

C:N:P stoichiometry in soil: is there a “Redfield ratio” for the microbial biomass?

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Abstract Well-constrained carbon:nitrogen:phosphorus (C:N:P) ratios in planktonic biomass, and their importance in advancing our understanding of biological processes and nutrient cycling in marine ecosystems, has motivated ecologists to search for similar patterns in terrestrial ecosystems. Recent analyses indicate the existence of “Redfield-like” ratios in plants, and such data may provide insight into the nature of nutrient limitation in terrestrial ecosystems. We searched for analogous patterns in the soil and the soil microbial biomass by conducting a review of the literature. Although soil is characterized by high biological diversity, structural complexity and spatial heterogeneity, we found remarkably consistent C:N:P ratios in both total soil pools and the soil microbial biomass. Our analysis indicates that, similar to marine phytoplankton, element concentrations of individual phylogenetic groups within the soil microbial community may vary, but on average, atomic C:N:P ratios in both the soil (186:13:1) and

the soil microbial biomass (60:7:1) are well-constrained at the global scale. We did see significant variation in soil and microbial element ratios between vegetation types (i.e., forest versus grassland), but in most cases, the similarities in soil and microbial element ratios among sites and across large scales were more apparent than the differences. Consistent microbial biomass element ratios, combined with data linking specific patterns of microbial element stoichiometry with direct evidence of microbial nutrient limitation, suggest that measuring the proportions of C, N and P in the microbial biomass may represent another useful tool for assessing nutrient limitation of ecosystem processes in terrestrial ecosystems.

Keywords Carbon · Microbial biomass · Nitrogen · Phosphorus · Soil · Stoichiometry

The environment not only determines the conditions under which life exists, but the organisms influence the conditions prevailing in the environment.—Alfred Redfield (1958)

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Introduction

In 1958, Alfred Redfield presented evidence of what are now two of the most powerful and useful principles in biogeochemistry: (1) that marine plankton are composed of carbon (C), nitrogen (N), and

phosphorus (P) in a characteristic molar ratio; and (2) that the abundance of C, N and P is regulated by reciprocal interactions between marine organisms and the ocean environment. Redfield (1958) observed that, on average, planktonic biomass contains C, N and P in an atomic ratio of 106:16:1, similar to the ratio of C, N and P in marine water. The elegant simplicity of this stoichiometric relationship—the Redfield ratio—belies its incredible utility. The consistent stoichiometry of C, N and P in the ocean informs our understanding of ocean-atmosphere carbon dioxide (CO₂) exchange, provides valuable insight into the nature and extent of nutrient limitation of marine net primary production (NPP) and ocean C storage, and contributes to our knowledge of biogeochemical cycling of N and P in the world's oceans (Cooper et al. 1996; Field et al. 1998; Hecky and Kilham 1988).

The predictive power of the Redfield ratio has prompted ecologists to search for similar patterns and relationships in terrestrial ecosystems, and has even inspired a new discipline—*ecological stoichiometry*—which seeks to understand the balance of multiple chemical elements in ecological interactions (Elser et al. 2000; Sterner and Elser 2002). Similar functional relationships between soil microbial chemistry and soil processes were identified even before Redfield's canonical ratio was presented (e.g., Waksman and Starkey 1931), but our current understanding of stoichiometric relationships and their significance in terrestrial ecosystems is still relatively limited.

Recent data, however, do suggest parallel interactions between the terrestrial environment and organisms. Element ratios in terrestrial systems appear to be more variable than those in the ocean, but parallels between the nutrient abundance of organism and the environment seem to exist in plant communities and forest ecosystems worldwide (Reich and Oleksyn 2004; Hedin 2004; McGroddy et al. 2004; Reiners 1986). For example, using a dataset of more than 1,200 plant species from ~450 unique sites, Reich and Oleksyn (2004) showed that plant foliar N:P ratios increase from high to low latitudes, coincident with biogeographical gradients of soil substrate age (i.e., soil nutrient availability) and climate. Until now, the existence of similar ratios and patterns in the soil microbial biomass has not been thoroughly investigated.

Important physical, chemical, and biological differences between soil and aquatic habitats may preclude the emergence of constrained microbial element ratios in soil (e.g., McGroddy et al. 2004). Many marine nanoplankton are composed primarily of protoplasm and thin cell walls composed of C, N and P, and thus represent an “ideal organism stoichiometry from which others may be derivatives” (Reiners 1986). In contrast, the soil microbial biomass is characterized by an anatomically and physiologically diverse community of organisms that spans all the major life domains. Nonetheless, a long history of soil microbiological research does suggest that: (1) microbial biomass varies as a function of soil C content (Wardle 1992, 1998); and (2) microbial biomass C:N ratios (on a mass basis) are relatively consistent, typically varying between 8:1 and 12:1 (Paul and Clark 1996; Wright and Coleman 2000). However, while the relationships between soil and microbial C and N content have been documented, data from terrestrial ecosystems also indicate that variations in organismal N:P ratios are more informative than C:N ratios for understanding many important terrestrial ecosystem processes (Reich and Oleksyn 2004; Townsend et al. 2007).

Sterner and Elser (2002) presented a conceptual model describing the potential stoichiometric relationships between organisms and the environment (Fig. 1). First, organisms may be characterized by strict *homeostasis*, where changes in resource stoichiometry have no influence on organism stoichiometry. In a strict homeostasis, organism nutrient ratios are rigorously established, and in turn, organism growth is strongly regulated by the most limiting nutrient. Alternatively, an organism may show identical stoichiometry to its resources, with changes in resource stoichiometry driving corresponding changes in organism stoichiometry (*no homeostasis*). Finally, changes in resource stoichiometry may influence organism stoichiometry in a manner that varies from a 1:1 relationship (Sterner and Elser 2002). Here, our goal was to examine global-scale patterns of C:N:P ratios in soil and in soil microbial biomass, and to investigate the relationships between environmental and organismal element abundance. We “extracted” microbial biomass C, N and P data from the primary literature to address the following questions. First, is there a consistent ratio of elements—akin to the Redfield

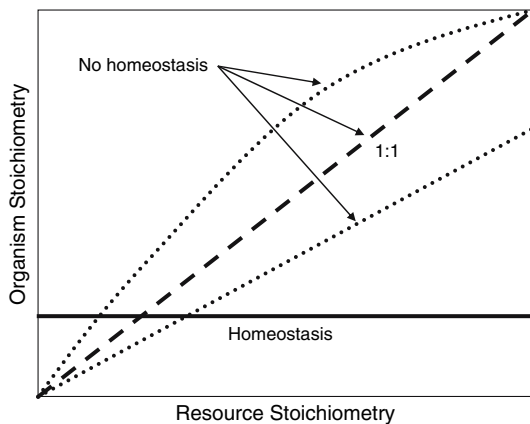


Fig. 1 Potential patterns relating resource to consumer stoichiometry. The stoichiometry of *homeostatic* organisms (solid line) is strictly defined, and changes in resource stoichiometry do not influence organism stoichiometry. The stoichiometry of *non-homeostatic* organisms may match resource stoichiometry in a 1:1 relationship (large dashes) or in a relationship (small dashes) that diverges from the 1:1 line (Adapted from Sterner and Elser 2002)

ratio—in the soil microbial biomass? Second, what is the relationship between environmental and soil microbial biomass element abundance? And third, do environmental and microbial element concentrations vary in predictable ways across latitudes and distinct vegetation types?

