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The Significance of Soil Microbial Biomass Estimations

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I. INTRODUCTION

It has long been recognized that soil organisms are the driving force behind nutrient transformations in soils and, thus, have a major role in soil fertility and ecosystem functioning. However, without a quantitative method for estimating microbial biomass, nutrient flux models were necessarily empirical. Since the mid-1970s, there has been a surge of interest in measuring soil microbial biomass, spurred by the development of rapid estimation procedures.

The new procedures developed were (1) the chloroform fumigation incubation method (CFIM) [1], (2) the respiratory response (RR) method [2], and (3) ATP measurement [3,4]. These are fairly simple, rapid laboratory methods that provide biomass values for investigations of microbially mediated processes. By measuring both the biomass and the flux of nutrients of interest, a specific process could be described on a pool-size basis. This approach provides a mechanistic analysis of such dynamic systems as nutrient cycles. However, this measurement approach ignores the interaction of the many different individual microbial components that make up the entire system [5]. These individual interacting components may affect and alter process estimations based on whole-system measurements. For example, the C:N ratio of fungal biomass can be quite different from that of bacteria; both groups of organisms are known to have different decomposition rates and also to differ in their abilities to degrade other organic compounds [5].

Microbial biomass estimations have proved useful in a variety of comparative studies of different ecosystems. Comparative studies

have generally measured temporal fluctuations in microbial biomass in natural [6,7] and perturbed [8] systems. The change in microbial biomass values due to single effects such as tillage, soil type, climate, and crops has been the focus of much research [9-11]. Soil microbial biomass measurements have also been used in studies of degradation of added organic chemicals [12,13], residue decomposition [14], and polluted soils [15]. These studies have greatly increased our knowledge of soil system functioning. Even though we have the reasons for and the methods to measure microbial biomass, the values have mainly been used for comparative purposes.

A substantial number of the microbial biomass papers published since 1981 [5] have been entitled, "The effect of . . . on soil microbial biomass" or "The relationship between . . . and soil microbial biomass." In 1984, Paul and Voroney [16] stated, "These [biomass] measurements when combined with tracer techniques and mathematical modeling will help answer questions concerning soil processes of importance to agricultural management and understanding of ecosystem functioning." Basically, the use of biomass values for these important pursuits has been limited to steady-state and comparative conditions. We now seem to understand the significance of microbial biomass values, but the question remains, "What do our microbial biomass values represent and how can be use them to study nutrient cycling?" [17].

In this chapter, we discuss the significance of utilizing microbial biomass values for investigating nutrient cycling in disturbed and nondisturbed ecosystems. We compare the magnitude of the microbial biomass and its role as a source-sink of nutrients. In addition, the contribution of biomass to global C and N cycles is presented to gain a perspective on managing the soil microbial biomass for plant productivity.

II. CYCLING OF SOIL NUTRIENTS BY MICROBIAL BIOMASS

A. Biomass as a Source-Sink for C, N, P, and S

To assess the magnitude of the soil microbial biomass as a source-sink for nutrients, it is necessary to develop a set of standard procedures for measuring each constituent present in the cells. The CFIM procedure is by far the most widely used method for determining soil microbial biomass carbon (C). The major limitation of the method is the definition and use of a proper unfumigated control sample. This problem has recently been addressed by using ^{14}C-labeled straw as an internal standard of the decomposition of native organic matter in fumigated and unfumigated samples [17]. The

use of an internal standard provides a more realistic control for CFIM and reduces instances where negative biomass C values result.

The CFIM has also been used to measure microbial biomass nitrogen (N) by extracting the incubated samples with a concentrated salt solution, such as 2 N KCl [18], and measuring net inorganic N mineralized. As the net mineralized N accounts for only a fraction of the biomass N, a k_N factor is needed. The determination of the k_N factor is not straightforward, as k_N values range between 0.32 and 0.59 for bacteria [18-20], with little N being mineralized from fungi. In subsequent analyses, linear and nonlinear ratios were used to estimate a k_N of 0.68 [21] and a variable k_N dependent on C_F:N_F ratios [22]. With this variation in k_N values, it is difficult to compare biomass N values from different published papers. At the same time, this k_N value, or percent of microbial N mineralized, provides a powerful tool in mineralization-immobilization calculations.

The RR method, which measures CO_2 evolved over short periods after the addition of substrate, is a rapid procedure that has been calibrated against the CFIM. However, the RR method provides only biomass C values. This method can provide estimates of active biomass C when used with tracers, though the results may change over time due to the changing nutrient status of the soil [23].

Methods that measure the ATP content of microbial cells can give variable results because of differing available phosphorus (P) concentrations and other amendments. Similar to the RR method, it provides only biomass C values and must be calibrated through the CFIM or direct microscopy. These three methods have been compared in detail elsewhere [5,24].

Soil P is important in the nutrition of green plants, and its cycling in soils plays a major role in crop production. The method development for soil microbial P has focused on chemical extraction after chloroforming soil. Several extractants, including neutral salts and weak acids, were tested, and 0.5 M $NaHCO_3$ (pH 8.5) appears to be the most efficient extractant [25,26]. In this method, inorganic P is extracted from both a fumigated and a nonfumigated soil, and the difference in extractable P is divided by a k_P factor that has been determined to be approximately 0.40 [27].

The measurement of microbial biomass sulfur (S) has paralleled the methodology development for P. Sulfur in many soils is substantially in organic forms and, hence, subject to microbial mineralization-immobilization cycles. The extraction procedures for S have used 0.01 M $CaCl_2$ or 0.1 M $NaHCO_3$ as the extractant [28,29]. As in the N and P extraction methods, fumigated and nonfumigated samples are extracted, and the quantitative difference in S between the samples is divided by k_S to determine biomass S values. The k_S factor, determined by recovery of S from cells added to soil, was shown to range from 0.35 to 0.41, depending on the extractant [28].

Usually, each of the biomass nutrient extractions is done individually. The $NaHCO_3$ extraction procedure for P and S may be modified to include N. Thus, one extraction procedure would provide estimations of the major nutrient content of the soil biomass. This would give useful information for managing soil biomass for crop production. Direct extraction methods have recently been published for both C and N. These methods show reasonable correlations with the results from CFIM [30-32], and are also more straightforward and becoming widely used [33]. The CFIM, although tedious and subject to misinterpretation (i.e., use of a control and specific k_N), will continue to be used in situations where there are significant short-term changes in both the size and composition of the microbial populations.

Inasmuch as we consider the microbial biomass to be the catalyst in the cycling of C, N, P, and S, the magnitude of the biomass pool will directly affect the nutrient flux. Most measurements have been concerned with microbial C, although in the last few years, microbial N, P, and S pool estimations have been reported in the literature. Most biomass estimations are from temperate zone soils under agricultural cultivation, grassland, or forest. Biomass C and N values from various locations and ecosystems are presented in Table 1, which has been expanded from Smith and Paul [17] to include N values. A significant number of biomass estimations are reported in μg biomass C g^{-1} soil and generally for only the 0- to 10-cm soil depth. In compiling this table, it was sometimes necessary to estimate a bulk density for conversion to kg ha^{-1}. In addition, where biomass conversions were missing, the following values were used: $k_C = 0.41$, $k_N = 0.3$ to 0.4, and cell C content = 40%.

