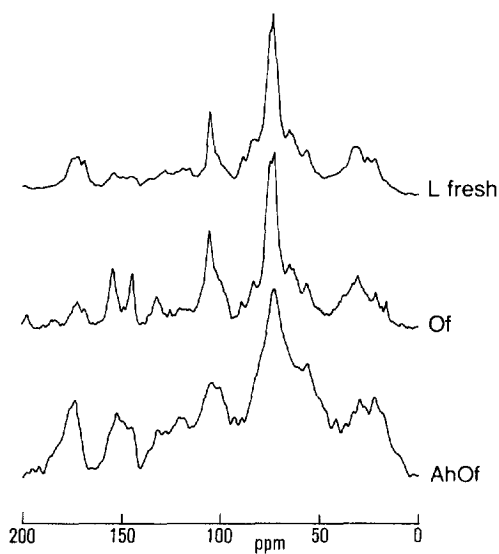


Fig. 5. CPMAS ^{13}C NMR spectra of bulk soil samples from the L, Of, and AhOf horizons below a perhumid tropical rain forest in the lowlands of northern Costa Rica.

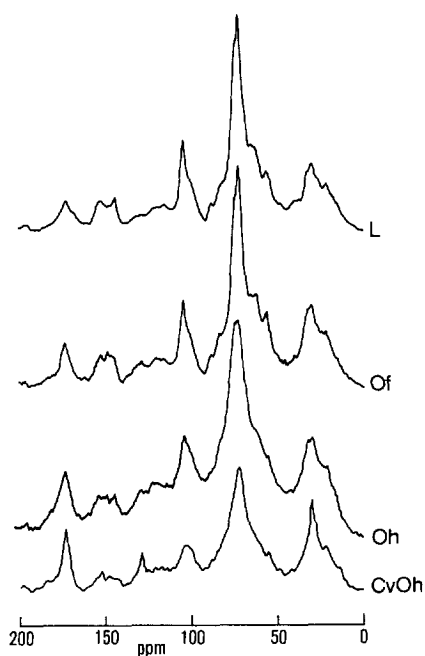


Fig. 6. Changes in carbon-species distribution during humification in a Histosol-like soil below a tropical rain forest (Hawaii, 1140 m a.s.l.) according to CPMAS ^{13}C NMR spectroscopy.

1994) and the Mediterranean zone (Miltner et al., 1996), a pronounced increase of signal intensities due to phenolic C (150 ppm) and methoxyl C (56 ppm) during humification was observed. In German and Mediterranean forest soils, as well as in the Histosol-like soils of Hawaii (Fig. 6), both signals generally decrease during humification.

Despite some uncertainties these findings can be explained in the following way:

(1) Decrease of O-alkyl carbon during humification from L to Ah may be mainly attributed to the preferential mineralization of polysaccharides. The polysaccharide C determined with wet chemistry (Table 1) decreased from 25% (L) to 8% (Ah) in the Liberian soil, whereas O-alkyl C decreased only from 57% to 42% (Fig. 4). Either fractions of O-alkyl C were not accessible to hydrolysis because of physico-chemical stabilization, or non-polysaccharide, yet not identified structures, contributed to the NMR signal. Further, the O-alkyl-C fraction not accounted for by wet chemistry appeared to increase during humification.

(2) The increase of alkyl-carbon contents (0–50 ppm) during humification (Figs. 4–6) can be explained by enrichment of extractable and bound lipids (Hempfling and Schulten, 1989; Ziegler and Zech, 1989) or plant-derived biopolyesters and non-saponifiable aliphatic biomacromolecules of plant and microbial origin (Tegelaar et al., 1989). Using dipolar dephasing ^{13}C NMR spectroscopy, Kögel-Knabner et al. (1992) were able to show that mobile alkyl components are degraded with soil depth, whereas the rigid ones appear to be selectively preserved, probably due to cross-linking of aliphatic polymers.

(3) Increase of the aromatic carbon (110–160 ppm) contents generally is not very pronounced. In temperate forests, aromaticity has even been shown to decrease during litter decomposition and humification (Zech et al., 1992). Figs. 4–6 indicate that in humus layers of tropical forests aryl-carbon contents are much lower than O-alkyl-carbon contents and usually lower than alkyl-carbon contents. There is some discrepancy between the behaviour of aryl C identified

Table 1

Characterization of the L, Of and Ah horizons of a Lithic Hapludoll (fine-loamy, mixed, isohyperthermic) below tropical rainforest in Liberia

	L	Of	Ah
pH (0.01 M CaCl_2)	6.4	5.7	4.6
C_{org} (g kg^{-1})	501	413	32
N (g kg^{-1})	14.7	16.2	2.2
C/N	34.1	25.5	14.4
CuO-lignin (V + S + C in g kg^{-1} C)	46.2	34.8	26.3
(ac/al) _v	0.21	0.29	0.83
Polysaccharide-C (g kg^{-1} C)	24.8	15.6	7.8

with NMR spectroscopy in the Liberian Hapludoll (Fig. 4) and the decrease of CuO-lignin from L to Ah (Table 1). Presumably, these findings indicate a relative enrichment of non-lignin aromatic structures with progressive decomposition and humification. Less is known about the nature of these non-lignin aromatic structures. In general, there is a concurrent increase of C-substituted aryl C (130 ppm) with decreasing O-aryl-C intensities (phenolics, 150 ppm) in temperate forest A horizons. According to Figs. 4–6, all three tropical soils show some increase of the signal intensities near 130 ppm during humification, but the O-aryl-C signals in the Ah horizons are more pronounced than in the L layer in the Liberian and the Costa Rican soils.

(4) Increase of carboxyl-C contents (175 ppm) may be partly related to the oxidative cleavage of lignin side-chains and of the aromatic ring itself during degradation. This is confirmed by the results of CuO oxidation, which indicate an increase of the acid-to-aldehyde ratio of the vanillyl units (ac/al)_v from L to Ah (Table 1). Additional processes like oxidation of polysaccharides and the

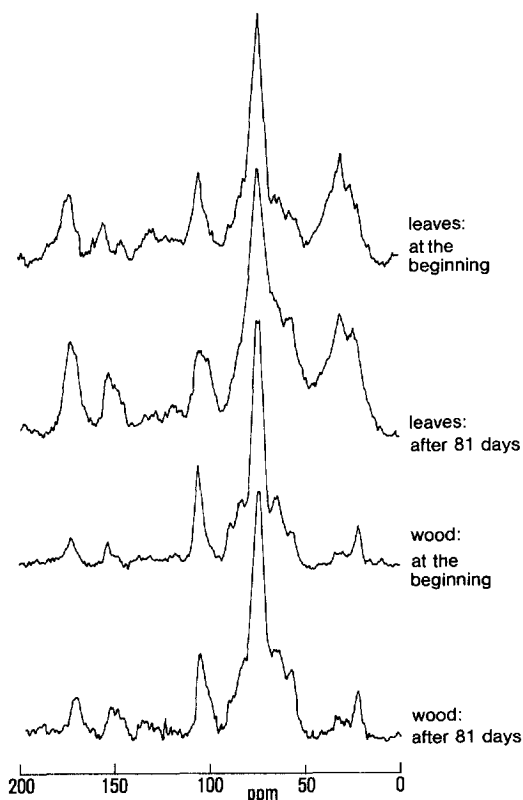


Fig. 7. CPMAS ^{13}C NMR spectra of *Cajanus cajan* leaves and wood at the beginning and after 81 days of a litter-bag experiment in Central Togo.

accumulation of fatty acids may contribute to the increase of carboxyl groups during humification.

The chemical pathways derived from soil profile studies are generally confirmed by the preliminary results obtained on the carbon-species distribution from litter-bag experiments (Fig. 7). After 81 days of incubation, both leaf and wood samples revealed higher signal intensities due to carboxyl C, phenolic C, methoxyl C and alkyl C, but lower ones due to O-alkyl C (W. Zech, unpubl. results). Again, the increase of the phenolic (150 ppm) and methoxyl C (56 ppm) signals seems to indicate the existence of some differences in comparison to initial stages of humification in temperate zones.

Other elements undergo significant transformations during humification besides carbon. For example, the transformation of phosphorus species from litter to mineral B horizon in a Dystric Cambisol of Rwanda is shown in Fig. 8. With soil depth, inorganic P (signal at 6.5–7.1 ppm) increased, and monoester and diester phosphates decreased (signals at 5.5 ppm and 0.3–1.0 ppm, respectively).