Methods

Literature review

We compiled a database of soil and microbial C, N and P concentrations and ratios by conducting a thorough review of the primary literature. Our strategy for collecting data was to search the ISI Web of Science online database (<http://isiknowledge.com/>), and our final dataset included 186 observations from 48 unique, published sources. For this analysis, we were interested in microbial C, N and P. Because estimates of microbial P frequently include estimates of microbial C and N (while estimates of microbial C and N often do not include microbial P data), we constrained our survey by searching for published literature that cited the most common method for estimating microbial biomass P concentrations in soil. Specifically, we searched for

literature in the database that cited at least one of the following microbial P methodological studies: Jenkinson and Powlson (1976); Brookes et al. (1982, 1984); Hedley and Stewart (1982); Oberson et al. (1997); or Morel et al. (1996).

Quantifying soil microbial biomass:
the chloroform fumigation and extraction
(FE) technique

The most common technique used to estimate microbial biomass P (and biomass C and N) is the chloroform fumigation-extraction method (FE). Briefly, moist soil samples are split into two subsamples; one set of soil samples is immediately extracted (0.5 M K_2SO_4 for microbial C and N or 0.5 M $NaHCO_3$ for microbial P), and the other set is fumigated with chloroform and then extracted (Brookes et al. 1982, 1984, 1985). Following centrifugation, samples are digested (for N and P), analyzed for C, N and P concentration, and microbial biomass element content is calculated from the difference between fumigated and non-fumigated soil samples.

The majority of published estimates of microbial C, N and P have utilized the FE technique, but the method does have several limitations that may lead to errors in microbial C, N and P estimates (Jenkinson et al. 2004). First, persistent enzymatic activity during the fumigation (and variations in enzyme activity between sites and soil types) may drive variations in available N that are unrelated to soil microbial biomass concentrations N per se. Next, chloroform exposure may yield more than just biomass C, N and P by rendering non-microbial biomass (e.g., plant material) extractable. Finally, only a fraction of the microbial biomass is solubilized during chloroform fumigation. Thus, estimates of microbial biomass must be adjusted using experimentally-derived conversion factors for C, N and P (e.g., 0.45, 0.45, and 0.40 for C, N and P, respectively; Jenkinson et al. 2004; Brookes et al. 1984). While the most commonly used conversion factors have been experimentally shown to represent the proportions of C, N and P that are mineralized from a small selection of organisms in pure culture (e.g., Jenkinson et al. 2004), they may not be accurate for a diverse soil community, and they may vary significantly between soil types. Nonetheless, for the

purposes of this analyses, we used published “microbial biomass” values that reflect the specific chloroform FE conversion factors used for estimating microbial C, N and P in each of the published estimates.

In addition to microbial biomass C, N and P, concentrations of total soil C, N and P were also gathered from the primary literature sources when available. In most cases, we used estimates of microbial biomass and soil element pools obtained from surface soils (typically 0–10 cm mineral soil samples). At some sites, however, slightly deeper or shallower soil samples were collected. For example, in several of the high-latitude sites, 0–10 cm soils represented organic horizons, and in others, soil samples were collected from both the organic (e.g., 0–10 cm) and mineral horizons (e.g., 10–20 cm). When sources reported both organic and mineral soil biomass estimates separately, both measurements were included in our analysis. Finally, we included data only from sites that were untilled, unfertilized and free of intensive agriculture, and we used only data obtained from field fresh soil samples. Microbial biomass and total soil element pool estimates generated from samples collected across years were averaged to generate a single data point, but estimates generated from samples collected across multiple seasons within a year were treated as unique observations (e.g., Cleveland et al. 2004).

Incomplete climate data in many of the sources prevented a detailed climate—microbial biomass analysis. However, because latitude serves as a general proxy for climate, we investigated possible latitudinal variation in microbial element ratios (e.g., Reich and Oleksyn 2004). For the purposes of the vegetation-type analysis, vegetation was classified based on the reported description as either grassland or forest, the two vegetation classifications that we expected would be most likely to show significant differences in soil and microbial element ratios. Data from other vegetation types were excluded from this analysis.

Data analyses

We calculated average molar ratios (C:N, C:P and N:P) of both the total soil and the microbial biomass element pools and tested several hypotheses. First, we

tested differences between the mean soil and microbial biomass ratios (C:N, C:P, N:P) with one-way analysis of variance (ANOVA). Next, we examined differences among microbial and soil element ratios in the two most common vegetation types—forest and grassland—using a one-way ANOVA. Finally, we used one-sample *t*-tests to test for significant differences between the three element ratios in soil the soil microbial biomass, and in the ocean (i.e., the Redfield ratio [106:16:1]). Prior to all analyses, nutrient ratios were \log_{10} transformed to improve the distribution and homogeneity of variance, but all means and standard errors were back transformed into the original units.