In general, biomass C values increase in the order: arable < forest < grassland. However, the ranges overlap quite significantly. Arable soils range from a low in a Polish oat system of 110 kg biomass C ha^{-1} to a high of 1940 kg C ha^{-1} in a Canadian wheat system. Soil type is a major factor in producing this broad range in microbial biomass values. Forest ecosystems range from 500 to 2180 kg C ha^{-1} in locations from the United States to England. The grassland locations are more varied geographically and contain 280 to 2240 kg biomass C ha^{-1}. The average microbial biomass pool size is 700, 850, and 1090 kg C ha^{-1} for arable, forest, and grassland systems, respectively.

As previously observed, microbial biomass C accounts for 2 to 5% of the total soil C [5], and this continues to hold over a wide range of locations and ecotypes (Table 1). It will be important to determine the relationship of biomass size not only to total organic matter but also to the fraction of organic matter that is active.

Fewer microbial biomass N values than C values have been reported in the literature, but the acceptance of N flush values as an

Table 1 Microbial Biomass Values for Different Vegetation and Soil Types from Various Locations

Biomass (kg ha^{-1})		Soil C (%)	Vegetation type	Soil texture or type	Location	Ref.
C	N					
110	—	0.7	Oats	Loamy sand	Poland	35
170	—	2.1	Scrub	Podzol	Australia	36
225	—	9.7	Maize	Muck	Poland	35
230	—	1.6	Wheat	Clay	England	37
280	40	0.7	Pasture	Sandy loam	Australia	38
288	48	4.7	Cereal-grass	Silt loam	Canada	34
352	108	2.3	Wheat	Loam	Canada	39
430	—	3.5	Pasture	Podzol	Australia	36
440	260	5.6	Barley	—	Scotland	40
460	96	—	Fallow	Clay loam	Sweden	10
460	84	2.6	Sugarcane	Spodosol	Brazil	16
500	146	3.9	Grain	Gleys	Ireland	19
500	130	4.0	Forest	Alfisol	United States	17
523	157	1.5	Wheat	Silt loam	Canada	39
563	—	0.7	Wheat	Mollisol	United States	41
590	273	3.2	Grassland	Silt loam	New Zealand	42
600	—	1.1	Grass	Loam	Pakistan	43
600	80	—	Wheat	Alfisol	England	21
615	—	0.8	Wheat	Aridisol	United States	41
647	116	6.7	Bromegrass	Silt loam	Canada	44
660	—	2.9	Wheat	Silt loam	England	1
700	287	2.7	Bush	—	Nigeria	45
750	100	1.3	Pasture	Clay	Australia	38
760	—	5.5	Cereal	—	Scotland	46
760	216	1.9	Forest	—	Nigeria	45
800	309	6.8	Pasture	Silt	New Zealand	47
910	—	2.8	Arable	Chernozem	Germany	2
1200	—	5.6	Grassland	—	Scotland	46
1200	85	2.6	Grassland	Alfisol	United States	17

Table 1 (continued)

Biomass (kg ha^{-1}) C	N	Soil C (%)	Vegetation type	Soil texture or type	Location	Ref.
1200	240	—	Cereals	Clay loam	Sweden	10
1225	485	5.6	Grassland	Acid browns	Ireland	19
1300	262	2.0	Cultivated	Sandy loam	Poland	48
1500	—	4.7	Grassland	Silt loam	England	50
1600	360	6.5	Wheat	Chernozem	Canada	16
1825	496	5.6	Pasture	Clay loam	New Zealand	42
1850	—	—	Heath	Bog	Norway	49
1940	385	4.6	Wheat	Clay loam	Canada	39
2180	—	6.5	Forest	Silt loam	England	1
2240	—	7.0	Grassland	Silt loam	England	1

indication of biomass N has promoted the determination of biomass N. Microbial biomass N estimates ranged from 40 to 385 kg biomass N ha^{-1} for arable systems, 130 to 216 kg N ha^{-1} for forest systems, and 40 to 496 kg N ha^{-1} for grasslands. The average biomass N is 195, 170, and 225 kg N ha^{-1} for arable, forest, and grassland systems, respectively. These averages should be used with restraint, because of the limited observations in the data base; i.e., forest n = 2. Generally, the microbial biomass N represents 1 to 5% of the total soil N and constitutes a similar pool size across different ecosystems. The C:N ratio of the biomass pool is lower in cultivated systems (3.7) than in forests (5.0) or grasslands (4.8). The lower C:N ratio in arable land can be attributed to the mineralization of soil organic matter caused by tillage together with the extensive use of N fertilizer on cultivated soils.

Phosphorus and S transformations are controlled by both abiotic and biotic factors. In a wide range of soils, 40 to 60% of the P and >90% of the S is associated with the soil organic matter (SOM) component and, thus, interacts with the soil microbial biomass. There is scant information on microbial P and S pools. The data available are presented in Table 2. These biomass P and S values represent arable, forest, and grassland soils. Several values listed in Table 2 were extracted from the literature with some difficulty and should be viewed as relative trends only.

Table 2 Microbial Biomass Phosphorus and Sulfur Pools

kg ha^{-1}					
Biomass					
P	S	Total soil P	Total soil S	% of total P or S	Reference
83	—	—	—	—	51
11	—	360	—	3.0	50
39	—	297	—	13.1	50
67	—	350	—	19.1	50
20	—	734	—	2.7	52
65	—	1400	—	4.6	53
26	—	—	—	—	26
—	6	—	381	1.6	29
—	7	—	308	2.3	28
—	23	—	1420	1.6	54

As a first approximation of the total nutrient content of soil biomass, Anderson and Domsch [51] measured biomass C and used C:N, C:P, C:K, and C:Ca ratios of pure culture organisms to obtain total nutrient contents. For 26 agricultural soils, the average biomass nutrient contents were 108, 83, 70, and 11 kg ha^{-1} for N, P, K, and Ca, respectively. These correspond to ratios of 5.3 and 7.0 for biomass C:N and C:P, respectively. In contrast, Brooks et al. [50] reported biomass C:P ratios of 25, 18, and 11 for cultivated, grassland, and woodland soils, respectively. Wide variations in biomass C:P ratios between ecotypes may be caused by erroneous k_P values or varying C:P ratios. Biomass C:P ratios for pasture soils have been reported to range from 21 to 24 [52,55], whereas for several acid organic soils the average ratio was 10 [53]. More research is needed to refine the methods for analyzing soil microbial P. The studies cited show a range of microbial biomass P to total P of 2.7 to 19.1%, which accounts for a substantial pool of potentially available P for plant growth.

Many agricultural and forest soils have been found deficient in S, particularly in semiarid regions and regions where acid rain is low or nonexistent. Only a few studies have measured soil microbial S (Table 2). The values range from 7 kg S ha^{-1} in arable systems [28,29] to 23 kg S ha^{-1} in some acid organic soils [54].

Approximately 3 to 8% of the total S was estimated to be in an active pool (i.e., a rapidly turning over labile pool) that contributed to S cycling [56,57]. Estimates of the soil organic S in the biomass fraction have ranged from 1.3 to 2.3% over significantly different soils [28,29,54]. The C:S ratios in two studies were calculated to be 52 for eight arable soils in Scotland [29] and 84 for two cultivated prairie soils in Canada [58]. The overall magnitude of the microbial S pool is generally lower than that of the N and P pools, although the proportion of microbial NPS to total NPS is similar.