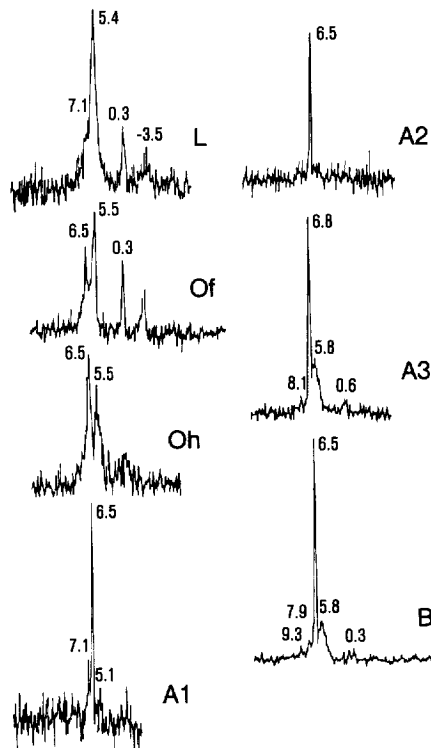


Fig. 8. ^{31}P NMR spectra of NaOH extracts from different soil horizons of a Dystric Cambisol in Crête Zaire Nil, Rwanda (L, litter; Of, fermentation layer; A1, A2, A3, humified mineral surface soil; B, mineral subsoil).

Organic free radical concentration and content of Al, Fe, S, and Mn increased and that of Mg decreased with depth when passing from the uppermost layer (Oi) to the lower layer (Oa) in a ponderosa pine litter collected in a mixed-conifer forest in lower Sierra Nevada, California, USA (Tam et al., 1991). Aqueous extracts of ponderosa pine litter showed increases in pH and decreases in organic C concentration, carboxyl groups, and free organic acids with depth, some of the changes being as large as an order of magnitude (Tam et al., 1991). Water extractability of elements such as Al, Mg, Ca, P, and Mn decreased with increasing depth, with a 20-fold decrease measured for Al (Tam et al., 1991). These differences together with variations observed in fluorescence spectra of the litter with depth, were interpreted as reflecting the gradual transformation of relatively labile litter materials into more stable, humified compounds.

3.3.2. Identification by chemical structural analyses of SOM fractions

Compared to the CPMAS ^{13}C NMR spectra of Figs. 4–6, the liquid-state ^{13}C NMR spectra of NaOH-soluble substances extracted from the horizons of a Dystric Cambisol in Rwanda show similar but better resolved signals (Fig. 9).

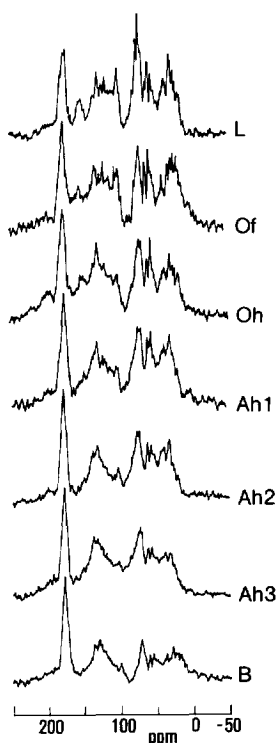


Fig. 9. Liquid ^{13}C NMR spectra of NaOH extracts from the humic horizons of a Dystric Cambisol in Rwanda.

With increasing humification from L to Ah1, the following alterations are detectable:

- weak increase of alkyl carbon;
- decrease of methoxyl C, O-alkyl C, and O-aryl C; and
- increase of C-substituted aryl C (130 ppm) and carboxyl C.

In the mineral soil profile, signals due to carboxyl C and C-substituted aryl C further increased from Ah1 to B, whereas signals induced by phenolic C, O-alkyl C, methoxyl C, and alkyl C decreased. These findings suggested that lignin structures are considerably modified during humification, mainly by demethylation, loss of phenolic moieties, side-chain oxidation, and increasing dominance of C-substituted recalcitrant aromatic structures with signals near 130 ppm. Using pyrolysis–field ionization–mass spectrometry, Hempfling and Schulten (1989) have shown that C–C linked lignin moieties are selectively preserved in forest soils of the temperate zones in comparison to the less resistant ether-linked structures.

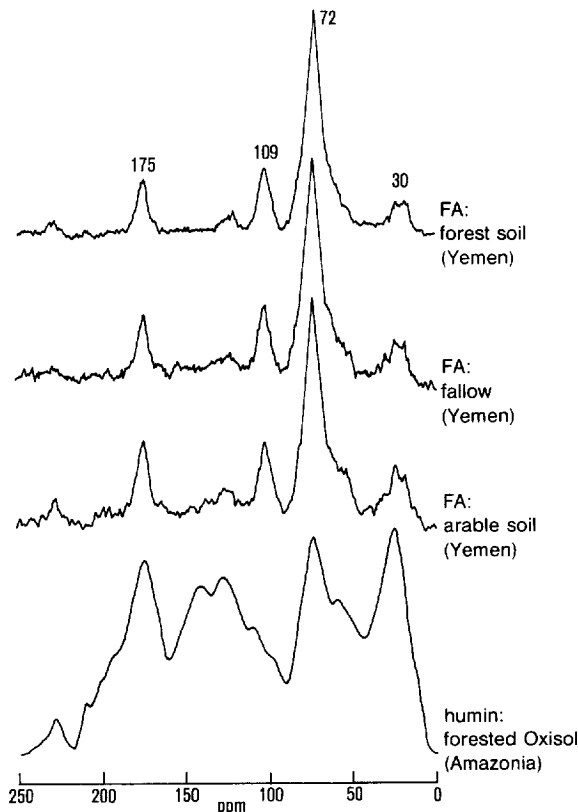


Fig. 10. CPMAS ^{13}C NMR spectra of fulvic acids (FA) extracted from the A horizons of highland soils under different landuse (Yemen) and of humin from a forested Oxisol (Amazonia).

Fractionation of German and Mediterranean surface soil horizons into humic acids (HAs), fulvic acids (FAs), and humins (Kögel-Knabner, 1992; Wiedemann, 1993) revealed that the major part of total C remains in the humin fraction (L = 63–72%, Ah = 27–46% of total C). With soil depth, the FA fraction did not change significantly (1–12% of total C) but the HA fraction increased from 24–29% (L) to 50–60% (Ah) of total C.

^{13}C NMR spectroscopy revealed that FA fractions are composed mainly of polysaccharides and contain only small amounts of alkyl C. Landuse practices did not significantly influence C species distribution of FAs extracted from A horizons of highland soils of Yemen (Fig. 10).

Humins generally contained high amounts of only slightly altered lignin and polysaccharides (Fig. 10). The composition of FA fractions and humins varied only slightly from L to Ah. For humins this is due to their marked content of plant residues in the O horizons and stabilized residues in the mineral horizons.

In contrast to FAs, NMR spectra of HAs showed typical lignin signals with resonances near 150, 130, 117, and 56 ppm, besides signals due to carboxyl and O-alkyl C (Fig. 11). HAs from the semiarid soils of the Yemen highlands were

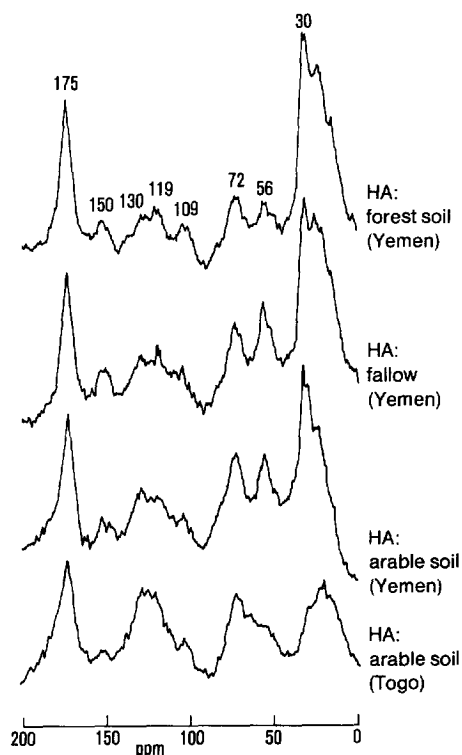


Fig. 11. CPMAS ^{13}C NMR spectra of HAs extracted from soils under different landuse in Yemen and Togo.

extremely rich in alkyl C, compared with the HAs extracted from the cropped Ultisol Ah horizon in Togo. These results indicated that carbon-species distribution of HAs can vary considerably according to differences in site conditions. This was not the case for FAs. Thus, HAs probably are more sensitive to environmental changes than FAs or bulk soils (Zech et al., 1990). With increasing humification from the L to the Ah horizon, HA structures change in a way similar to that described above for the NaOH extracts.

According to these results, it can be concluded that the study of NaOH extracts and HA fractions provides additional information about humification in comparison to the analysis of bulk soil samples and FAs. ^{13}C NMR spectra of NaOH extracts and of HAs revealed that phenolic substances and methoxyl groups are depleted in these fractions due to increasing humification. Concurrently, there was an increase in carboxyl groups and non-lignin aromatic structures with C-substituted aryl-C moieties. The comparison with results from temperate and subtropical environments indicated that the chemical pathways during humification are similar, but turnover rates differ due to the variation of controlling factors like temperature, water regime, and chemical parameters.