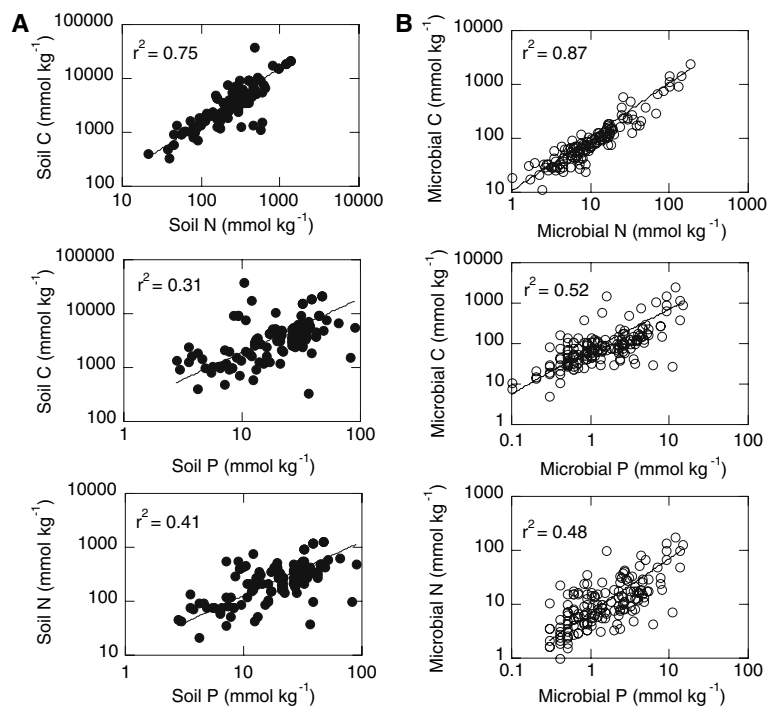
The relationships among the nutrients for soils and microbial biomass were examined using standardized major axis (SMA) estimation (Warton et al. 2006). Unlike ordinary least-squares regression, the SMA technique assesses the “best fit bivariate line” between two variables instead of predicting one variable from the other and fits a slope and an intercept for the model. Because of the \log_{10} -normal distribution of nutrient ratios, stoichiometric relationships were analyzed on a log–log scale with the model: $\log y = a + b (\log x)$. This relationship is commonly used for allometric analysis on size-based measures, such as biomass, and is based on the power function, or the allometric equation: $y = a x^b$ (Reiss 1989). When the slope (*b*) of this model does not significantly differ from one, the relationship is described as isometric, indicating the special case of a linear relationship between the two variables. Relationships among the three soil nutrient pools, the three microbial biomass pools, and the soil-microbial biomass relationships for the three nutrients (soil C versus microbial C, soil N versus microbial N, soil P versus microbial P) were evaluated using the software SMATR (Falster et al. 2006).

Results and discussion

Total soil C:N:P ratios

Redfield (1958) observed that both the abundance and ratio of elements in ocean water are constrained, and suggested that close interactions between organisms and the environment drive the observed similarities in their element ratios. Our analysis suggests a similar

Fig. 2 Relationships between C, N and P in (A) the soil and (B) the soil microbial biomass



pattern in soil (Fig. 2). At the global scale, the abundance of total C, N and P in soil varies by orders of magnitude. Across the entire database, total soil C varies from 1,108 mmol kg⁻¹ to 39,083 mmol kg⁻¹ and total soil N varies from 21 mmol kg⁻¹ to more than 1,300 mmol kg⁻¹ (Fig. 2). However, although total soil element content is highly variable, our analysis indicates that total soil C:N:P ratios are remarkably constrained (Fig. 2A; Table 1). Across all data, total soil C:N ratios vary between 2 and 30, and total soil N:P ratios from a low of 1 to a high of 77, with log-normal distributions (Fig. 3). In addition, in spite of observed differences in plant element ratios across broadly-defined vegetation types and latitudes (Reich and Oleksyn 2004; McGroddy et al. 2004), soil nutrient ratios did not vary significantly between forests and grasslands (Table 1).

In general, biological organisms have ordered chemical composition (Reiners 1986), and recent analyses show that like marine plankton, terrestrial plants have relatively constrained element ratios (McGroddy et al. 2004; Reich and Oleksyn 2004). Fixed soil C:N ratios across large geographical distances are consistent with the fact that plants are the major source of total soil C and N in terrestrial ecosystems, but fixed C:P and N:P ratios in soil are

more surprising. In contrast to total soil C and N, weathering of primary rock minerals provides the dominant, albeit highly variable, source of total P in terrestrial ecosystems (Walker and Syers 1976; Chadwick et al. 1999). Nonetheless, the results of the SMA indicate that on the global scale, there are significant, positive associations between total soil C, N and P (overall, $P < 0.0001$ for all models; Table 2). The strength of the relationship varied between elements, but r^2 -values ranged from 0.31 (soil C:P) to 0.75 (soil C:N; Table 2). The relationship between soil C and N was isometric with a slope not significantly different than 1 ($P > 0.05$), but the relationships between C and P and N and P were non-linear, with concentrations of P increasing slower than C and N ($P < 0.05$). In other words, it appears as though when organic matter accumulates in an ecosystem, soil C and N concentrations become increasingly decoupled from total soil P concentration. This observation may reflect a more efficient use of P released from the cycling of organic P pools in the mineral soil and forest floor, rather than on weathering of inorganic P from primary minerals; organic P pools are thought to be an important source for labile P in forest soils, especially for tropical forests (Johnson et al. 2003). In any case, the strong,

Table 1 Atomic (molar) nutrient ratios in the microbial biomass and total soil element pools

	C:N	C:P	N:P	References
<i>Microbial biomass</i>				
Overall	8.6 ± 0.3 (132)	59.5 ± 3.6 (157)	6.9 ± 0.4 (150)	This study
Grassland	8.3 ± 0.3 (57)	47.3 ± 3.4 ^a (77)	4.9 ± 0.4 ^a (57)	This study
Forest	8.2 ± 0.4 (57)	74.0 ± 6.2 ^b (63)	8.9 ± 0.8 ^b (67)	This study
Bacteria	6.5	46	7	Reiners (1986)
Fungi	5–17		15	Sterner and Elser (2000); Reiners (1986)
<i>Soil (total pools)</i>				
Overall	14.3 ± 0.5 (146)	186.0 ± 12.9 (135)	13.1 ± 0.8 (150)	This study
Grassland	13.8 ± 0.4 (75)	166.0 ± 12.2 (72)	12.3 ± 0.7 (72)	This study
Forest	14.5 ± 1.2 (55)	211.7 ± 28.4 (47)	14.6 ± 1.8 (47)	This study
<i>Tree foliage</i>				
Overall	43.6 ± 3.5	1334.1 ± 137.6	27.8 ± 1.4	McGroddy et al. (2004)
Temperate broadleaf	35.1 ± 3.7	922.3 ± 77.3	28.2 ± 1.5	McGroddy et al. (2004)
Temperate coniferous	59.5 ± 7.0	1231.8 ± 140.3	21.7 ± 1.7	McGroddy et al. (2004)
Tropical	35.5 ± 4.1	2456.9 ± 503.7	43.4 ± 4.6	McGroddy et al. (2004)
<i>Tree litter</i>				
Overall	66.2 ± 6.3	3144 ± 341.9	45.5 ± 3.2	McGroddy et al. (2004)
Temperate broadleaf	58.4 ± 3.8	1702.4 ± 170.3	29.1 ± 2.0	McGroddy et al. (2004)
Temperate coniferous	87.8 ± 6.9	2352.9 ± 350.3	26.0 ± 4.6	McGroddy et al. (2004)
Tropical	60.3 ± 13.2	4116.0 ± 577.4	62.7 ± 4.9	McGroddy et al. (2004)

Data represent the geometric mean ± 1 SE; Sample numbers are shown in parentheses. Differences between the two vegetation types (grassland and forest) were tested with a one-way ANOVA on log₁₀-transformed data, and significant differences ($\alpha = 0.05$) are indicated with lowercase letters. Previously published element ratios in specific soil microbial groups, tree foliage, and tree litter are included for comparison

bivariate relationships among the three elements indicates that even though organisms may not directly regulate total soil P, total soil P ultimately influences the amount of biologically active P that is available for plant productivity, thus indirectly linking the abundance of total P to the abundances of total C and N in soil.