The estimates of pool sizes for microbial biomass C, N, P, and S suggest that these pools are large enough to have significant impacts on plant nutrient availability. In the Pacific Northwest, a winter wheat crop will produce 16 tonnes ha^{-1} of dry matter for a 6.7 tonne (100 bu Ac^{-1}) grain yield. Using average nutrient concentrations of wheat N, P, and S, we calculate that 302, 36, and 32 kg ha^{-1} of N, P, and S, respectively, are taken up and utilized by the aboveground plant biomass. The average N, P, and S contents of the microbial biomass pool for these silt loam soils are 180, 17, and 9 kg ha^{-1}, respectively. Thus, 60, 47, and 28% of the N, P, and S requirements of the aboveground plant biomass are contained in the microbial biomass. Paul and Voroney [16] have provided a similar calculation for C and N turnover in a Canadian wheat-fallow system, Rothamsted long-term wheat plots, and a Brazilian sugarcane field. The estimated microbial N pool was significantly larger than the amount of N removed by a low grain yield wheat crop but only 38% of the annual requirements of the sugarcane crop.

A major supply of N for plant growth is obtained from SOM through microbially mediated mineralization processes. The entire process of mineralization-immobilization turnover (MIT) can provide 50% or more of the annual N needs of an agricultural crop, while resulting in an internal N cycling of two to four times that of plant uptake. In terrestrial ecosystems, MIT is the limiting constraint on yearly N availability. The MIT process was recognized as being affected by temperature and moisture and, thus, predictive efforts focused on relating N availability to abiotic parameters, even though a biological process was involved. Upon further model refinement, soil properties, such as SOM, pH, and clay content, were considered in estimating the N-supplying power of soils, although biological tests, mainly incubations, to determine mineralizable N appear to be the most reliable method of determining N-supplying capacity. In developed countries, the cost of N fertilizer has been so low that tests for mineralizable N have not been deemed economically prudent. Residual inorganic N in the root zone and estimates of N mineralized (1 to 3% of SOM) provide the information necessary for determining crop fertilization.

Table 3 Nitrogen Mineralization Rates from Incubation or First-Order Kinetic Analysis

Ecotype	Nitrogen mineralization: Daily rate[a] (μg N g^{-1} soil day^{-1})	Nitrogen mineralization: First order[b] (wk^{-1})	Reference
Eucalyptus	0.07	—	59
Forest	—	0.061	60
Conifer	0.21	—	61
Range	—	0.057	62
Grassland	0.26	—	63
Tea	0.19	—	64
Arable	—	0.051	65
Cultivated	0.03	—	66
Arable	—	0.123	67
Arable	—	0.130	68
Arable	—	0.040	69
Hardwood	0.55	—	61
Cultivated	—	0.100	70
Cultivated	—	0.100	71
Cultivated	0.40	—	72
Arable	0.40	—	73
Cultivated	—	0.054	74
Arable tropics	0.54	—	75
Coastal plain	0.82	—	76
Arable	—	0.193	77
Arable	1.11	—	44
Grassland	1.05	—	65
Arable	3.00	—	78

[a]Most commonly based on net production from incubation studies, i.e., μg N g^{-1} soil during X weeks of incubation.

[b]Based on first-order kinetic analysis, such that $N_t = N_0(1 - e^{-kt})$, N_t being the N mineralized over the entire year.

With increasing interest in cropping system efficiency and concern about ground water contamination by agricultural chemicals becoming a national issue, renewed interest in mechanistic studies of N MIT has arisen. The development of laboratory procedures for microbial biomass determinations has advanced our capabilities to study MIT on a more refined level and to expand our knowledge of the biological processes involved. This, incorporated with site management techniques that involve alternative sources of N such as legumes, N applications to coincide with peak uptake periods, varying the NH_4/NO_3 fertilizer ratio, and possibly leaf tissue analysis, can have a major input into sustainable agriculture.

Table 3 represents a variety of studies that determined N mineralization rates as net mineralization over various time periods or that performed a kinetic analysis based on first-order kinetic theory [74]. There are no definable trends of mineralization rates between different systems or even within the same ecotype. Mineralization of organic reserves does not occur as a steady-state process over the course of the year, but then neither does plant uptake. A limited analysis of various crop N uptake patterns has shown the N uptake rates to range between 0.5 and 2.0 kg N ha^{-1} day^{-1} [81]. Mineralization rates for agricultural soils calculated from Table 3 are 0.7 kg N ha^{-1} day^{-1}. However, the rates will be higher during the maximum plant uptake period, with ultimately 50% of the N needed by the plant coming from mineralized soil N.

In contrast to N mineralization, few studies have been conducted to analyze rates of P and S mineralization. The procedures for studying and interpreting P and S mineralization rates are complicated by chemical precipitation and occlusion, which increases apparent biological immobilization. Table 4 gives several references for P and S mineralization rates. Phosphorus production rates apparently increase fivefold from arable to woodland systems. Sulfur mineralization production was variable in the arable land and highest for a grassland system.

Mineralization of plant nutrients from SOM is a major function of the soil microbial biomass. This mineralization, if timely, can supply a growing crop's need for major nutrients. However, the biomass can also cause immobilization, which competes for plant nutrients. Fluctuations in microbial biomass can cause significant increases or decreases in nutrient pool size and turnover, which can control the fate of nutrients in the system.

B. Energy Flux Through Microbial Biomass

Generally, the growth and functioning of the soil microbial biomass is limited by C. The substrate availability in microbial habitats is low but fluctuares throughout the year influenced by abiotic factors.

Table 4 Phosphorus and Sulfur Mineralization Rates for Various Systems

Ecotype	Nutrient	Mineralization rate ($\mu g\ g^{-1}$ soil day^{-1})	Reference
Arable	P	0.02	50
Grassland	P	0.06	50
Woodland	P	0.19	79
Arable	S	0.04	57
Cropped	S	0.09	80
Arable	S	0.10	72
Grass	S	0.12	73

When flushes of substrate C are input into the system, the microbial biomass increases in size until the substrate is depleted. The system does not immediately return to equilibrium with native C substrate availability, as the biomass has doubled or tripled in size. The system will return to equilibrium according to the relaxation rate constant, which describes the rate of return to steady state. The return to a static level of biomass is controlled not only by C substrates but also by the clay protection level [82]. This pulse-relaxation cycle occurs during periods of rapid C solubilization and/or C input, such as precipitation on dry soil or a freeze-thaw cycle, or upon residue incorporation. In contrast, the input of C during plant growth, from fine root turnover and root exudation, will cause a semipermanent change in microbial biomass levels rather than a pulse-relaxation event. This continuous "feeding" of the soil biomass differs from the rapid C input in affecting nutrient cycling. In the feeding mode, the population may either increase to a new stationary level and immobilize significant amounts of nutrients or become more active and, thus, put through greater amounts of organic compounds rich in N, P, and S. The rapid C input causes immediate uptake with a slow release.

Energy flux through microbial biomass is the driving force for the decomposition of residue and detrital material. This energy flux determines whether the system is building or depleting the SOM pool. If the decomposition rate is equal to the rate of litter input on an annual basis, the system is at steady state. If decomposition exceeds C inputs, the soil organic matter will decline and C and N will be lost over time. These C and N increases or decreases will be dependent on residue substrate quality, the fluctuation of microbial biomass, and the kinetic decomposition rate.