3.4. Chemical factors controlling humification

Humification, as well as litter decomposition, are primarily microbially mediated processes, mainly controlled by site-specific variables like temperature, soil water regime, pH, and available nutrients. Besides these external variables, internal ones like resource quality are of importance. They control the composition of the decomposer community, and their activity and distribution in the soil (Swift et al., 1979). The external factors help to explain differences in the turnover rates of a given SOM pool at different sites, whereas the resource quality should, in addition, be responsible for differences occurring at the same site (Swift, 1987; Palm and Sanchez, 1990; Camire et al., 1991). In this section emphasis is given to chemical control, which can be studied under field conditions or in the laboratory with similar methodological approaches as the chemical pathways discussed in the previous section.

Only a few field-related soil profile studies tackle the influence of chemical parameters on humification. To find out to what extent aromaticity of SOM is controlled by site factors, Zech et al. (1989) studied eight soil profiles from temperate, subtropical, and tropical regions. Correlating chemical SOM characteristics (e.g. aromaticity) of bulk samples with site factors, they found that temperature and the temperature/precipitation ratio are primarily influencing the aromaticity of bulk soil samples. Chemical factors like pH and C/N ratio were of minor relevance. In soil horizons with high pH values and low C/N ratios, aromaticity tended to be somewhat higher, probably due to increasing turnover rates. These studies (Zech et al., 1989, 1992) showed that advanced stages of humification are characterized by higher aromatic carbon contents,

although aromaticity remains nearly constant during initial stages. Since about 73% of the variation of aromaticity could be explained by the variation of the temperature/precipitation ratio and a smaller percentage by the variation of pH and the C/N ratio (Zech et al., 1989), it was suggested that the chemical control of humification under field conditions may be relatively less important. Studying the HAs of five Kenyan soils, Arshad and Schnitzer (1989) also found a positive relationship between the temperature/precipitation ratio and aromaticity. But no influence of chemical factors on HA chemistry could be identified either in subhumid Kenya or in the subtropical Mediterranean zone where Miltner and Zech (1994) studied bulk soil samples and density fractions, and Wiedemann (1993) the HAs.

The chemical composition of the primary resources control decomposition and humification, not by altering the overall chemical pathways, but by changing the turnover rates. Resources rich in phenols, waxes, and lignins are known to decompose more slowly and to contribute markedly to the recalcitrant SOM pool, in comparison to proteins and sugars (Swift et al., 1979). Residues if young plants are more rapidly decomposed than older ones, the latter often containing more stable cell-wall compounds. Different parts of plants also differ in the decomposition rate, e.g. root xylem, epidermis, and leaf veins are rich in lignin and thus decompose more slowly.

Such effects of decomposition can be studied by litter-bag experiments (Wieder and Lang, 1982), but, up to now, these experiments have been mainly carried out to study decomposition, mineralization, and nutrient release. The use of litter-bag experiments for identifying factors controlling humification are scarce.

3.5. SOM stabilization by interaction with minerals

Organic matter stabilization by minerals may play a much more important role in tropical soils than in temperate soils (Nayak et al., 1990). As many tropical soils are dominated by variable-charge minerals with low cation exchange capacity (CEC), organic matter is very important for the nutrient status of the soils because it lowers the point of zero charge (PZC) and increases the CEC. Since the climatic conditions of the tropics favour decomposition of organic matter, especially after forest clearing, tropical soils would be very poor in organic matter without this stabilization process. First we refer to the stabilization of SOM on clay minerals.

3.5.1. Influence of clay minerals

Organic molecules can be adsorbed by clay minerals. The adsorption to (generally) negatively charged minerals mainly takes place via cation exchange for positively charged organic compounds, hydrophobic bonding (neutral molecules) to already existing organic coatings of the minerals, and polyvalent cation bridges (organic anions) (Mortland, 1986). Soils with a high PZC may be

positively charged at ambient conditions and therefore can directly adsorb organic anions via anion exchange. The functional groups of the organic matter interacting with the minerals are mainly carboxyl groups.

The adsorbed organic matter is protected against microbial degradation. The protecting effect depends on the kind of mineral the organic matter is sorbed to. Smectites are very effective protectors, whereas the effect of kaolinite is rather weak (Martin and Haider, 1986). This agrees with the view of Duchaufour (1977) who stated that the protective effect of clay minerals is related to their swelling properties.

Only few results refer to the stabilization of SOM in kaolinitic soils. One example is reported from the Amazonia basin, where soils similar to Mollisols occur with low C-mineralization rates. ^{13}C NMR spectroscopy revealed that the organic matter of this so-called 'Terra preta do indio' is extremely rich in aryl carbon. Up to now little is known about possible interactions with the inorganic phase (Zech et al., 1990).

Theng et al. (1986) showed that organic matter can enter the interlayers of clay minerals. The structure of this organic matter is of polymethylene chain character, and it is stabilized against thermal and chemical oxidation. Thus, the effect is at least partly a physical one. SOM can also be enclosed in micropores that cannot be entered by microorganisms. Extracellular enzymes are sorbed by the clays and therefore are not able to reach their substrates in the micropores (Nguyen Kha, 1982). For this reason, clay minerals with high porosities and high proportions of fine pores such as allophane or imogolite are very effective stabilizers. Allophanic soils generally are rich in organic matter, and the decomposition rates, determined as CO_2 losses, are lower than in non-allophanic soils. The mechanism of this stabilization may be partly due to phosphate limitation, but also to the adsorption of organic compounds. All kinds of easily decomposable compounds are stabilized. The greatest stabilization occurs with polysaccharides and proteins (Martin and Haider, 1986). The lower decomposition rates in allophanic soils were also demonstrated by Boudot et al. (1986). However, Zech et al. (1994) reported that Andosol SOM is highly aromatic but poor in O-alkyl carbon species. Since highly aromatic SOM is more stable than polysaccharide-rich organic matter, advanced humification, resulting in high aromaticity and probably catalyzed by allophanic compounds, may additionally contribute to the high stability of SOM in Andosols.

The protective effect of clay minerals depends on the amount of the organic compound sorbed to the mineral. McKeague et al. (1986) and Martin and Haider (1986) showed that with higher protein/clay ratio there is a weaker protein protection against biodegradation. The authors suggested that there is a stronger adsorption of the first layer of protein, which led to a better protection. The second layer was held more loosely and therefore was less protected than the first one.

Part of the stabilization may be due to the influence of clays on the microbial

activity. Clays change the microenvironment of microorganisms. They have influence on pH, ionic strength, and substrate availability as well as on enzyme production and activity. In the early stages of decomposition, clays generally increase the microbial number and activity. The oxygen consumption is increased, whereas CO_2 loss is lowered. Microorganisms are able to convert substrate C more efficiently to biomass and synthesize more humic acid-like polymers in the presence of clays (Martin and Haider, 1986).

3.5.2. *Influence of sesquioxides*

Sesquioxides play an important role in the SOM dynamics of many tropical soils, such as Andosols, Oxisols, and Ultisols, because of their abundance in these soils.

The main mechanisms for the adsorption of organic matter to Fe and Al oxides are electrostatic attraction, hydrogen bonds, and ligand exchange reactions (Oades et al., 1989). As is the case for the clay minerals, the carboxyl groups of the organic matter control adsorption (Oades et al., 1989). The organic matter sorbed to sesquioxides is dominated by aliphatic and O-alkyl constituents, whereas aromatic entities are less prominent (Baldock et al., 1992), or nearly missing (Oades et al., 1989). The bonds between sesquioxides and organic constituents are very stable. Therefore, the protective effect of sesquioxides may be relatively strong, and is comparable to that of allophane (Boudot et al., 1986).

Incubation experiments conducted in our laboratory showed that the decomposition of beech litter is retarded in the presence of amorphous $\text{Al}(\text{OH})_3$. The weight loss during 90 days was only about half of that of the control (beech litter without mineral addition). Ferrihydrite acted in the same way, but the effect was much weaker. It caused a reduction in weight loss of 15% compared to the control. On the contrary, birnessite tended to increase the weight loss slightly (A. Miltner and Zech, 1997).

Boudot et al. (1989) conducted incubation experiments with Fe and Al complexes of model organic compounds (citric acid, fungal melanin HAs and FAs) and found that decomposition rates are lower for complexes with high metal/functional group ratios. The metal contents exceeded the complexing capacity of the organic compounds. Thus, the authors concluded that the stabilization is not mainly related to chemical binding per se, but to the loss of solubility and to 'trapping and wrapping' of the organic compounds by insoluble iron or aluminium hydroxides, i.e. physical protection of the organic compounds.