C:N:P ratios in the soil microbial biomass

The biogeochemical cycles of C and N are tightly coupled in terrestrial ecosystems. For example, high N requirements during photosynthesis, combined with low N availability in many terrestrial ecosystems, means that increases in primary production are dependent on the availability of N to fuel increased photosynthetic C acquisition (Vitousek and Howarth 1991; Asner et al. 1997). Fairly consistent plant litter element ratios (e.g., McGroddy et al. 2004)—and hence consistent element ratios in the non-woody

organic matter inputs available for microbial decomposition and metabolism—could suggest that the soil microbial biomass may also be characterized by distinct C:element ratios. However, several important differences between soil and aquatic habitats may preclude the emergence of constrained soil microbial element ratios. First, the potential for element mobility and mixing is high in aquatic ecosystems. In marine ecosystems in particular, regional and global ocean currents and upwelling lead to well-mixed, relatively homogeneous conditions (Redfield 1958). In contrast, relative element immobility within a fixed (non-fluid) soil medium, significant spatial differences in soil nutrient concentrations driven by state factor variation (Jenny 1941), and nutrient redistribution mechanisms that operate only on small-scales (e.g., litterfall) perpetuate soil nutrient heterogeneity (McGroddy et al. 2004). Next, marine element ratios are strongly influenced by the growth demands of photoautotrophic organisms (Falkowski et al. 2000) that assimilate nutrients and inorganic

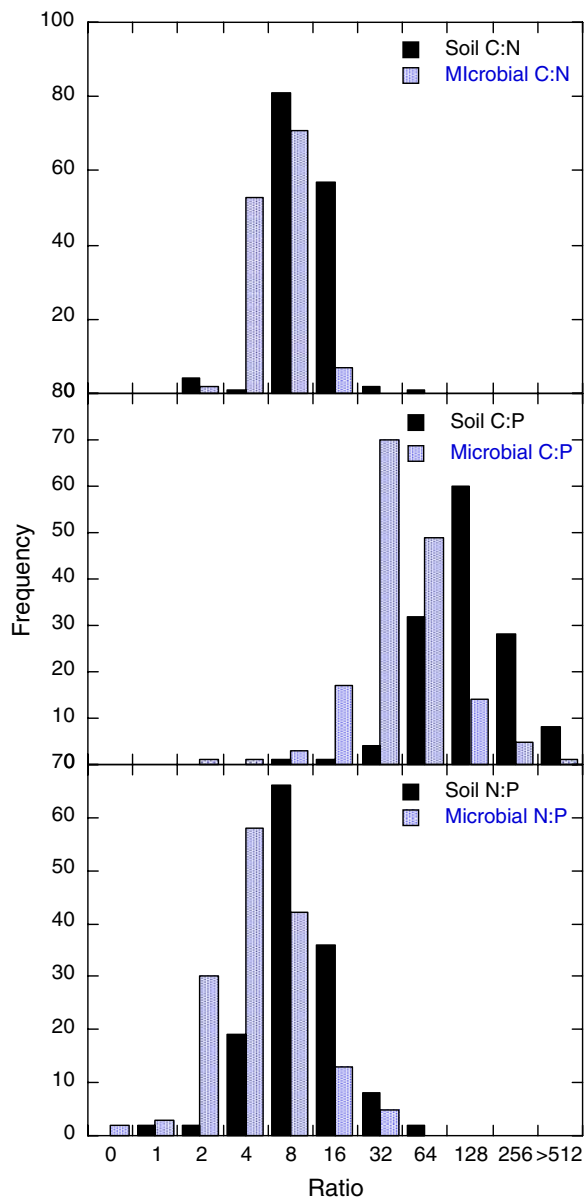


Fig. 3 Frequency distribution of nutrient ratios (C:N, C:P, N:P) in the soil and the soil microbial biomass. The X-axis of the histogram is presented using a \log_2 scale to highlight the lognormal distribution of the soil and microbial element ratios

carbon (CO_2) to build biomass, but the soil microbial biomass is dominated by heterotrophic organisms that must metabolize a tremendous diversity of plant-derived organic compounds, many of which are characterized by extreme variations in nutrient content (Paul and Clark 1996). Third, the planktonic biomass is dominated by unicellular organisms

lacking mechanical structures (i.e., plankton is composed primarily of cytoplasmic materials; Reiners 1986), but the soil microbial biomass consists of a diverse community of organisms occupying vastly divergent phylogenetic lineages and showing significant variation in form and physiology (Table 1). Finally, several known sources of error when using the FE method in soil may further mask the presence of consistent element ratios in the soil microbial biomass (Ingham and Horton 1987; Ross 1989; Sparling and West 1989; Ross 1990; Badalucco et al. 1997).

Despite the relative complexity of the soil medium, soil microbial community structure, and potential methodological limitations, our analysis revealed highly constrained C:N:P ratios in the soil microbial biomass (Fig. 2B). As was the case with total element concentrations, soil microbial biomass concentrations across the entire database spanned several orders of magnitude; soil microbial C, N and P concentrations varied from 5–2,500 $\mu\text{mol kg}^{-1}$, 1–178 $\mu\text{mol kg}^{-1}$, and 0.1–14 $\mu\text{mol kg}^{-1}$, respectively. However, the SMA analysis indicated linear relationships between all three elements in microbial biomass (Table 2). Thus, even though the ranges of nutrient concentrations in microbial biomass were large, element ratios scaled isometrically and were well-constrained; C:N ratios averaged 8.6 ± 0.3 (geometric mean ± 1 SE) and ranged from 3 to 24, and N:P ratios averaged 6.9 ± 0.4 , ranging from 1 to 55 (Fig. 3; Table 1).