In modeling C and N dynamics, such as the fate of plant-assimilated C, residue decomposition, N mineralization, or microbial biomass growth, the mechanism of choice has been the first-order rate reaction [74,71,83]. A first-order rate process is assumed to be dependent on the concentration of a single variable. Even though the microbial biomass is a catalyst in decomposition dynamics, it is often considered to be at a constant level throughout the process. The actual kinetics of decomposition, biomass growth, or N mineralization can also be described by second-order kinetics, catalysis reaction equations, or enzyme reaction theory. With various assumptions, these biochemical reaction equations reduce to similar sets of mathematical estimations. In a chemical kinetic model, the substrate changes according to

$$\frac{dS}{dt} = -k[B][S] \tag{1}$$

where S = substrate, B = biomass catalyst, and k = reaction rate constant. If the catalyst is constant, the requirement that the concentration of one reactant is not significantly changed by the reaction is satisfied. Thus, equation (1) is reduced to a pseudo-first-order rate reaction that combines k and B into an apparent rate constant (k'_{app}), with a first-order form of

$$\frac{dS}{dt} = -k'_{app}[S] \tag{2}$$

Equation (2) is a time-rate law rather than a true concentration rate law, where k is constant and B and S vary.

Using equations developed for catalyst reactions, the product formation can be described as

$$\frac{dP}{dt} = \frac{kC_0S_0}{S_0 + K_m} \tag{3}$$

where P = product, k = rate constant, C_0 = initial catalyst concentration, S_0 = initial substrate concentration, and K_m = a rate constant ratio. This equation is the Michaelis-Menten equation for enzyme kinetics, where $V_{max} = kC_0$. Equation (3) reduces to

$$\frac{dP}{dt} = \frac{k}{K_m} C_0S_0 \tag{4}$$

if $S_0 <<< K_m$, which is first order with respect to S_0 but is second order if both reactants are fluctuating. Viewing the Michaelis-Menten equation, the same situation reveals a first-order equation, as the total enzyme or catalyst concentration is implicitly expressed in V_{max}. In the case that $S_0 >>> K_m$,

$$\frac{dP}{dt} = kC_0 \tag{5}$$

which is zero order with respect to S_0, but the product formation is dependent on the concentration of C_0. Microbial growth models are similar to equation (5) where substrate input is much greater than the biomass population, resulting in a first-order exponential population increase to V_{max}.

In laboratory experiments designed to monitor microbial growth, residue decomposition, or product formation, environmental parameters can be adjusted to influence the rate of reaction. In this situation, the microbial biomass or catalyst can be maintained constant over periods of weeks. In field situations, microbial biomass may be visualized as a constant catalyst in the short term but not necessarily over an annual cycle, when biomass fluctuations occur. Thus, laboratory incubations may be best described by first-order or zero-order reaction rates [84] and yearly field processes by second-order kinetics. In any ecosystem, the entire annual cycle must be considered, in order to balance energy inputs with microbial growth and residue decomposition. Assuming the microbial biomass to be constant and at a maximum will overestimate C and N processes affecting the yearly C and N flux values.

One of the major problems associated with characterization of C flux has been the inability to balance the input C substrate to the microbial energy requirement on an annual basis. The basic process of energy flux through organisms is dependent on the energy needs of the organisms for growth and maintenance. The soil microbial biomass is generally C limited; thus, the priority for energy flux is to satisfy the maintenance requirement. The maintenance energy concept for microbes in soil has been debated since the early 1970s. Maintenance energy is required for internal cell functions, such as RNA turnover and osmotic work [85]. It is assumed that all organisms require energy to maintain biochemical functions. In soil, this concept is complicated by the fact that only a small segment of the total microbial population is active at any particular time [3]. In addition, it is not known whether active and inactive organisms have the same maintenance energy requirements [41,86,87]. If the biomass is not considered to have active and inactive phases, it is not surprising that on an annual basis the calculated maintenance energy requirement for the soil microbial biomass exceeds the C input [86, 88,89]. The maintenance equation is

$$m = \frac{a}{Y} \tag{6}$$

where m = the substrate maintenance coefficient, a = the specific maintenance rate, and Y = the assimilation yield. The specific maintenance rate (a) is related to biomass energy use for maintenance activities, whereas the maintenance coefficient (m) is the total substrate utilized for assimilation and maintenance. When considering C flux, we are interested in the total C use or m. Values for the specific maintenance rate in different soil systems span two orders of magnitude, from 3.4×10^{-4} to 4.0×10^{-2} h^{-1} for temperatures near 20°C [41,86,90-92]. Most of the values were extrapolated from the literature or estimated from substrate inputs and steady-state assumptions. Recently, an approach was used to calculate maintenance energy from product formation, which can be measured accurately [41]. The values from this approach, 3.2×10^{-4} to 4.6×10^{-4} h^{-1}, are the lowest that have been reported for active organisms at steady state. Specific maintenance values for dormant organisms were estimated to range from 1.0×10^{-4} to 1.9×10^{-4} h^{-1}, two to three times lower than those for active organisms [86,87].

A summary of annual substrate C relative to microbial maintenance requirements in soil is shown in Table 5. The substrate input estimates usually included those for roots and root exudates. The use of an average specific maintenance rate of 2.0×10^{-3} indicated that, in no case, would the substrate input meet the C requirements. The second approximation was based on a specific maintenance of 3×10^{-4} h^{-1} [41]. In this scenario, there were several instances where C input equaled or exceeded maintenance C requirements. The third estimate used the concept that 40% of the biomass is active with a maintenance requirement of 3×10^{-4} h^{-1} and 60% is inactive with specific maintenance being 1.5×10^{-4} h^{-1} [41,86]. Even though this reduced the annual C requirement of the biomass for maintenance, in most instances there was still little C remaining for growth. The fourth estimate was calculated using 15% active and 85% inactive organisms, a ratio often found from staining procedures using fluorescein diacetate and one reported from the isotopic dilution calculations of Paul and Voroney [16]. Reducing the active population reduces the maintenance requirement, although larger reductions occur from decreased biomass values or maintenance rates.

The biomass values used in the above calculations are assumed to be a yearly mean. However, as C flux is calculated over time, maintenance requirements should be based on temporal biomass values. In many systems, the decomposition of plant material added to soil is 50% complete within 1 to 2 months [83,93], during which time the microbial biomass is maximal. During the rest of the year, biomass values may be less than half the maximum values.

Table 5 Annual Substrate C Input and Microbial Maintenance Requirements in Soil

Microbial biomass (kg C ha^{-1})	Substrate input (kg C ha^{-1} yr^{-1})	Maintenance requirement[a] (kg C ha^{-1} yr^{-1})				Reference
		a = 0.002 h^{-1}	a = 0.0003 h^{-1}	b	c	
570	1200	16,644	2497	1748	1439	5
240	2500	7,008	1051	735	605	90
184	3820	5,373	806	565	465	91
1472	3100	42,982	6447	4513	3707	82
1122	2380	32,762	4914	3440	2825	82
200	3540	5,840	876	613	503	37
600	740	17,420	2628	1839	1511	89

[a]Calculated using m = axt/Y; t = 1 year; Y = 0.6; see Section II.

[b]Assuming that 40% of the biomass is active [41], with a = 0.0003 h^{-1}, and that 60% of the biomass is inactive, with a = 0.00015 [86].

[c]Assuming that 15% of the biomass is active and 85% of the biomass is inactive, with the same maintenance rates as in footnote b.

C. Constraints Controlling Microbial Biomass Size

Although the size of the soil microbial biomass is principally related to C inputs, other mitigating factors can suppress the growth and activity potential of the native microflora. This situation is illustrated by subarctic systems with significant C reserves and relatively small microbial biomass populations [94]. Other constraining factors include N, P, and S, water potential, soil aeration and pH, substrate quality, clay type, and osmotic pressure.