In addition to physical protection, the influence of sesquioxides on the microenvironment of microorganisms plays a role similar to that outlined for the clay minerals. An additional reason is the extremely low solubility of Al and Fe complexes of organic matter which makes it impossible for the microorganisms to use the organic matter as a substrate.

3.6. Dissolved organic matter dynamics

Dissolved organic matter (DOM) is supposed to represent the most active and mobile form of organic matter in soils. It exerts a profound influence on denitrification, the acid/base chemistry of soil solution, cation leaching, and mobilization of heavy metals as well as organic xenobiotics. Almost all DOM studies in terrestrial ecosystems have been conducted in temperate and cool mixed deciduous forests, and in temperate, cool, montane and boreal coniferous forests. Again, there is a great gap concerning soil DOM investigations in the tropics. To our knowledge, Frangi and Lugo (1985) are the only ones who examined the DOM dynamics in a subtropical floodplain forest.

Most important compartments for DOM mobilization are the forest canopy with DOC (dissolved organic carbon) concentrations between 8 and 22 mg C l⁻¹, and especially the forest floor with DOC concentrations between 20 and 60 mg C l⁻¹ (Cronan and Aiken, 1985; McDowell and Likens, 1988; Guggenberger and Zech, 1993). Calculated DOC fluxes from the forest floor into the mineral soil vary between 150 and 370 kg ha⁻¹ yr⁻¹ (Guggenberger and Zech, 1993). In Spodosols the A horizon serves as an additional DOM source (David and Zech, 1990; Guggenberger and Zech, 1992). All authors observed DOC maxima during the growing season, suggesting a biotic control of DOC release. This hypothesis was confirmed by investigations of the chemical structure of DOM. Chemical composition of DOM fractions indicated that DOM is mainly comprised of by-products of organic matter mineralization and of products of microbial resynthesis (Guggenberger et al., 1994).

Microbial activity, however, is strongly influenced by the chemical environment. So, liming of a coniferous forest (Höglwald, Germany) increased significantly the microbial activity (Kreutzer and Zelles, 1986), and DOC concentrations (Göttlein and Pruscha, 1991). Guggenberger (1994) also showed for soils in the Fichtelgebirge (Germany) that high N deposition increased DOC concentrations and fluxes significantly.

The solubility of DOM, mainly polyacidic organic macromolecules, has been shown to depend upon its chemical composition. ¹³C NMR spectroscopy and chemical degradative methods like CuO-oxidation and acid hydrolysis showed a dominance of sugars and only small amounts of lignin (Guggenberger and Zech, 1993). The ionic composition of the soil solution also was found to exert a profound influence on DOC release (Hayes, 1985). DOM mobilization is reduced at low pH, which gives rise to contraction and precipitation of organic matter by reduction of the electrostatic repulsion due to protonation of functional groups. High ionic strength also reduces the DOM solubility by decreasing electrostatic repulsion between organic molecules (salting out). Polyvalent cations lead to intra- and intermolecular bridging, and thus decrease solubility of organic molecules.

From the above it is clear that solubilization of DOM results from the

interaction of various abiotic and biotic processes. They can act in parallel or opposing fashions. For instance, liming increases the negative charge of DOM and microbial activity, both resulting in increasing DOC concentrations. Acid N deposition, however, decreases negative charge of DOM but appears to stimulate microbial activity.

In the mineral soil, DOM is usually retained very effectively. DOC concentrations in the subsoil vary between 0.5 and 12 mg C l⁻¹ (Cronan and Aiken, 1985; McDowell and Likens, 1988; Guggenberger and Zech, 1993). Corresponding DOC fluxes are in the range of about 5 to 60 kg ha⁻¹ yr⁻¹ (Guggenberger and Zech, 1993). McDowell and Wood (1984) showed that DOM retention in the mineral soil is mainly controlled by the content of Fe and Al oxides/hydroxides. According to Dalva and Moore (1991) and Guggenberger (1994), Fe oxides retain DOM more effectively than Al oxides. To a lower extent, clay can also immobilize DOM. Jardine et al. (1989) showed that the main adsorption mechanism is hydrophobic interaction driven by favourable entropy changes. Besides the DOM retention by the soil mineral phase, biotic controls are of minor importance for DOM concentrations in the soil solution. Qualls and Haines (1992) showed that only hydrophilic neutral compounds (= free carbohydrates) are mineralized to a considerable extent.

Since investigations on soil DOM in the tropics are very scarce, we can only speculate on DOM chemistry and budgets. However, comparing DOC mobilization and retention in Dystric Cambisols of Rwanda and Germany by establishing initial mass isotherms, we found that about 50 mmol kg⁻¹ DOC were released from the surface horizons and only approximately 15 mmol kg⁻¹ from the B horizons. DOC retention capacity was similar in both soils (Fig. 12). An

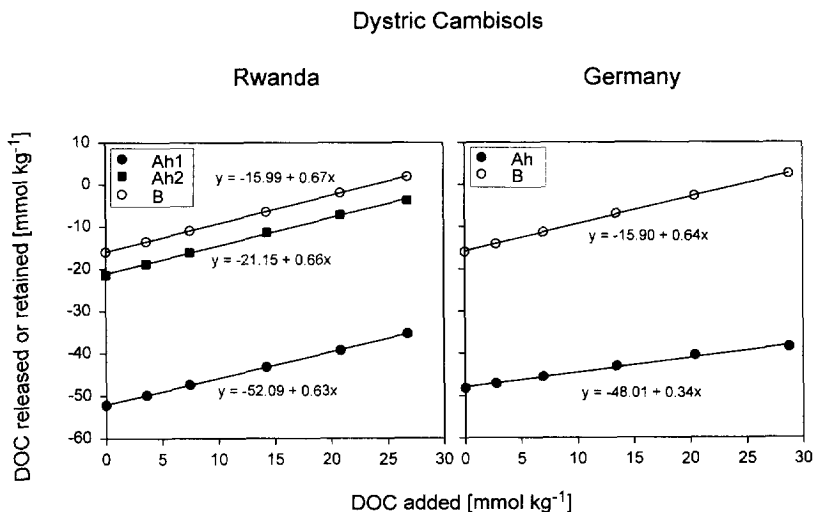


Fig. 12. Dissolved organic carbon (DOC) sorption by Dystric Cambisols from Rwanda and Germany. Sorption isotherms are plotted as initial mass relationships (Nodvin et al., 1986).

alternative approach is to draw some conclusions from the DOM dynamics of the main rivers and their tributaries.

In the humid tropics, DOC fluxes in the canopy floor are expected to be higher than in temperate zones due to higher precipitation and higher leaf area indexes. Also in the mineral soil DOC input and fluxes may be higher in the tropics. Upland soils rich in oxides (Oxisols) are expected to retain DOM effectively. In contrast, Spodosols with thick E horizons (Giant Podzols) export great amounts of DOM into rivers, thus creating black water streams. Thus, mean DOC concentration of the Amazon river (representing mainly Oxisol soil series) is 4.8 mg l^{-1} , and mean DOC concentration of the Rio Negro (representing mainly Spodosol soil series) is 10.8 mg l^{-1} (Ertel et al., 1986). In floodplain soils, frequent flooding causes intensive leaching of carbon from the soil profile, leading to DOC concentrations in ground waters and rivers of about $2\text{--}30 \text{ mg C l}^{-1}$ (Frangi and Lugo, 1985). The authors calculated a watershed export of $380 \text{ kg DOC ha}^{-1} \text{ yr}^{-1}$, which far exceeds DOC export in temperate zones.

4. Mineralization in relation to SOM chemistry

4.1. Definition

Mineralization is the microbially mediated transformation of organically bound elements (like C, N, S, P) into inorganic compounds (like CO_2 , CH_4 , NH_4^+ , NO_3^- , SO_4^{2-} , H_2S , HPO_4^{2-}). Nutrient release is generally related to decomposition and mineralization. Mineralization affects the different SOM pools, like above- and belowground primary resources, the secondary resources, humic compounds, and also DOM (Fig. 1). The speed of mineralization and amount of nutrients released differ greatly between these SOM fractions.

For mathematical modelling purposes the following SOM pools are commonly distinguished: (i) the microbial fraction (alive and dead); (ii) the labile SOM fraction; and (iii) the recalcitrant SOM pool. The microbial fraction can be assessed with the fumigation method (Jenkinson and Powlson, 1976). No adequate method has been developed for the determination of recalcitrant pools. They can only be estimated from simulation models (Duxbury et al., 1989).

In this section, after discussing labile versus stable SOM components, we focus on aspects of nutrient release and greenhouse gas evolution during SOM mineralization.