Relationships between soil and microbial element ratios

Unlike the pattern for soil nutrients, there were significant differences in microbial biomass element ratios between grasslands and forests (Table 1). The microbial biomass in the forest soils had significantly higher C:P and N:P ratios, largely due to lower concentrations of microbial biomass P. One possible explanation for the difference in element ratios between the two vegetation types may be the presence of a well-developed litter layer (with relatively high C:P and N:P ratios) in many forests. At sites that reported values for both the litter layer and the mineral soil, microbial biomass was consistently higher in former, with microbial biomass element ratios reflecting the relatively high C:P ratios

Table 2 Summary of standardized major axis analysis of \log_{10} -transformed molar nutrient concentrations in microbial biomass and soils

Variable		<i>n</i>	r^2	Intercept	Slope
<i>x</i>	<i>y</i>				
Soil C	Soil N	146	0.75	−0.92	0.93
Soil C	Soil P	135	0.31	−1.62	0.82
Soil N	Soil P	135	0.41	−0.82	0.87
Microbial C	Microbial N	133	0.87	−0.93	0.99
Microbial C	Microbial P	161	0.52	−1.79	1.00
Microbial N	Microbial P	153	0.48	−0.81	0.97
Soil C	Microbial C	145	0.39	−2.07	1.11
Soil N	Microbial N	118	0.15	−1.99	1.26
Soil P	Microbial P	135	0.08	−1.77	1.50

For all the nutrient relationships, the bivariate relationship was significant ($P < 0.001$). Slopes not significantly different than 1 are displayed in boldface font indicating an isometric (i.e., linear) relationship between nutrients

of the decomposing plant material (Santruckova et al. 2004; Ross et al. 1999; Chen et al. 2000a). For example, sites in New Zealand where pine forest was replaced with native grasses, microbial biomass C declined by ~50%, and the soil microbial biomass C:P changed by 33% (Yeates and Sagar 1998; Chen et al. 2000a), suggesting that changes in vegetation type have the potential to influence microbial biomass element stoichiometry. Alternatively, differences between vegetation types may be related to variations in litter quality, litter quantity or relatively consistent differences in the biomass proportions of major groups within the soil microbial community (e.g., higher bacterial:fungal ratios in grassland versus forest; Paul and Clark 1996). While the precise mechanism is unclear, our analysis indicates that profound differences in plant element ratios correspond with measurable changes in microbial biomass ratios between plant community types.

Overall, soil microbial biomass C and total soil C were strongly and linearly related (Table 2, $r^2 = 0.39$, overall $P < 0.0001$). This corroborates previous research showing strong correlation between microbial biomass and soil C availability (e.g., Wardle 1998). However, our analysis also indicated that microbial biomass C concentration was strongly associated with the soil microbial N and P content, suggesting that the stoichiometry of the soil microbial biomass is strictly defined. Similarly, while plant foliar element ratios do reflect the low-to-high latitude increases in the relative abundance of soil

N versus soil P (Reich and Oleksyn 2004), microbial N:P ratios in soil microbial biomass do not vary with latitude, and do not correlate with the soil N:P supply ratio (Fig. 4); instead, microbial N:P ratios appear fixed in “Redfield-like” proportions, indicating homeostatic control of nutrient ratios. The relatively strict nutrient requirements of the soil microbial biomass—combined with the relative P-poor status of many low latitude soils—provides an explanation for the observation that P often limits both microbial biomass and activity in these ecosystems (e.g., Gallardo and Schlesinger 1994; Cleveland et al. 2002; Cleveland and Townsend 2006). In any case, strong linear relationships between all elements also indicate that increases in soil microbial biomass C depend on the abundance of sufficient soil N and P to maintain the required microbial element stoichiometry.

Do Redfield-like ratios exist for the soil microbial biomass?

Our data suggest that as a broadly-defined group, the soil microbial community is homeostatic. Overall, microbial C, N and P ratios are strongly and positively related, and variations in soil element ratios do not significantly affect soil microbial biomass element ratios (Fig. 4B). The lack of significant variation in soil microbial element ratios with changing environmental ratios (i.e., homeostasis)

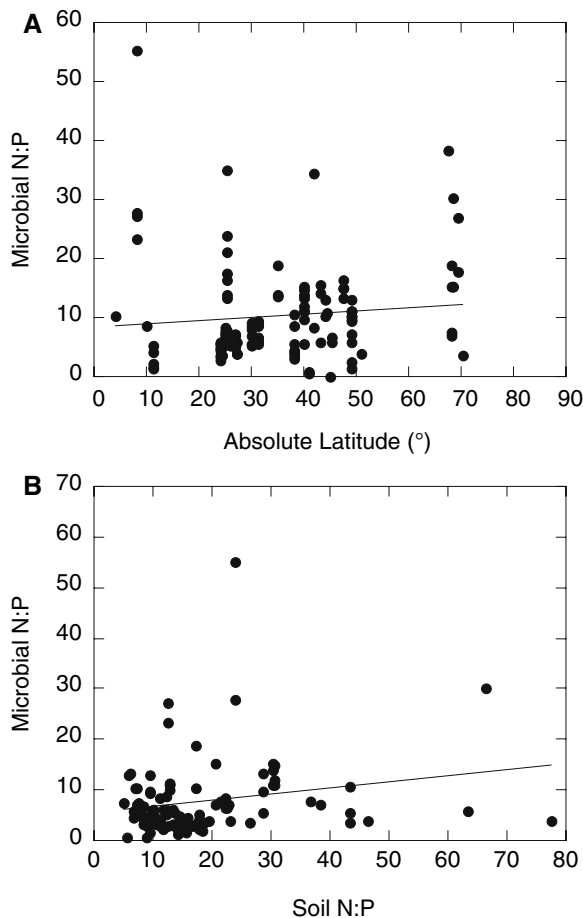


Fig. 4 (A) Microbial N:P ratios as a function of absolute latitude; (B) relationship between soil N:P supply ratio and the N:P ratio of the soil microbial biomass

suggests that constrained ratios—akin to Redfield ratios—do exist in the soil microbial biomass. As is the case in other environments, element ratios do vary significantly between specific groups of organisms

(e.g., bacteria versus fungi) within the soil microbial biomass (Reiners 1986; Paul and Clark 1996; Table 1). On average, however, it appears that soil microbial element ratios are essentially fixed.

Based on our analysis, our best estimate of the soil microbial biomass C:N:P molar ratio is 60:7:1 (Table 3), and this value does differ significantly from the Redfield ratio. Our data indicate that as a group, the soil microbial biomass has a higher C:N ratio than planktonic organisms, and a lower N:P ratio (Table 3). Differences in the C:N ratios likely reflect a greater overall investment in structural cellular material by the soil microbial biomass (e.g., relatively high C:N ratios in fungal biomass) than in the planktonic biomass (Paul and Clark 1996; Reiners 1986). The lower N:P content of the soil microbial community may reflect a higher P demand (and hence lower N:P ratios) of soil bacteria relative to marine algae. Alternatively, high N:P ratios in marine phytoplankton may reflect the higher N demands of chlorophyll-rich, photosynthetic organisms that dominate marine waters (and exert primary control over Redfield stoichiometry; Redfield 1958). However, perhaps more striking than the differences between the Redfield ratio and microbial element ratios in soil are the similarities. Despite the high phylogenetic diversity of the soil microbial community, a suite of potential errors associated with the FE technique, and an enormous range of element ratios among specific plants and plant groups (Table 1), C:N:P content in the soil microbial biomass is constrained in a ratio that is surprisingly similar to the Redfield ratio (Table 3).