Soil water potentials of -0.01 to -0.05 MPa are close to optimum for both bacteria and fungi. As the system becomes drier, bacteria start to lose activity at -0.5 MPa to a lower limit of -8.0 MPa. Fungi, however, have a lower activity threshold, still being active at -4.0 to -10.0 MPa. Although the range of potentials from -0.01 to -0.4 MPa provides for an active environment for biomass, as the water potential changes so does the composition of the microbial population, mainly due to substrate availability. This population shift is also seen with soil aeration.

A major constraint on the microbial biomass pool size in soils is the magnitude of the soil carrying capacity. The carrying capacity is defined as the level of biomass that a soil can sustain under steady-state conditions. As energy is the major limiting factor for microbial growth in soil, the carrying capacity has generally been related to C inputs. However, other factors, such as soil aggregation and clay content, influence the magnitude of the biomass by altering ecological niches and providing protection from predation. In modeling C dynamics in grassland systems, it was found that decomposition products and recalcitrant organic matter were physically protected from rapid decomposition [95]. Physical protection had more influence on equilibrium C levels than on decomposition of plant residues. Four years after addition of labeled plant material, more residual ^{14}C and ^{15}N were found in the biomass of soils higher in clay content [93]. After eight years of decomposition, only 12% of the ^{14}C input and 35% of the ^{15}N input was recovered; however, the differences in biomass ^{14}C and ^{15}N between soils with varying clay contents still existed. Incubation of one of the same soils with ^{14}C- and ^{15}N-labeled plant material showed lower immobilization-mineralization rates and more labeled biomass in the clay-textured soil [96].

Different management practices can cause variations in SOM and constrain native soil biomass levels [10]. These findings suggest that the carrying capacity of a soil is dictated by the dynamic interaction of mineral particles, soil organic matter, and soil microbial biomass. In some systems, biomass capacity is low, process rates are accelerated, and microbial biomass does not accumulate. In other systems, organisms are protected from predators and extreme environmental fluctuations, creating an environment where higher levels of biomass can exist.

D. Rhizosphere Versus Nonrhizosphere Nutrient Cycling

Carbon flux through plant roots may release appreciable amounts of photoassimilated C into the root rhizosphere zone [97-99]. This carbon input is thought to fuel microorganism growth until the substrate is exhausted. The rhizosphere zone is one of intense activity, with competition for nutrients between organisms and plant roots being a dominant process. The magnitude of the carbon flux will influence microorganism growth, nutrient flux, and the efficiency system with respect to nutrient cycling.

In sand culture with $^{14}CO_2$ exposure to growing plants, 20 to 25% of the total C fixed was lost from the roots of barley and wheat [97]. Other studies found that 16, 33, and 30% of total assimilated C were transferred to the belowground system. Most of the carbon was respired as CO_2, a significant amount was in the root system, and usually little was deposited directly in the soil [99,101]. A recent study with tree seedlings showed 17% of the assimilate in the soil microbial biomass and 33% in the SOM [98]. These high levels were attributed to the extensive occurrence of ectomycorrhizal fungi. The rhizodeposition of C is affected by plant species, age, and development, as well as by environmental factors and nutrient levels [102,103]. Total C input to the soil (CO_2 + roots + soil) for cereal crops ranges from 941 to 2300 kg C ha^{-1} [104-106]. Comparing these values with litter substrate input (Table 5) shows that rhizodeposition of C can double the total yearly input of C to soil systems.

Microbial growth in the rhizosphere is rapid but only for a few days for a particular segment of root material [107]. Thus, for a single root growing through the soil, the biomass in the rhizosphere of the growing segment may be growing rapidly, whereas biomass farther up the root is declining. This situation is complicated by the interaction between roots, particularly fibrous roots systems, where organisms may be affected by more than one root. Most studies assume that the rhizosphere encompasses a thin area around the root of 1 to 3 mm where most of the substrate is consumed. However, the zone of influence is related to soil diffusion properties and nutrient availability.

A model that simulates rhizosphere organism growth shows substrate decreasing away from the roots and, thus, declining populations away from the roots [107]. Few studies have actual data showing that this situation exists, although in one study of the ratio of rhizosphere to root-free soil organisms, the ratio for fungi was 12 and for bacteria 23 [108]. This describes the situation where the rhizosphere is dominated by bacteria, which may be more dependent

on the close proximity of substrates. In a rye system, the numbers of bacteria did not differ in rhizosphere and bulk soil; however, the measured CO_2 evolution was almost three times greater for soil taken close to the roots [109].

Carbon flow from plants to the belowground soil system has been sufficiently demonstrated for a number of plant species, although quantities and distributions differ substantially due to varying conditions. The hypothesis of many C flow studies is that C flow to stimulate rhizosphere organisms is a plant strategy to increase favorable conditions for growth and increase nutrient uptake [109-111]. In this C flow scenario, mycorrhizae and rhizobia are not considered, as C flux to the root is a cost borne by the plant for a symbiotic relationship. If the plant is exuding C to the rhizosphere microflora, what are the benefits? If most of the C exudates are sugars and organic acids, we would expect a great deal of immobilization of N and P by the rapidly developing biomass population. This, it would appear that the plant is inducing competition for nutrients—an unlikely successful strategy. The other hypothesis is that intense microbial rhizosphere activity increases nutrient turnover and plant uptake. Microbial biomass and phosphatase activity have been shown to be increased by plant roots in several zones adjacent to the roots [110, 111]. In general, few studies report the effects of C flow on nutrient dynamics. Most studies have measured enzyme activity, biomass increases, and specific organism concentrations [112]. The actual nutrient transformations and transfers have eluded our attention.

III. MICROBIAL BIOMASS AS AN ECOLOGICAL MARKER

In the last several years, there has been increasing concern over the role of man-made chemicals in the degradation of the natural environment. The concern resulted in an environmental movement that is worldwide, unified, and politically strong and is demanding a halt to the degradation of the environment, accountability by polluters, and reclamation of devastated lands. Part of the concern is focused on toxic chemical waste dumps, both legal and illegal. In addition to toxic dumps, the clear-cutting of forests, acid rain pollution, and agricultural soil disturbance are other examples of ecosystem perturbations. The impacts of these ecosystem disruptions are sometimes difficult to determine, because each system has differences in sensitivity and resilience. However, a commonality of these disturbances is that the soil microbial biomass is affected to varying extents and may provide a measurable ecological marker for perturbed systems.

A. Effect of Tillage and Management Practices on Microbial Biomass

It is well documented that tillage reduces soil organic matter C and N levels. In North American prairies, the loss of C and N is estimated to have been 60 to 70% over the last 70 years [113]. In Queensland, Australia, Dalal and Mayer [114] found that both C and N losses averaged 36% in soils cultivated for 20 to 70 years. In addition, they found that 17% of the P and 30% of the soil S were lost. Tillage-induced SOM losses directly reduce microbial substrates and, thus, soil microbial biomass levels.

Comparisons of no-till and conventional till (moldboard plowing) have generally shown lower microbial biomass levels in tilled soils. Lynch and Panting [6,37], comparing biomass values from plowed and direct drilled wheat fields at various times during the year, found greater amounts of biomass in the direct drilled fields than in the plowed fields. When N was applied, microbial biomass increased in direct drilled plots but not in plowed plots. The need for more N fertilizer in no-till systems has been attributed to the immobilization of N by the microbial biomass present in the surface of these plots.