4.2. Labile versus stable SOM components

Although 55 to 70% of all plant and animal residue C returned to the soil is released into the atmosphere as CO_2 after 1 year, different rates of mineraliza-

tion occur among different constituents. SOM may be divided into labile and stable components based on the rate of decomposition in soil. The labile pool averages about a quarter to a third of the total SOM in temperate region soils but is probably smaller in tropical soils (Duxbury et al., 1989). Labile constituents of SOM decompose within a few weeks or months and are suggested to include comminuted plant litter, macroorganic matter or light fraction, non-humic substances not bound to mineral constituents, water-soluble forms, macroorganisms (fauna), and microbial biomass (Theng et al., 1989). The stable components of SOM may persist in soil for hundreds to thousands of years and are largely represented by humic substances and other organic macromolecules which are intrinsically resistant to microbial attack or physically protected by association with mineral surfaces or trapped within mineral aggregates or clay layers. In general, as C is lost as CO_2 from a given substrate, more residual C will be found in the soil microbial biomass, and less C will be stabilized in the soil humus.

The relative pool sizes, i.e. the amount and composition of the various SOM constituents, are mainly controlled by residue inputs and climate gradients, edaphic factors, soil mineral types and contents, and other physical and chemical properties of the soil that affect the activity of decomposer organisms (Theng et al., 1989). The chemical composition and physical state of the residue, the site of placement in soil, and tillage operations are additional factors which affect the decomposition pattern and SOM lability. For example, animal manures are much more effective than plant residues in contributing to the labile SOM pools, because they have already been subjected to the rapid initial decomposition.

In absolute terms, the size of the labile SOM pool derived from plant residue additions will be smaller and will respond quicker to changes in residue inputs in tropical soils than in temperate soils (Sauerbeck and Gonzales, 1977). With constant annual residue inputs of $1000 \text{ kg C ha}^{-1}$, the labile SOM pool is estimated to contain a maximum of $2500 \text{ kg C ha}^{-1}$, 250 kg N ha^{-1} , and 25 kg P ha^{-1} , if the C/N and C/P ratios are 10 and 100, respectively.

Labile SOM constituents rapidly decline after a natural soil is first placed to cultivation and new equilibrium levels are attained. Balesdent et al. (1988) have compared soil C content in a native prairie under grass with that of the same soil under wheat for about 100 years. The higher level of organic C measured in the former was ascribed to the presence of more labile but physically protected C, whereas the lower level of original native C in the latter was imputed to result from loss of protection through tillage operations. The decline of the prairie SOM initially was rapid, due to the loss through mineralization of the most labile SOM, and then reached a steady state. Similarly, labile and stable SOM pools have been distinguished for a tropical soil in which sugar cane was grown after deforestation (Cerri et al., 1985).

Lability of SOM was also shown to be related to soil particle-size, with the coarse clays being mainly responsible for stabilizing SOM (Theng et al., 1989).

4.2.1. Litter

The turnover time of litter in tropical rain forests is generally less than one year, whereas turnover times in temperate deciduous forests usually range between one and two years. The marked overlap in decomposition rate constants indicates, however, that the litter-decay rate in the tropics is not always greater than in temperate regions (Anderson and Swift, 1983).

Litter quality also influences degradability, as shown by the comparison of data for leaf litter with those for litter containing 30–40% of woody materials having a relatively high lignin content. Decomposition rate is known to correlate well with both initial lignin content and the C/N ratio of leaf litter over a range of forest ecosystems (Meentemeyer, 1978; Laishram and Yadava, 1988). Litter-decay rate may also be related to content, type, and activity of soil organisms (Dietz and Bottner, 1981).

4.2.2. Light fraction

The light fraction is an intermediate between plant litter and stable humus. It consists of slightly to moderately decomposed but still discernible plant or animal residues. The amount and lability of the light fraction vary widely among both tropical and temperate soils, depending on several factors including pH, temperature, water, plant litter quality, aeration, soil mineralogy, and nutrient status of the soil (Stout and Lee, 1980; Theng et al., 1989). Variations of the light fraction in soil are also indicative of the consequences on SOM dynamics caused by changes in soil management (Janzen et al., 1992).

The chemical composition of the light fraction in the soil is similar to that of plant tissues (Molloy and Speir, 1977; Skjemstad et al., 1986). The variability of C and N contents measured in the light fraction of SOM in temperate soils has been shown to depend on the C/N ratio of the parent plant material (Sollins et al., 1984), and other factors such as soil C content, pH, earthworm abundance in soil, and season (Spycher et al., 1983). Similar relationships are expected to occur in tropical soils.

The labile character of the light fraction is important because of its large contribution to the plant-available N pool, especially if its C/N ratio is low (Sollins et al., 1984). The rate of loss of organic C is also much greater from the light fraction than from the heavy fraction, especially in tropical soils (Dalal and Mayer, 1986).

4.2.3. Other labile SOM constituents

So-called non-humic substances comprise a wide variety of chemically defined natural biopolymers including, among others, lignin, tannins, waxes, pigments, various polysaccharides, and pectins. These compounds are attributed to the labile SOM pool, at least in soils where biological processes are not restricted (Theng et al., 1989). In general, the lability of non-humic substances in soils is inversely related to their molecular size and complexity (Haider and

Martin, 1981). Most of these compounds may persist for years, especially in soils with low biological activity, because of their polymeric recalcitrant structure or chemical stabilization through interactions with minerals or other substances, such as protein–tannin complexes (Oades, 1988).

Potentially labile forms of organic P may accumulate largely as orthophosphate diesters of microbial origin in soils with restricted biological activity (Tate and Newman, 1982), whereas in tropical soils, which are characterized by intense biological processes, a small, steady supply of P may be contributed from this source. In temperate soils the amount of orthophosphate diesters was shown to decline under cultivation (Tate, 1984).

By definition, available C is readily usable by heterotrophic microorganisms as an energy and C source, because it is mostly water-soluble and originates mainly from dissolution of litter components, plant root exudates, microbial metabolites, and hydrolysis of more stable forms of SOM (McGill et al., 1986). This form of C amounts to about 0.2 g kg^{-1} in temperate soils, while much less is probably present in most tropical soils (Theng et al., 1989). Dynamics of water-soluble C is discussed in Section 3.6.

4.2.4. Macro- and microorganisms

Soil macroorganisms (fauna), especially earthworms and termites, play a primary role in comminuting surface litter, mixing and incorporating the fragmented products into the soil, facilitating and accelerating the successive microbial attack and decomposition, and converting it into excreta (Herbillon, 1980; Lee, 1983). It has been estimated that soil fauna contribute to nutrient cycling by processing 20–40% of the annual litterfall in this way (Kitazawa, 1967).

The amount of C contained in the soil microbial biomass mostly ranges from 1 to 3% of the total soil organic C, with C/N ratios between 5 and 15 depending on the dominating microbial population, that is, bacteria or fungi, respectively (Theng et al., 1989).

The low biomass levels indicated by the limited data available for tropical soils suggest a rapid turnover of biomass in these ecosystems. In contrast, soils developed on volcanic ash and rich in allophanes are characterized by high biomass contents. In these soils organic substances decompose slower and are in general less labile than in other soils (Zunino et al., 1982). These results may be ascribed to the stabilizing effect exerted by allophanes which may adsorb and protect organic substances by complex formation with Al and Fe (Theng, 1987), and even stabilize the biomass itself and its metabolites.

Studies with isotopically labelled microbial biomass have revealed that turnover times increase from less than 6 months during the first weeks, to several years after the first year of decomposition (Ladd et al., 1981). The biomass appears to be more labile and to decompose faster than non-living

SOM, thus the proportion of residual C and N from the biomass in the soil decreases with progressive decomposition.

In most soils the activity of microorganisms is largely restricted to the rhizosphere, probably because the rapid turnover of microbial biomass requires large supplies of available C. In some tropical ecosystems, however, the large inputs of organic matter and rainfall, and the related high potential for SOM leaching, seem to warrant SOM turnover and microbial population in both the rhizosphere and non-rhizosphere soil (Theng et al., 1989).

4.3. Nutrient release

4.3.1. Amounts, distribution, and forms of nutrients in SOM

Nutrients are present in SOM in the following forms: (i) as part of complex organic polymers which may include N, P, and S; (ii) as exchangeable inorganic cations on its surface, e.g. the basic nutrients Ca, Mg, K; or (iii) as organically complexed cations, such as most transition metal micronutrients (e.g. Mn, Cu, Fe, Zn). Nutrients are stored in or released from SOM by two types of fundamental processes that are mainly biological processes for N, P, and S, and physico-chemical processes for macro- and micronutrient cations (Duxbury et al., 1989). It should be noted, however, that SOM mineralization decreases the total retention capacity of available cations in tropical soils where SOM is often the major source of negative charge.