An ecosystem is described as “stoichiometrically balanced” when the C:N:P ratios of autotrophs approximate the Redfield ratio of 106:16:1 (Sternner and Elser 2002), and this generalization seems

Table 3 Total soil and microbial biomass C, N and P ratios in soil (molar ratios), compared to the Redfield ratio using \log_{10} -transformed data

Ratio	Redfield	Microbial biomass					Soil				
		LL	Mean	UL	<i>t</i>	<i>P</i>	LL	Mean	UL	<i>t</i>	<i>P</i>
C:N	6.6	8.1	8.6	9.1	8.38	<0.001	13.5	14.3	15.5	21.58	<0.001
C:P	106	52.5	59.5	66.1	−10.06	<0.001	162.2	186.0	213.8	8.24	<0.001
N:P	16	6.2	6.9	7.8	−13.71	<0.001	11.7	13.1	14.8	−3.27	<0.01
C:N:P	106:16:1	60:7:1					186:13:1				

The columns labeled *t* and *P* are the test statistic and probability values associated with the one sample *t*-tests comparing the microbial biomass and soil element ratios to the Redfield ratio (Redfield 1958). LL and UL represent the lower and upper confidence limits respectively for the means of the microbial biomass and soil ratios

broadly applicable to the majority of aquatic ecosystems. One could argue, however, that differences between aquatic and terrestrial environments may limit the relevance of the Redfield ratio for defining balanced stoichiometry on land. For example, difficulties quantifying “available” soil nutrients could confound comparisons of terrestrial organism element ratios to the nutrient element ratios of the soil. Nonetheless, while reported C:nutrient ratios in tree foliage are nearly an order of magnitude higher than the Redfield ratio, in both the microbial biomass and the total soil nutrient pools, it does appear that: (1) there are constrained—and thus predictable—ratio of C, N, and P; and (2) the C:N:P ratio of the soil microbial biomass approximates the Redfield ratio remarkably well (Table 3). These observations suggest that the Redfield ratio per se may be an inappropriate standard for defining the stoichiometric balance in terrestrial ecosystems, but the predictable, “Redfield-like” element ratios we observed indicate that soil may indeed be stoichiometrically balanced. If so, spatial, temporal or site-specific differences in microbial biomass element ratios from the average microbial ratio could potentially provide insight into the nature of nutrient limitation in terrestrial ecosystems, just as the Redfield ratio does in marine ecosystems.

Soil microbial biomass element ratios as indices of nutrient limitation

Several studies (Aerts and Chapin 2000; Koerselman and Meuleman 1996; Reich and Oleksyn 2004) have hypothesized a foliar N:P “breakpoint” between N limitation ($N:P < 14$) and P limitation ($N:P > 16$), indicating that plant N:P ratios may provide a reliable index of nutrient limitation in terrestrial ecosystems. In many temperate and high latitude sites, relatively low average plant N:P ratios (i.e., <14 , suggesting ecosystem N limitation) are consistent with data from myriad nutrient manipulation experiments that show direct evidence of N limitation of ecosystem processes. Unfortunately, although high average foliar N:P ratios (i.e., >16) in tropical forests would suggest P limitation, direct evidence of P limitation of ecosystem processes in mainland tropical ecosystems is rare. Complicating matters, recent analyses indicate that within tropical rain forest sites, foliar N:P

ratios vary widely around the hypothesized N:P breakpoint (Townsend et al. 2007), further confounding their use as accurate predictors of nutrient limitation in these ecosystems.

Our analysis indicates that N:P stoichiometry of the soil microbial biomass is well-constrained (Fig. 4), suggesting that measured, site-specific microbial N:P ratios that diverge from the calculated average (i.e., 6.9 ± 0.4) may provide insight into the nature of ecosystem nutrient limitation, at least within lowland tropical ecosystems. For example, at a tropical rain forest site on highly weathered, P-poor soil in Costa Rica, plant N:P ratios vary widely between individual plant species. In addition, the range of measured foliar ratios bracketed the N:P breakpoint (Townsend et al. 2007), thus limiting their usefulness for assessing N versus P limitation at that site. However, at the same site, relatively high measured microbial N:P ratios (suggesting P limitation) are supported with direct evidence showing that low soil P availability strongly limits microbial biomass, activity, and other ecosystem processes (Cleveland et al. 2002; Cleveland and Townsend 2006; Reed et al. 2007; Cleveland and Townsend 2006). Therefore, a more complete picture of nutrient limitation within ecosystems—as well as an improved understanding of how they are likely to respond to anthropogenic nutrient inputs (Galloway et al. 2004; Okin et al. 2004)—could both be gained via a more comprehensive approach that includes measuring not only N:P ratios in plants, but also by assessing variability in soil and microbial biomass N:P ratios at multiple scales.

Our analysis indicates that N:P stoichiometry of the soil microbial biomass may be even more constrained than plant N:P ratios, and therefore suggests that an average soil microbial N:P ratio (i.e., 6.9 ± 0.4) may be perhaps a more appropriate index of ecosystem nutrient limitation than plant N:P ratios, at least within lowland tropical ecosystems. For example, at a tropical rain forest site on highly weathered P poor soil in Costa Rica, plant N:P ratios varied widely between individual plant species, and the range of observed foliar ratios included the N:P breakpoint (Townsend et al. 2007). However, at the same site (where relatively high microbial N:P ratios suggest P limitation), direct evidence indicates that low soil P availability strongly limits microbial biomass, activity, and ecosystem processes

(Cleveland et al. 2002; Cleveland and Townsend 2006). At this site, analysis of plant N:P ratios alone would provide an unclear picture of nutrient limitation in this tropical rain forest. However, much higher than average soil microbial N:P ratios (suggesting P limitation) are consistent with multiple lines of data showing P limitation of soil microbial biomass and processes (Reed et al. 2007; Cleveland and Townsend 2006). We therefore suggest that a more complete picture of nutrient limitation within ecosystems—as well as an improved understanding of how they are likely to respond to anthropogenic nutrient inputs (Galloway et al. 2004; Okin et al. 2004)—could both be gained via a more comprehensive approach that includes measuring not only N:P

ratios in plants, but also in the soil and the soil microbial biomass.