Redistribution of microbial biomass occurs when no-till practices are used. With reduced tillage, residues are concentrated in the surface layer, causing an increase in microbial biomass as the result of concentrated substrate input. Carter [34] found that zero tillage increased the microbial biomass C and N in the 0 to 5 cm zone by 10 to 23% over shallow tillage. The biomass in the lower depths of the zero-tilled soil decreased with time, probably because of lack of substrates. Doran [115] showed differences in the number and types of microorganisms in soil under no-till. He also determined that the average metabolic status of the greater population under no-till was less oxidative and that differences in biomass levels were related to soil water content, concentrations of organic C and N, and pH. When N mineralization potentials for seven U.S. locations were measured, the N_0 potentials of no-till soils were 20 to 101 kg ha^{-1} greater than those of conventional-till soils, most likely due to increased levels of microbial biomass in no-till systems [116]. Carter and Rennie [39] reported significantly greater mineralization potentials in the 0 to 5 cm depth of zero-tilled versus conventional-tilled soils of western Canada. However, the mineralization potentials in the 5 to 10 cm depth were higher in the tilled soils, due to a larger biomass pool, than in the no-till soils at this depth.

The concentration of biomass in the surface layer of no-till soils could be beneficial from the standpoint of organism versus root competition for fertilizer N. With most of the biomass in the top 5 cm, it should be possible to place fertilizer below this active zone. Less

immobilization would allow enhanced plant uptake but might also promote N leaching. In a field study using ^{15}N-labeled urea fertilizer, Carter and Rennie [117,118] investigated soil microbial N transformations in no-till and shallow-tillage systems. Microbial biomass levels in the 0 to 5 cm soil depth of no-till systems were 48% higher and inorganic N levels 62% lower than those of shallow-tillage systems. Less residual fertilizer N remained in the biomass and more was transformed to SOM in no-till compared with shallow-tilled soil. This pool distribution resulted in three times more residual N uptake by spring wheat from shallow-tilled and no-tilled soil in a subsequent pot test.

Crop rotations affecting microbial biomass would make it possible to manage residues and rotations for the benefit of each crop. McGill et al. [89] studied the nutrient dynamics in a Canadian luvisol after 50 years of cropping to a 2-year rotation (wheat-fallow) or a 5-year rotation (wheat-oats-barley-forage-forage). Their results showed that the soil cropped to the 5-year rotation contained greater amounts of SOM C and N and microbial biomass. Microbial turnover in the 2-year rotation was twice as fast, even though the 5-year rotation had twice the input of C into the soil and a greater percentage of C and N in biological form. Carter [34] found significant reductions in microbial biomass in wheat-fallow rotation compared with continuous wheat, which suggests that substrate depletion causes parallel reduction in biomass. Granatstein et al. [119] found differences in biomass levels related to tillage but little difference when comparing rotations. The lack of significant differences between rotations may have been due to having a legume in each rotation, as on a short-term basis, a current crop affect on biomass levels was evident.

B. Microbial Biomass as an Indicator of Chemical Toxicology

Public awareness of chemical contamination of the environment has increased because of publicity and increased awareness of the resulting manifestations. Poisoning of lakes and streams by acid rain, ground water contamination by herbicides, and toxic waste spills have raised fundamental questions concerning suitable monitoring procedures to determine the effects on the environment. To determine the effects of chemical contamination on specific environmental parameters, a sensitive test related to biological components is needed. For soils, microbial biomass measurements may provide the information needed for ecosystem-level monitoring for initlal disturbance and recovery.

Microbial biomass of plots receiving sewage sludge over an 8-year period increased with increased addition [120,121]. There was also a decrease in the C:N ratio in the treated plots, showing an elasticity

in the microbial pool which can damp the surge of mineral N release. Soils contaminated with heavy metals from sewage sludge showed lower levels of biomass than soils treated with manure low in metals [122]. Malik and Azam [43] showed significant differences in microbial biomass and plant decomposition in saline and saline-sodic soils. The biomass concentration decreases in the order normal > saline > saline-sodic.

In addition to periodic toxic chemical problems, a significant proportion of cropped land receives regular applications of herbicides and insecticides. These chemicals can upset the microbial ecology of soils and damage nontarget organisms. Anderson et al. [123], using the respiration response method, determined the relative ratios of bacteria to fungi in the presence of several fungicides. They found that as little as 5 $\mu g\ g^{-1}$ caused a 40% reduction in biomass levels. At 50 $\mu g\ g^{-1}$, long-term damage to the microflora occurred, with all fungicides altering the ratios of bacteria to fungi. The use of population diversity measurements in conjunction with total biomass estimates is a powerful management tool in ecological systems. In a study using fungicides [124], it was shown that initial CO_2 production from soil increased, followed by a decrease after another fungicide application. Increased activity (CO_2) could be shown for up to 10 weeks in the treated soil compared with the untreated control. Measurements to determine the decomposition of diallate and triallate at various moisture contents showed a significant relationship between water content, biomass quantity, and decomposition of herbicide [125].

Deposition of atmospheric chemicals is a serious problem for industrialized nations, as it is directly related to fossil fuel combustion. By the nature of the vector, the atmosphere, the problem can move vast distances with mass airflow. The effect on surface waters has been devastating; however, little information concerning soil systems has been gathered. Two constituents of acid rain, SO_2 and NO_2, have been shown to decrease the pH of surface soils [126,127], but only SO_2 significantly reduced microbial populations and heterotrophic activity. Another study exposed unpolluted soil cores to heavy atmosphere pollution (125 $\mu g\ SO_2\ m^{-3}$) for 1 year; no significant differences in enzyme activities, soil respiration, or microbial numbers were found [128].

Much of the research on acid rain has been conducted by subjecting soil samples to various concentrations of mineral acids, such as H_2SO_4 and HNO_3, measuring such effects as reductions in CO_2 production and enzyme activities. Most studies have not included microbial biomass measurements, possibly due to problems associated with using the fumigation method with acid soils. Bewley and Stotzky [129,130] found that acidification had little effect on respiration until the pH of the soil was reduced to below 3.0. Increasing the pH, after lowering, restored activity unless the pH had previously

decreased below 1.5. Their study also showed that clay minerals, specifically montmorillonite, reduced the effects of acid rain. In a forest soil of neutral pH, little inhibition of respiration or enzyme activity occurred until the soil pH was lowered to 2 [131]. Stimulation of enzyme activity at pH values of 3 and 4 occurred, although responses of specific enzymes varied. The authors postulated that stimulation of activity by acid rain may be due to alteration of the C and N availability to the microbial biomass. In two field studies in Florida, enzyme activities and respiration were not significantly reduced when simulated acid rain reduced the soil pH to 3 to 3.7 [132,133]. The varying effects of acid rain on soil microbial biomass shown in these studies are most likely due to variations in soil properties, such as buffering capacity and clay content, rather than to differences in the makeup of the organism population.

C. Microbial Biomass and the Recovery of Disturbed Areas

As an ecological marker, soil microbial biomass measurements are useful in determining the degree of disturbance and also subsequent system recovery. From the viewpoint of soil productivity, the soil biomass controls the major processes involved in nutrient transformation and cycling, SOM maintenance, and macroaggregation for favorable water and aeration characteristics.