Generally, SOM contains 95% or more of the N and S, and between 20 and 75% of the P in surface soils (Duxbury et al., 1989). A definite relationship is observed between organic C, total N, organic P, and total S in soils. The mean value of the C/N/S ratio of natural soils, both grassland and forest, is fairly constant at about 200:10:1, whereas the average proportion of C/N/P/S in agricultural soils is about 140:10:1.3:1.3 (Stevenson, 1986). These differences are ascribed to one or more reasons including: (a) preferential mineralization of C relative to N and S, and of N relative to S, in cultivated soils; (b) the generally higher nutrient contribution from agricultural crop residues; and (c) differences in the retention capacity for the various elements in the soil–plant system after mineralization. The gradual transformation of raw plant material into stable SOM (humus) leads to the establishment of a more consistent relationship between C, N, P, and S, approaching that of native humus.

The mean P content in SOM is close to that for S, but is more variable than the other elements, especially in tropical soils. Thus C/P and N/P ratios of SOM can vary widely on dependence of several factors including the relatively greater independence in the cycling of SOM-P relative to organic C, N, and S. In contrast, the greater constancy of soil N/S ratios would indicate coupling of their cycling in the soil–plant system (Biederbeck, 1978).

Only about 40–50% of the organic N in soils can be identified in components of definite chemical classes, with amino acids usually dominating over amino

sugars (Freney, 1986; Stevenson, 1986). Although newly added and immobilized N has a different chemical composition than native soil N (e.g. more amino N and unidentified hydrolysable N, and less non-hydrolysable, mainly heterocyclic N), it is rapidly converted to chemical forms similar to those present in the native SOM. Thus, the more rapid mineralization of recently added N should be ascribed more to differences in substrate lability and availability or protection than to differences in the structural composition of added and native N. This conclusion is supported by results from long-term field experiments that show limited impact of either tillage practices or cropping systems on the distribution of N forms in SOM (Duxbury et al., 1989).

The most abundant forms of organic S in soil are sulphur-containing amino acids, mainly including methionine, cysteine and cystine, which also account for up to 30% of the SOM-S (Freney, 1986). Between 30 and 70% of SOM-S is in the form of HI-reducible ester sulphates (C–O–S) and C–N–S and C–S bonded sulphur. C-bonded S is not reduced by HI and comprises a smaller proportion of total SOM-S.

NMR measurements have shown that most of the organic P extractable from soil is in the form of monoesters of orthophosphoric acid and that phosphate esters of inositols are the most abundant class of identifiable compounds, ranging from 5 to 80% of SOM-P (Tate and Newman, 1982; Hawkes et al., 1984). Small amounts of diesters and phosphonates containing C–P bonds have also been detected by NMR, together with minor contributions of nucleotides and phospholipids. The capacity of inositol phosphates to form insoluble precipitates with Fe, Al, and Ca, and to strongly adsorb on amorphous Fe and Al oxide surfaces, may explain their accumulation in some soils (Anderson and Arlidge, 1962). Tropical soils usually contain 60–80% of P in organic forms, thus underlining the potential importance of SOM-P as a source of P for plant growth in these soils.

N, P, and S are generally released in plant-available forms in ratios different from those in which they occur in SOM. Differences in apparent mineralization–immobilization rates for N, P, and S may be due in part to their occurrence in different organic compounds and SOM fractions, and to variations in the N, P, and S contents of applied crop residues (Duxbury et al., 1989).

Contrasting results from different workers have been obtained on the dependence of SOM, associated nutrient content, and susceptibility to mineralization on the size of soil aggregates. Most studies have shown that organic C, N, S, and P contents and mineralization increase while C/nutrient ratios decrease with decreasing aggregate size (Chichester, 1969; Cameron and Posner, 1979; Anderson et al., 1981; Lowe and Hinds, 1983). However, results showing an opposite trend for the nutrient content and mineralization have been obtained (Elliott, 1986). For example, S was found to be preferentially associated with fine clays (Anderson et al., 1981), P to accumulate more than C and N in fine

fractions less than 50 μm during wet sieving (Elliott, 1986), and N to accumulate preferentially in coarse clay/fine silt fraction (Ladd et al., 1977a,b).

No substantial differences were shown to exist between tropical and temperate soils when comparing results of elemental ratios and the distribution of structural forms of nutrients present in SOM. However, more detailed information is needed on the organic forms of P and S in tropical soils and on their interactions with soil mineral components. It is expected that these results will be more likely produced by applying chemical and physico-chemical (NMR) analyses of soil fractions separated by particle-size and density fractionation procedures than by studies with whole soil.

Microbially mediated processes, including turnover of nutrients in plant and animal residues in unprotected SOM pools, will be greater in tropical soils under warm and humid climates than in temperate soils, but this may not be true in dry tropical regions. Although few tropical sites have been studied, large differences have been observed among sites, which are probably related to differences in quantity and quality of litterfall. The net N mineralization and subsequent nitrification rates were greater in tropical forests than in temperate forests, also indicating more rapid nutrient turnover under these conditions (Robertson, 1984; Jordan, 1985; Vitousek and Sanford, 1986; Vitousek and Matson, 1988).

The labile SOM nutrient pool is generally smaller in humid tropical soils than in comparable temperate-region soils, thus resulting in a smaller fraction of the total organic N, P, or S mineralized (Duxbury et al., 1989). The tendentially lower C/N ratio in tropical soils (Post et al., 1985) is also consistent with a more complete degradation of unprotected SOM. Accelerated turnover of unprotected, labile SOM pools in the humid tropics implies a faster release of nutrients which can lead to greater nutrient losses if sinks, such as vegetation, are removed.

In contrast, the size of the oldest, colloiddally or chemically protected SOM pools will probably be larger. Both size and turnover will be relatively insensitive to moisture and temperature, but highly sensitive to soil mineralogy and texture in highly weathered acid tropical soils dominated by amorphous Fe and Al oxides with large mineral surfaces compared to temperate-region soils dominated by layer silicate clays (Duxbury et al., 1989). Physical disturbance, and in particular, intensive tillage generally results in a partial removal of SOM protection and a rapid release of organic C, N, P, and S in the humid tropics. This is a major reason for the higher fragility of humid tropical soils (e.g. Oxisols) and for the quicker loss of their fertility than temperate-region Molisols demonstrate after initial cultivation.

4.3.2. General aspects of nutrient cycling and turnover in SOM

Nutrient mineralization and immobilization result from interacting factors involving heterogeneous substrates, functionally diverse organisms, chemically different elements, and multiple environmental controls. Important environmen-

tal factors controlling nutrient turnover and cycling through SOM pools include chemical and mineralogical soil properties, soil and vegetation management, climatic factors, such as temperature and moisture, and seasonal and short-term environmental variations (Theng et al., 1989). For example, fluctuations in both temperature and moisture are known to accelerate SOM decomposition and N mineralization (Ladd et al., 1977a,b), possibly through disruption of physically protected SOM and accelerated turnover of microbial biomass.

The knowledge of amount, quality, availability, and activity of organic nutrient substrates is a key for understanding and describing mineralization–immobilization processes in soil. Thus, it is apparent that SOM cannot be considered homogeneous with regard to potential for mineralization. Although a continuum of reactive organic constituents exists, six conceptual interrelated organic pools may be identified in soil (Stevenson, 1986): (a) plant and animal residues, which provide nutrients for plant growth upon decomposition; (b) the soil biomass, which functions as a temporary storage unit for C and nutrients; (c) water-soluble compounds, which have a physiological function and act as carriers for micronutrient cations; (d) bound and free enzymes; (e) a ‘labile’ component of humus; and (f) the ‘resistant’ humus fraction.

Models are being developed for following the flow of C and nutrients (especially N) through the various pools as influenced by soil management practices and changes in the soil environment (Stevenson, 1987). Isotopic studies using ^{15}N , ^{32}P , and ^{35}S have provided information on the distribution of N, P, and S in the various SOM pools as influenced by microbial activity and environment alterations. Methods are developed for determining the dynamics of N, P, and S transformations (from the biomass) to more stable humus forms (Stevenson, 1987).

The biological turnover of organic N, P, and S through mineralization–immobilization processes leads to incorporation of N, P, and S first into the biomass and then into labile and stable humus forms. Studies with ^{14}C -labelled substrates have shown that about one-third of the C arriving to the soil as crop residues remains behind in the soil at the end of the growing season (Stevenson, 1986). Similarly, field studies with ^{15}N have shown that about one-third of the applied fertilizer-N remains in the soil in organic forms after the first growing season. No more than 15% of this residual N becomes available to plants during the second growing season, and availability decreases even further for succeeding crops (Stevenson, 1986). Residual C and N have a mean residence time (MRT) of about 5 years, following which the MRT approaches that of the native soil C and N. A similar effect has been observed for N in crop residues. The value of crop residues in conserving N is due not so much to their capacity to provide large amounts of immediately available N, but rather to long-term effects whereby soil N levels are maintained or increased, thereby ensuring an adequate supply of N by slow decomposition of stable organic forms. The decay of crop residues is often accompanied by a small ‘priming’ effect on native soil

C, although a general priming action has never been substantiated (Stevenson, 1987).