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Appendix

Appendix A Studies used in analyses of soil and microbial biomass C, N and P

Latitude	Vegetation type ^a	Soil nutrients (mmol kg ⁻¹ soil)			Microbial biomass (μmol kg ⁻¹ soil)			Citations
		Carbon	Nitrogen	Phosphorus	Carbon	Nitrogen	Phosphorus	
11	Grassland	1091.7	63.3	6.3	32.8	2.9	0.7	Agbenin and Adeniyi (2005)
11	Grassland	1991.7	118.6	7.6	29.9	3.4	2.0	Agbenin and Adeniyi (2005)
11	Grassland	1083.3	61.1	6.2	24.9	4.4	0.8	Agbenin and Adeniyi (2005)
11	Grassland	1100.0	78.0	5.5	43.2	5.1	3.5	Agbenin and Adeniyi (2005)
11	Grassland	1216.7	85.1	7.3	32.8	8.5	3.6	Agbenin and Adeniyi (2005)
26	Forest	4916.7	428.6	–	137.4	15.6	0.7	Arunachalam and Arunachalam (2000)
26	Forest	4333.3	285.7	–	107.8	15.4	0.6	Arunachalam and Arunachalam (2000)
26	Forest	4166.7	285.7	–	107.0	16.3	1.0	Arunachalam and Arunachalam (2000)
26	Forest	4833.3	428.6	–	109.5	16.1	1.2	Arunachalam and Arunachalam (2000)
26	Forest	3250.0	214.3	–	106.0	15.9	0.9	Arunachalam and Arunachalam (2000)
26	Forest	3250.0	214.3	–	111.0	15.8	0.5	Arunachalam and Arunachalam (2000)
26	Forest	2316.7	171.4	–	24.5	8.4	0.6	Arunachalam et al. (1996)
27	Forest	1375.0	450.0	9.7	66.7	5.6	1.4	Barbhuiya et al. (2004)
27	Forest	1533.3	571.4	9.0	50.0	6.6	1.1	Barbhuiya et al. (2004)
27	Forest	1258.3	321.4	13.9	58.3	3.4	0.9	Barbhuiya et al. (2004)
27	Forest	1108.3	550.0	7.1	91.7	5.7	1.5	Barbhuiya et al. (2004)
43	Grassland	6375.0	328.6	33.4	140.8	–	0.5	Chen et al. (2000a)
43	Forest	5250.0	250.0	30.6	79.1	–	0.4	Chen et al. (2000a)
29	Forest	2833.3	212.1	14.2	32.6	–	0.5	Chen et al. (2000b)
43	Grassland	6500.0	305.7	31.6	118.1	–	1.2	Chen et al. (2003)
43	Forest	5500.0	240.0	27.1	67.3	–	0.9	Chen et al. (2003)
43	Grassland	1625.0	71.4	3.7	22.1	–	0.2	Chen et al. (2004)
43	Grassland	3275.0	271.4	12.9	30.7	–	0.3	Chen et al. (2004)
43	Grassland	10866.7	521.4	19.3	103.7	–	2.6	Chen et al. (2004)
43	Grassland	4416.7	335.7	20.3	41.6	–	0.4	Chen et al. (2004)
43	Grassland	4083.3	221.4	21.4	40.4	–	0.5	Chen et al. (2004)
43	Grassland	2083.3	142.9	22.3	20.4	–	0.3	Chen et al. (2004)

Appendix A continued

Latitude	Vegetation type ^a	Soil nutrients (mmol kg ⁻¹ soil)			Microbial biomass (μmol kg ⁻¹ soil)			Citations
		Carbon	Nitrogen	Phosphorus	Carbon	Nitrogen	Phosphorus	
43	Grassland	3000.0	235.7	26.2	45.8	–	0.4	Chen et al. (2004)
43	Grassland	2416.7	214.3	27.8	47.1	–	1.0	Chen et al. (2004)
43	Grassland	6500.0	478.6	29.2	102.1	–	2.1	Chen et al. (2004)
43	Grassland	4166.7	342.9	30.3	71.2	–	0.5	Chen et al. (2004)
43	Grassland	3333.3	271.4	34.1	67.1	–	1.2	Chen et al. (2004)
43	Grassland	7416.7	442.9	36.4	56.1	–	0.6	Chen et al. (2004)
43	Grassland	4583.3	314.3	42.3	45.8	–	0.6	Chen et al. (2004)
43	Grassland	7750.0	607.1	51.1	71.1	–	1.1	Chen et al. (2004)
43	Grassland	5583.3	500.0	88.6	49.2	–	0.6	Chen et al. (2004)
24	Grassland	616.7	45.0	12.3	13.8	–	0.2	Chen and He (2004)
24	Forest	483.3	37.1	7.1	7.8	–	0.1	Chen and He (2004)
24	Forest	916.7	54.3	12.9	15.5	–	0.2	Chen and He (2004)
24	Forest	333.3	39.3	36.1	11.0	–	0.1	Chen and He (2004)
45	Forest	–	–	–	491.7	32.1	3.0	Christ et al. (1997)
8	Forest	5416.7	428.6	18.0	79.3	17.9	0.6	Cleveland et al. (2004)
8	Forest	5416.7	428.6	18.0	163.9	23.1	0.4	Cleveland et al. (2004)
8	Forest	5666.7	428.6	33.9	79.3	16.5	0.7	Cleveland et al. (2004)
8	Forest	5666.7	428.6	33.9	108.9	15.8	0.6	Cleveland et al. (2004)
25	Forest	3666.7	385.7	26.5	69.3	5.9	1.2	Devi and Yadava (2006)
25	Forest	3583.3	357.1	13.5	44.5	3.4	0.9	Devi and Yadava (2006)
40	Grassland	19583.3	1178.6	38.5	125.0	17.1	1.5	Holland (2006)
40	Grassland	21750.0	1321.4	46.3	233.3	29.3	5.4	Holland (2006)
40	Grassland	15583.3	964.3	31.7	141.7	15.0	1.0	Holland (2006)
40	Grassland	19583.3	1178.6	38.5	233.3	34.3	2.3	Holland (2006)
40	Grassland	21750.0	1321.4	46.3	291.7	66.4	5.0	Holland (2006)
40	Grassland	15583.3	964.3	31.7	125.0	15.0	1.1	Holland (2006)
40	Grassland	19583.3	1178.6	38.5	116.7	13.6	1.1	Holland (2006)
40	Grassland	21750.0	1321.4	46.3	125.0	19.3	2.0	Holland (2006)
40	Grassland	15583.3	964.3	31.7	108.3	9.3	0.8	Holland (2006)
51	Forest	–	–	14.8	75.4	7.8	2.0	Joergensen et al. (1995)
68	Other	1900.0	100.0	38.7	1158.3	100.0	13.2	Jonasson et al. (1996)
68	Other	1608.3	100.0	80.6	1500.0	100.0	1.6	Jonasson et al. (1996)
68	Other	–	–	–	–	49.9	7.1	Jonasson et al. (2006)
49	Grassland	9500.0	550.0	31.0	156.0	19.0	7.8	Kopacek et al. (2004)
49	Grassland	3100.0	200.0	21.0	39.0	3.5	2.3	Kopacek et al. (2004)
2	Grassland	–	–	–	4.9	–	0.3	Kwabiah et al. (2003)
48	Forest	2250.0	114.3	–	183.3	41.1	2.7	Lorenz et al. (2001)
48	Forest	–	–	–	216.7	43.6	2.7	Lorenz et al. (2001)
48	Forest	–	–	–	175.0	37.5	2.5	Lorenz et al. (2001)
48	Forest	–	–	–	133.3	32.5	2.4	Lorenz et al. (2001)
25	Other	3000.0	285.7	12.6	27.8	4.1	0.6	Maithani et al. (1996)
25	Forest	4500.0	357.1	16.8	56.8	6.4	0.8	Maithani et al. (1996)