A 5-year study in New Zealand on plots stripped of topsoil showed that restoration of the soil could be related to changes in biochemical properties of the soil [134,135]. During the initial 3-year period after disturbance, the seven enzyme assays and three different methods for biomass measurements correlated with herbage production on plots stripped of 10 and 20 cm of topsoil. Microbial biomass, as well as most enzyme activity measurements, increased over the 3 years after disturbance, with invertase and sulfatase showing the most significant correlation with crop yield. Microbial biomass continued to increase after herbage yield had leveled off in the second year of the study, which decreased the correlation between the two parameters. This biomass buildup of C may provide a better index than plant yield for soil restoration and stability.

In mine spoils of various age and states of restoration, microbial activity was lower than in native sites [136]. The accumulation of C and N was related to increased microbial activity and increased to levels similar to that of native soils after 20 years of recovery. Mineralizable N recovered rapidly, although after 20 years, it was still 50% of the value for the undisturbed soil. In reclaimed coal strip-mine spoils, ATP was the most useful indicator of microbial activity [137].

Forest clear-cutting can be the most drastic disturbance that large areas will encounter. Significant land areas are being cleared yearly, and yet the ecology of the recovering soil is little understood. There was a 40% reduction in fungal biomass after clear-cutting in central Sweden, with a smaller reduction if the slash was not removed [138]. This effect had also been reported for a spruce forest after cutting [139]. Land treatment after clearing affected not only microbial biomass values but also N transformations [140]. In an ^{15}N study, less biomass, less immobilization of N, and greater nitrification rates in treatments were found when tree residues were raked and the soil disked compared with chopping the residue in situ.

It has been argued that biomass measurements are not uniform across systems and may only be relative, but as an ecological marker, relative biomass change over time should be sufficient for prediction of system recovery. With the addition of monitoring changes in ratios of fungi to bacteria and in species diversity, biomass estimation could be a powerful prediction method.

VI. SIGNIFICANCE OF MICROBIAL BIOMASS IN GLOBAL C AND N CYCLES

A. Soil C and N in Terrestrial Ecosystems

A significant number of soil microbial biomass values are available for temperate systems but few or none for tropical or tundra ecosystems. Work has focused on agricultural land, which constitutes only 10% of the total terrestrial land area. With the CO_2 concentration of the earth's atmosphere increasing, it will be important to estimate the effect of global warming on C fluxes between major C pools.

The total terrestrial land area has been estimated to be 149×10^{12} m^2. Excluding ice, rock, and streams, the surface area is 122×10^{12} m^2 [141]. This area has been divided into the 12 ecosystem types shown in Table 6. Carbon and N densities were taken from an exhaustive study by Zinke et al. [142], where more than 3500 soil profiles were analyzed. From the density to a depth of 1 m, the total C and N contents of each ecotype are calculated and presented as gigatons (Gt = 10^{15} g) of C and N.

The land areas of the boreal forest, tundra, and swamp marshes account for 18% of the total land area but contain 37% of the soil C and 31% of the soil N storage. Tropical forest land contains 25 and 22% of the terrestrial C and N, respectively, while temperate forest and cultivated land contain 8 and 13%, respectively. The total global soil C has been estimated to be 700 to 3000 GtC; however, the most cited estimate is 1400 Gt [143]. In Table 6 the lower value of 1348 GtC reflects the merging of ecotypes and small variations in reported land areas.

Table 6 Total Carbon and Nitrogen Content of Terrestrial Soil Systems

Ecosystem type	Area (10^{12} m^2)	Carbon[a] density (kg m^{-2})	Nitrogen[a] density (kg m^{-2})	Soil carbon (Gt)	Soil nitrogen (Gt)
Tropical rain forest	17.0	15.3	0.76	260	12.9
Tropical seasonal forest	7.5	10.6	0.94	80	7.0
Temperate evergreen forest	5.0	12.7	0.78	64	3.9
Temperate deciduous forest	7.0	7.1	0.66	50	4.6
Boreal forest	12.0	15.5	1.10	186	13.2
Woodland and shrubland	8.0	5.4	0.32	43	2.6
Savanna	15.0	5.4	0.32	81	4.8
Temperate grassland	9.0	10.5	0.79	95	7.1
Tundra and alpine	8.0	21.8	1.15	174	9.2
Desert scrub	18.0	3.3	0.26	59	4.7
Cultivated land	14.0	7.9	0.84	111	11.8
Swamp and marsh	2.0	72.3	2.90	145	5.8
Totals	122.5	—	—	1348	87.6

[a]To a depth of 1 m.

Sources: From Refs. 141 and 142.

B. Global Biomass Estimates

Only a few values of global microbial biomass C and N exist, most being derived from an estimate of microorganism density (100 g m^{-2}) multiplied by land area [144]. The estimates assume cell contents of 50% C and 4% N and range from 3.4 to 6.6 Gt C and 0.5 Gt N. In an earlier attempt, we estimated the global microbial biomass C to be between 2.8 and 8.8 Gt, depending on the method of calculation [17]. Table 1 showed a wide diversity of biomass values for different vegetation types and management systems. Even if some of these variations can be attributed to differences in methodology, one cannot take a single average biomass estimate and multiply it by the areas of the various ecotypes shown in Table 6. Similarly, although biomass N generally ranged between 2 and 5% of SOM, there was no overall significant correlation between these two parameters in Table 1. The ecosystem types shown in Table 6 have been merged into six systems, which make up 95 × 10^{12} m^2 and represent approximately 77% of the terrestrial land area. Woodland, desert scrub, and swamp areas are not included in the subsequent analysis, and cultivated land is included with temperate grassland. These condensed systems contain 82 and 86% of the total terrestrial soil C and N, respectively.

The biomass values shown in Table 7 represent a summation of available literature values for the total organism C and N in the surface 10 cm of soil. The temperate grassland has the highest concentration of biomass, followed by the temperate and tropical forest systems. The grassland has one of the lowest plant biomass pools, but litter input is relatively high. The low biomass C pools of the boreal forest and tundra reflect the influence of colder environments on biological pools. The grassland area is significantly higher in biomass N than any other ecosystem, producing the lowest organism C:N ratio. This high N content may be due to the efficiency of the decomposition of litter input, where the grassland system retains most of its N during the cycling process relative to other systems. Inasmuch as this also includes cultivated soils, the effect of N fertilization will also be shown.

The total biomass content of these terrestrial systems is 6.0 Gt C and 0.9 Gt N. These estimates for C are similar to previous estimates; however, they are twice as high for N. When estimating biomass content for the same land areas from organism density [144], the total global microbial C and N are 5.3 and 0.2 Gt, respectively.

C. Global C and N Cycling Through Microbial Biomass

For gross C flux calculations, the global terrestrial system is considered to be at steady state (i.e., C inputs = C outputs), emphasizing the role of microbial biomass in decomposition and C cycling. In

Table 7 Plant Biomass and Net Primary Productivity (NPP), Litter Input, Soil Organic Matter, and Microbial Biomass Pools of Major Global Vegetation Types[a]

	Tropical forest	Temperate forest	Boreal forest	Savanna	Temperate grassland[b]	Tundra	Total
Plant biomass, Gt C	460	175	108	27	13	2	785
NPP, Gt C yr^{-1}	20.4	6.7	4.3	4.7	6.1	0.5	43
Litter input							
Gt C yr^{-1}	17.4	4.6	3.0	5.4	6.0	0.6	37
Gt N yr^{-1}	0.46	0.18	0.14	0.18	0.16	0.02	1.1
Soil							
Gt C	340	113	186	81	205	174	1099
Gt N	20	12	13	5	19	9	78
Microbial biomass							
Gt C	1.23	1.38	0.42	0.90	1.94	0.16	6
Gt N	0.06	0.18	0.03	0.13	0.46	0.01	0.9

[a]Plant biomass and NPP from Refs. 141, 145. and 147; litter from [146]; soil C and N from Ref. 142.
[b]Includes cultivated land.