The distribution of the various organic N and S forms is somewhat similar for all soils and relatively unaffected by crop management practices. The chemical structure of organic molecules, by itself, seems insufficient to account for the extreme variation in age and turnover times. Components of the FA fraction of SOM may constitute the biologically active and transitory form of organically bound N, P, and S. Interactions among organic molecules and minerals at the molecular or colloidal level, as well as the chemical nature of the organic molecules are suggested to be the main reason for the stabilization of the old SOM constituents, such as HA and refractory non-humic compounds. The nutrient content of the older organic fractions and their contribution to nutrient release is largely undefined, except for the little information existing on N.

4.3.3. Nutrient release from organic versus inorganic inputs

Organic input of various nature and sources to soil has the function of supplying nutrients to plants and can be evaluated by the potential to increase plant yields to levels above that based on the application of an equivalent amount of nutrients as inorganic fertilizers (Avnimelech, 1986). Nutrient release and availability depend on the rate of decomposition, which is controlled in part by temperature, moisture, soil texture, and soil mineralogy. Manure and compost formulations, composting techniques and duration, application rates and techniques, placement and timing also affect OM decomposition. Slow nutrient release from soil added OM may provide a stable supply of ammonium. Available P can also be increased, as well as trace metal availability and solubility through complexation.

Major differences between organic and inorganic sources of nutrients are the form and availability of nutrients. A typical feature of SOM is to release nutrients gradually, thereby reducing leaching, fixation, and volatilization. The net release of nutrients from SOM is mainly a function of decomposition rates of the different SOM fractions and of the subsequent uptake of nutrients by the growing biomass. The decomposition process often results in an effective storage of nutrients by the developing biomass. Fast decomposition of labile SOM produces a high rate of nutrient release only when the SOM is rich in nutrients (low C/N and C/P ratios). Stabilized SOM will lead to a slow rate of nutrient supply while the presence of fresh SOM, rich in nutrients, will produce a fast supply of them. In similar material having high C/N and C/P ratios, nutrients will be first immobilized by the growing biomass, and only later released to the soil.

In conclusion, the main effects of SOM are to improve the plant-growing conditions and maintain the crop yields especially when soil conditions and other soil fertility parameters are not in the optimal range. Most information about the decomposition process of SOM derives from studies conducted in

temperate-region soils. Decomposition of organic inputs and subsequent nutrient availability are likely to operate differently in acid, infertile Oxisols and Ultisols with variable-charge minerals and with microbial populations often dominated by fungi (Sanchez et al., 1989). A better understanding of the processes that control nutrient availability of SOM from management (e.g. quantity, quality, placement, and timing), may allow for design of systems that produce more efficient use of organic inputs in tropical agroecosystems.

4.3.4. Nutrient cycling in natural and cultivated soils

The OM content of a soil developed under natural vegetation approaches to a steady state when organic inputs and decomposition are balanced. In cultivated soils, nutrient cycles are disturbed by agronomic practices including tillage, irrigation, and external inputs of nutrients, which generally accelerate nutrient release from SOM. When released, nutrients can either be taken up by plants or lost through leaching and/or volatilization. SOM content thus declines until a new steady state is reached, typical of the particular agroecosystem. The new steady-state SOM content is generally reached more rapidly in tropical than temperate soils.

The synchrony in nutrient cycling existing between plant growth and microbial activity in natural soils is disrupted in agricultural soils, since nutrients mineralized and released to soil during periods without crops are subject to loss by leaching and/or volatilization. Thus, the separation in time between the two processes of release and uptake results in lower nutrient-use efficiency, especially with N, where excess amounts may be lost by leaching, denitrification, or ammonia volatilization. Further, annual crop plants are not as effective in recovering nutrients from soils as perennial crops or natural perennial plants. In subtropical and tropical ecosystems, nutrient conservation strategies should be developed to conserve both mineralized nutrients and fertilizer.

4.3.5. SOM and cationic nutrients

The CEC of soils is of fundamental importance for the retention of basic nutrient cations (Ca, Mg, K, and Na) by electrostatic forces on the surfaces, in exchangeable and bioavailable forms. Most of the CEC of soils dominated by kaolinite and amorphous oxides is associated with SOM rather than with the mineral components. Thus, maintenance of SOM to provide CEC is more important in highly weathered soils in the tropics than in temperate regions. However, the amount of CEC contributed to tropical soils by SOM is lower than expected because of the extended degree of blockage of negatively charged sites at low pH values by Al and Fe. Thus, attempts to increase the CEC of acid soils by increasing SOM levels may lead to short-term benefits, but in the long-term the soil system will equilibrate to block newly formed exchange sites unless soil pH is raised by liming.

Although the older, more biologically stable SOM pools (e.g. humic sub-

stances) may contribute substantially to soil CEC, labile SOM pools are often considered to be the most important SOM source of CEC in tropical soils (Duxbury et al., 1989). Thus, maintenance of this SOM pool at high levels is important for maintaining CEC in these soils. Extended SOM mineralization will reduce CEC levels and have a negative impact on cation retention in tropical soils.

Transition metal ions (e.g. Zn, Mn, Fe, Cu) complexed by SOM are generally considered an important component of the labile and available reservoir of these micronutrients in soils. Further, soluble metal–SOM complexes, such as those formed by the fulvic acid fraction of SOM, play an important role in the transport of micronutrients to plant roots, especially in high pH soils where solubility of inorganic forms of all the micronutrients is low. Thus, micronutrient deficiencies, that are common in high pH tropical soils cultivated for long time periods, may be eliminated by increasing SOM contents.

4.3.6. *CO₂ evolution during mineralization*

Whereas net CO₂ release from agricultural sites due to land clearing and biomass burning is negligible in the temperate zones, in the tropics net loss of carbon still continues, amounting to $1.6\text{--}2.2 \times 10^{15}$ g C yr⁻¹ (Sauerbeck, 1993). In addition, 6×10^{15} g C are presently released world-wide during just one year, from fossil fuel alone. Jenkinson (1991) estimated that the yearly increase of temperature (0.03°C) also might lead to a loss of 1×10^{15} g C yr⁻¹ due to increasing mineralization.

The significance of chemical factors for the control of carbon mineralization was recently documented by Lehmann et al. (1995) in a study of the decomposition of leaves, twigs, and roots of agroforestry-relevant tree species in Central Togo. At a given site (Acrisol), the carbon loss was shown to be significantly correlated with the (polyphenol + lignin)/N ratio in leaves, twigs, and roots. Horner et al. (1988) pointed out that polyphenolic substances can directly inhibit microbial activity and the availability of N due to different ratios of the various plant components [(polyphenol + lignin)/N]. Agbim (1987) found a relationship between the initial lipid content and soil respiration after the addition of leaf litter in West African soils.

Lignin contents (Berendse et al., 1987; Berg and McClaugherty, 1987) or lignin/N-ratios (Melillo et al., 1982; Harmon et al., 1990) controlled carbon mineralization in litter-bag experiments. However, interpretation of these experiments in view of CO₂ production must be done carefully, because fine material may be lost from litter bags or be incorporated by animals.

The chemical quality of the above- and belowground litter has a significant influence on CO₂ release at a given site, whereas comparing different sites, generally the temperature and water regime may be more important. Less is known about the chemical control of C mineralization of labile SOM pools. High amounts of carbohydrates and proteins with a narrow C/N ratio may

promote C mineralization, whereas high aromaticity and high alkyl C contents apparently reduce turnover rates.

It should be mentioned here that according to Owensby (1993), elevated CO₂ concentration in the atmosphere reduces the litter quality of a tallgrass prairie by increasing its biomass production. The potential to reduce the decomposition rates is possibly related to higher SOM retention.

Microbial necromass is also a source of the total CO₂ output. During periods of severe droughts the microbial population dies and is readily mineralized when soil is rewetted by the succeeding rain. This can be observed when dry soil is incubated. After rewetting, day-1 respiration is ten times higher than during the following period. This increase can be attributed to the mineralization of the necromass of the microbes. An accelerated respiration during the first days of incubation was also observed by Janzen and McGinn (1991) with *Lens culinaris*.

With respect to the development of criteria for the selection of potential fallow tree species for soil improvement, Schroth et al. (1995) studied C mineralization in the surface horizons of 9 five-year old plantations in the Ivory Coast. They found an accelerated CO₂ production at the beginning (an average 0.55% of total soil C), indicative of the decomposition of low-stability organic compounds (Sparling and Ross, 1988). The control (soil invaded by *Chromolaena odorata*) produced significantly more CO₂ than the reforested soils. During the second respiration phase from 5 days onward, CO₂ production was much lower and continued to decrease in all samples until day 78, after which the control fell to an intermediate position, and differences were no longer significant. These results, however, give no information about the influence of resource quality on C mineralization.

4.3.7. Denitrification and SOM chemistry

Denitrification is defined as a microbially catalyzed, anaerobic respiration, occurring only if O₂ availability is reduced (Tiedje, 1988). It results in the reduction of NO₃⁻ and NO₂⁻ to NO, N₂O, and N₂. N₂O is assumed to promote global warming and the destruction of ozone. Several factors like pH, O₂, C, and NO₃⁻ availability regulate denitrification (Eichner, 1990; Aulakh et al., 1992). Here, we refer to the chemical control only.

Soil pH. Despite the fact that the majority of denitrifying organisms show optimum growth between pH 6 and 8, significant N losses were reported for acid soils even to pH 3.5 (Weier and Gilliam, 1986). It is still unknown, however, why denitrification decreases with decreasing pH. Probably toxic H⁺ and Al³⁺, and nutrient deficiencies at low pH can reduce vitality of the denitrifying microbes. In very acidic tropical soils (Ferralsols), molybdenum deficiency may occur due to adsorption on and diffusion into iron oxides. Consequently, less molybdenum is available for the synthesis of NO₃⁻ reductase. Koskinen and Keeney (1982) assumed that low pH does not influence denitrifi-

cation directly, but does so indirectly by reducing the amount of easily available organic compounds, which serve as a source for energy and the synthesis of cellular constituents. This may explain why available organic C supply is a controlling factor for denitrification.

Available organic C supply. Bremner and Shaw (1958) showed that denitrification is closely related to DOC contents. This result was not confirmed by Beauchamp et al. (1980), but it seems that under field conditions, denitrification is mainly limited by lack of organic compounds easily mineralizable under anaerobic conditions. It is clear that besides sufficient carbon, enough NO_3^- must be present. SOM rich in aromatic compounds like lignin will be less effective in promoting denitrification in comparison to carbohydrate-rich materials (Beauchamp et al., 1989). High inputs of plant residues and green and farmyard manures also stimulate denitrification, if soil N is not restricted.

In the subhumid and semiarid zones denitrification at the beginning of the rainy season may be relatively high due to the increased availability of C and N after the dry period. Roots are believed to support denitrification due to their exudates and consumption of O_2 (Smith and Tiedje, 1979; Mosier et al., 1988). Under field conditions, the rhizo-deposited C can rapidly enter the more stable SOM fraction (Haider et al., 1985, 1987), thus being not available for denitrification.

In most mineral soils, denitrification decreases with increasing soil depth due to limited carbon availability. Under tropical conditions, Vertisols may have high denitrification potentials, even in the subsoil, if easily decomposable organic material is washed in through the cracks at the beginning of the rainy season. Myers and McGarity (1971) reported appreciable denitrification activities from solonchic subsoils enriched by DOC leaching from the surface horizons.

C/N ratio. Aulakh et al. (1991) found that denitrification was inversely related to initial C/N ratio of different plant residues due to N immobilization. For 35 days, denitrification losses were 102 mg N kg^{-1} for vetch hay ($\text{C/N} = 8$) but only 70 mg N kg^{-1} for wheat straw ($\text{C/N} = 82$). In their experiments, incorporation of plant residues into soil as green manure increased initial denitrification rates compared with surface placement. However, after one month no differences between mulch and green manure were measured. To reduce soil erosion, tropical soils often are mulched, for instance, in coffee and banana plantations or in agroforestry systems. In some cases, even the use of mulch material with a wide C/N ratio may stimulate denitrification, due to the reduction of evaporation and the conservation of pore water.

Nitrate availability. Low N-mineralization and nitrification rates as observed in grazed humid tropical pasture (Scholes and Sanchez, 1990) restrict denitrification. In flooded and puddled rice soils with soil pH near neutrality, denitrification remains generally low because less NO_3^- is produced under anaerobic conditions and the majority of N is present as NH_4^+ (Aulakh, 1988). Only in the

vicinity of the plant roots is more O_2 available as compared with the surrounding soil, stimulating nitrification and, also, denitrification. According to Aulakh et al. (1992), up to 58% of applied N fertilizer are reported to be lost in rice soils, as estimated by the ^{15}N balance approach. However, Buresh and Austin (1988) and Buresh and DeDatta (1990), directly measuring denitrification with the ^{15}N chamber method, showed that denitrification losses in reality are probably much lower, and much of the N loss is due to NH_3 volatilization.

In contrast to nitrification, which has been studied extensively in tropical soils (e.g. Jacquemin and Berlier, 1956), less is known about denitrification in tropical environments. Greenland (1956) predicted that rates should be high in undisturbed rain forests, especially if soils are characterized by strong soil aggregates, promoting anoxic microenvironments in their interior (pseudosand, pseudosilt structure), combined with high amounts of easily decomposable organic compounds from litterfall. Actually, Robertson and Tiedje (1988) found in primary undisturbed forests of Costa Rica, using the acetylene inhibition technique, an annual outflux of $7.6\text{--}21\text{ kg ha}^{-1}\text{ yr}^{-1}$ gaseous N. Sites with secondary succession, 15 years after clearing the primary forest, produced only 25% of the above-mentioned values. However, at recently cleared forest sites, $N_2 + N_2O$ losses were even higher than in the undisturbed primary forest, at least during a few months after clearing.

Few results on denitrification are available from the tropics, and it seems that the same factors as in temperate zones are regulating denitrification (Groffman et al., 1988), but the ecological consequence may be different. Robertson (1989) pointed out that nitrification and denitrification may significantly influence ionic nutrient sorption in tropical soils with variable charge. Nitrification is accompanied by protonation, and denitrification by deprotonation. If nitrification is accelerated after forest clearing, the soil charge system may be close or even below the point of zero charge (PZC), at which exchangeable ions will be lost from the rooting zone. Our studies on the mineral nutrition of young forest plantations in the lowlands of Costa Rica revealed wide-spread N deficiency, Al-toxicity, and K/Mg-imbalances (W. Zech, unpubl. results).

Strategies for increasing food production in developing countries generally include the improvement of the N supplies of crops because besides P, N is often the limiting factor. Principally this is possible by planting legumes and applying N fertilizers. Both management practices significantly influence SOM pools, mineralization, nutrient release, and denitrification in soils in temperate climates (Eichner, 1990). However, information is scarce for tropical soils.

5. Conclusions

The composition and dynamics of soil organic matter (SOM) are generally the same in temperate and tropical soils, except that turnover rates in tropical

soils usually are higher than in colder climates. Therefore, many results from temperate soils can be transferred to explain SOM dynamics and their control in tropical soils. The main transformations occurring during litter decomposition and humification are loss of polysaccharides and phenolic moieties, modification of lignin structures, and enrichment in recalcitrant, non-lignin aromatic structures. The rates of these transformations are controlled primarily by climatic factors and only to a lesser extent by chemical factors such as pH, C/N ratio, or litter quality.

SOM stabilization by interaction with minerals probably is more important in tropical than temperate soils because of the more favourable climatic conditions for decomposition of organic matter. The protective effect of minerals is most pronounced for labile constituents such as polysaccharides or proteins.

Dissolved organic matter (DOM) is considered to be the most active and mobile SOM pool. Studies on its contribution to SOM dynamics in tropical ecosystems, however, are very scarce.

Labile forms of SOM are of primary importance as a reserve and a source of plant nutrients in tropical soils poor in weatherable minerals. Although relatively little information is available on their mineralization and consequent nutrient release and nutrient cycling in tropical soils, these processes appear to be generally controlled by the same chemical factors as in temperate regions. However, the size of the labile SOM pool is apparently smaller and shows a faster turnover with a faster release of nutrients in humid tropical than temperate soils. In contrast, the size of chemically protected SOM pools are probably larger. Intensive tillage, however, generally results in a partial removal of SOM protection, and in a rapid release of nutrients in the humid tropics. Further, the limited data available for tropical soils indicate a low biomass level and a rapid turnover of biomass in these ecosystems, except for soils developed on volcanic ash and rich in allophane. A more rapid nutrient turnover is also observed in tropical than in temperate forests.

Although elemental ratios and distribution of structural forms of nutrients present in SOM of temperate and tropical soils apparently are rather similar, more information is needed especially on the organic forms of P and S in oil mineral components. Chemical and physico-chemical analyses of soil fractions are expected to help elucidate this problem.

SOM is often considered to be the most important source of CEC in tropical soils dominated by kaolinite and amorphous oxides. However, the ability of SOM to retain nutrient cations is lowered in acidic soils to a great extent by blockage of negatively charged sites by Al and Fe ions. Extended SOM mineralization will reduce CEC levels and have a negative impact on cation retention in tropical soils. Maintenance of SOM to provide CEC is thus more important in highly weathered soils in the tropics than in temperate regions.

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