Table 8 Soil Microbial Biomass Turnover Time and Yearly Energy Requirements

	Tropical forest	Temperate forest	Boreal forest	Savanna	Temperate grassland	Tundra
Microbial biomass turnover, years						
C[a]	0.14	0.60	0.28	0.34	0.64	0.54
N	0.13	1.00	0.21	0.72	2.88	0.50
N[b]	0.06	0.44	0.09	0.32	1.27	0.22
Maintenance energy requirement, Gt yr^{-1}						
C	7.5	8.5	2.6	5.5	11.9	1.0
N	0.6	0.7	0.2	0.4	0.9	0.1

[a]Based on 60% yield of biomass per unit of litter C.
[b]Based on microbial N throughout of 2.3 times plant N uptake [144].

addition to microbial C cycling, 95% of the global N flow is between the soil and vegetation, as in the major flux in P and S. Litter input and net primary productivity (NPP) are by definition fluxes rather than pools, although when at steady state, they are often considered pools. Estimates of litter input are approximately 80% of NPP [146,148,149].

The six systems we have designated in Table 7 account for 77% of terrestrial land, 95% of the biota C, and 80% of the yearly global NPP. Total plant biomass ranges from 2 Gt C in the tundra to 460 Gt C in the tropical forest system. The NPP does not reflect as large a difference between systems as does total plant mass. For example, the ratio of plant biomass of tropical forest to temperate grassland is 35.4, whereas the ratio for NPP is 3.3. Turnover time of plant biomass within forest systems is approximately 25 years, compared with the relatively short residence times of plant biomass in grassland (2.1 years), savanna (5.7 years), and tundra (4.0 years) systems.

The role of the soil microbial biomass in the C cycling calculation shown in Table 8 is to decompose an amount of C equal to NPP, which is 43 Gt yr^{-1}. The litter contains 37 Gt C and 1.1 Gt N, with the decomposers containing 6 Gt C and 0.9 Gt N. Gross turnover times for microorganism C and N on a global basis would be 0.16 and 0.79 years, respectively. The longer residence time for N is a reflection of the fact that only litter N is considered an input, while inorganic pools of N are ignored. Because of internal N cycling, obtaining turnover rates for N is much more difficult than for C. Paul [150] calculated gross soil N mineralization of 2.6 Gt. This was obtained by relating the gross mineralization to plant uptake values of N for the major ecosystems.

Table 8 gives the calculated turnover time for microbial biomass on an ecosystem basis. The small residence time for tropical forest biomass is due to the relatively low levels of biomass and large litter inputs in contrast to the grassland, where the biomass is substantial compared with annual litter input and the residence time is much longer. In general, the turnover time for biomass C ranges between 0.2 and 0.6 years, corresponding to 2 to 5 times per year. The N turnover times calculated from only litter input showed longer residence times compared with C. A more meaningful N turnover time was calculated on the basis of a throughput of N, amounting to 2.3 times the plant N uptake, moving through the biomass immobilization/mineralization cycle [147,151]. These values (Table 8) are similar to the C turnover times, with the exception of the temperate grassland biomass, with a large N pool, which turns over at one-fourth the rate of its C. The large amounts of microbial biomass C and N in the temperate grassland systems and low amounts of C and N inputs suggest that the biomass is generally C limited and organism activity is suppressed.

Table 9 Comparison of Global Pool Magnitudes and Yearly Nutrient Uptake of C, N, P, and S by Plant Biomass

	C (Gt)	N (Gt)	P (Gt)	S (Gt)
Plant biomass	785	13	1.8	1.4
Yearly uptake	60	1.2	0.2	0.1
Microbial biomass	6.0	0.9	0.7	0.2

If the microbial biomass concentration in a steady-state system is known along with the specific maintenance rate and the net assimilation rate or yield, the amount of substrate necessary to maintain the organism population can be calculated. The maintenance C requirement for each ecosystem (Table 8) was calculated from equations and maintenance values given by Smith et al. [41]. In the tropical forest, boreal forest, and savanna systems, the maintenance C required for sustaining the microbial biomass was less than or equal to the yearly input from litter (Table 7). In the temperate forest, grassland, and tundra ecosystems, the maintenance C needed exceeded the C input to the system. Globally, the maintenance C totals 37 Gt, the same as litter input; however, the associated N requirement was 2.9 Gt, while litter N input was only 1.1 Gt. Much of the yearly C throughput is used for population maintenance, with little remaining for population growth. Thus, the microbial biomass is generally in a resting state with periodic flushes of activity and growth. The major limitation to the analysis of C flux through microbial biomass is lack of data on the magnitude of belowground C inputs. These inputs, even if only a small percentage of NPP, can have a substantial effect on microbial C pool size and turnover.

In addition to being a catalyst for organic matter transformations, the microbial biomass is large enough to act as a source and sink for plant nutrients. This source-sink concept is emphasized by the relatively fast turnover of microorganisms compared with plant biomass and soil organic matter pools. Table 9 shows global values of nutrient pools and yearly plant nutrient uptake. The nutrients, N, P, and S, in the plant biota all have a turnover time of approximately 10 years, compared with 13 years for plant C. The turnover time for plant N has been reported as approximately 5 years. The sink of nutrients in the microbial biomass represents 73, 372, and 130% of the annual nutrient needs of the total plant biota for N, P, and S, respectively. With turnover rates of 2 to 5 times per year, the generation of inorganic nutrients in quantities large enough to meet plant demands would be possible.

The role of microbial biomass in global nutrient cycles is well established, as significant N, P, and S transfers occur in terrestrial ecosystems. The magnitude of the biomass is small compared with soil and plant C and N pools; however, its rapid turnover can cause major fluxes of important plant nutrients, and its role as a decomposer makes the soil microbial biomass an important factor in the global C cycle. Appropriate data for the many ecosystems involved are still to be obtained.

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8

Soil Lipids: Origin, Nature, Content, Decomposition, and Effect on Soil Physical Properties

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I. INTRODUCTION

Soil organic matter refers to all organic carbon-containing substances in the soil, ranging from relatively undecomposed plant litter (leaves, stems, and roots) and microbial remains to highly polymerized, stable products of degradation and synthesis. The soil organic matter content varies appreciably from desert soils to typical mineral and organic agricultural soils. Similarly, the nature and the partition of the organic carbon in soil organic matter vary according to the botanical origin of plant materials and the characteristics of the soil faunal and microbial populations.

Soil organic matter can be subdivided into two major groups: nonhumic and humic substances. Nonhumic substances include those with still recognizable chemical characteristics, such as carbohydrates, proteins, amino acids, amines, alcohols, aldehydes, ketones, organic acids, phenolic compounds, lignin, alkaloids, antibiotics, auxins, vitamins, enzymes, and lipids (fats, oils, resins, and waxes) [1]. Humic substances, which make up the bulk of the soil organic matter, are characterized as polydispersed, acidic, amorphous substances ranging in molecular mass from a few hundred to several thousand daltons [2,3].

The literature dealing with carbohydrates and proteins in soils has been extensively reviewed [4-7]. The present review deals mainly with soil lipids and their relative biodegradability compared with other nonhumic components. Although the literature on soil lipids is scanty, the literature on the chemistry of waxes and on

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