Appendix A continued

Latitude	Vegetation type ^a	Soil nutrients (mmol kg ⁻¹ soil)			Microbial biomass (μmol kg ⁻¹ soil)			Citations
		Carbon	Nitrogen	Phosphorus	Carbon	Nitrogen	Phosphorus	
25	Forest	5166.7	428.6	19.2	90.7	8.9	1.4	Maithani et al. (1996)
45	Grassland	3583.3	185.7	–	100.3	10.1	0.9	McIntosh et al. (1999)
20	Grassland	950.0	43.4	2.9	–	–	–	Northup et al. (1999)
4	Other	2166.7	120.0	7.0	26.8	3.6	0.3	Oberson et al. (2001)
46	Grassland	7083.3	271.4	–	246.7	29.4	4.5	Ross et al. (1997)
46	Grassland	6750.0	285.7	–	242.5	25.9	4.4	Ross et al. (1997)
38	Forest	9666.7	400.0	9.3	133.3	17.3	3.1	Ross et al. (1999)
38	Grassland	6833.3	292.9	32.2	71.5	7.0	1.6	Ross et al. (1999)
38	Forest	9166.7	492.9	44.8	133.3	14.1	4.7	Ross et al. (1999)
38	Forest	9666.7	400.0	9.3	914.2	97.9	9.2	Ross et al. (1999) ^b
38	Forest	9166.7	492.9	44.8	946.7	126.4	14.8	Ross et al. (1999) ^b
38	Forest	9666.7	400.0	9.3	380.0	50.0	13.6	Ross et al. (1999)
38	Forest	9166.7	492.9	44.8	270.8	32.4	7.5	Ross et al. (1999)
25	Forest	2041.7	123.6	10.6	21.3	2.2	0.4	Roy and Singh (1994)
25	Forest	950.0	54.3	7.7	28.9	3.1	0.5	Roy and Singh (1994)
37	Forest	39083.3	476.4	10.3	1125.0	–	6.8	Saggar et al. (1998)
44	Grassland	1666.7	110.0	15.8	41.5	7.0	0.7	Saggar et al. (1999)
44	Grassland	1250.0	87.1	15.2	30.6	5.4	0.4	Saggar et al. (1999)
44	Grassland	1358.3	99.3	16.1	33.3	7.2	0.5	Saggar et al. (1999)
49	Forest	4833.3	278.6	21.6	–	3.6	0.3	Santruckova et al. (2004)
49	Forest	3583.3	192.9	27.1	–	2.2	0.3	Santruckova et al. (2004)
49	Forest	4416.7	157.1	16.8	–	5.1	0.5	Santruckova et al. (2004)
49	Forest	4833.3	278.6	21.6	–	25.8	2.3	Santruckova et al. (2004)
49	Forest	3583.3	192.9	27.1	–	28.9	2.8	Santruckova et al. (2004)
49	Forest	4416.7	157.1	16.8	–	27.6	2.9	Santruckova et al. (2004)
49	Forest	4833.3	278.6	21.6	–	33.1	3.3	Santruckova et al. (2004) ^b
49	Forest	3583.3	192.9	27.1	–	21.7	3.6	Santruckova et al. (2004) ^b
49	Forest	4416.7	157.1	16.8	–	53.8	4.2	Santruckova et al. (2004) ^b
–	Other	–	–	–	110.6	13.4	2.5	Sarathchandra et al. (1989)
30	Other	–	–	–	–	1.9	0.4	Sarig et al. (1996)
30	Other	–	–	–	–	3.9	0.4	Sarig et al. (1996)
30	Other	–	–	–	–	2.7	0.4	Sarig et al. (1996)
30	Other	–	–	–	–	1.7	0.3	Sarig et al. (1996)
30	Other	–	–	–	–	3.1	0.4	Sarig et al. (1996)
30	Other	–	–	–	–	6.1	0.7	Sarig et al. (1996)
31	Forest	–	–	–	26.1	2.9	0.7	Schilling and Lockaby (2005)
31	Forest	–	–	–	30.5	3.2	1.3	Schilling and Lockaby (2005)
31	Forest	–	–	–	43.0	4.5	0.9	Schilling and Lockaby (2005)
31	Forest	–	–	–	37.5	4.5	0.5	Schilling and Lockaby (2005)
31	Forest	–	–	–	70.7	6.7	1.0	Schilling and Lockaby (2005)
31	Forest	–	–	–	50.9	5.4	0.6	Schilling and Lockaby (2005)
68	Other	9470.8	306.0	8.3	666.7	69.5	9.1	Schmidt et al. (2002)

Appendix A continued

Latitude	Vegetation type ^a	Soil nutrients (mmol kg ⁻¹ soil)			Microbial biomass (μmol kg ⁻¹ soil)			Citations
		Carbon	Nitrogen	Phosphorus	Carbon	Nitrogen	Phosphorus	
68	Other	1402.8	47.6	2.7	770.8	81.9	4.3	Schmidt et al. (2002)
69	Other	7854.2	216.7	10.5	1508.3	138.8	9.1	Schmidt et al. (2002)
69	Other	17859.7	782.1	11.8	379.2	23.9	0.8	Schmidt et al. (2002)
27	Grassland	2666.7	202.9	26.8	72.0	10.1	1.4	Sharma et al. (2004)
27	Grassland	2166.7	176.4	21.3	59.3	6.9	1.0	Sharma et al. (2004)
27	Grassland	1250.0	170.0	21.0	63.7	5.1	1.0	Sharma et al. (2004)
25	Forest	1500.0	92.9	4.5	64.7	8.4	1.2	Singh and Singh (1995)
25	Forest	2483.3	135.7	3.5	73.0	9.9	1.4	Singh and Singh (1995)
25	Forest	1841.7	92.9	4.2	58.7	7.3	0.9	Singh and Singh (1995)
25	Forest	408.3	21.4	4.2	30.3	3.7	0.5	Singh and Singh (1995)
25	Other	1333.3	78.6	3.5	44.5	6.2	0.8	Singh and Singh (1995)
24	Other	833.3	78.6	5.5	32.9	2.5	0.5	Singh et al. (1991)
24	Other	1000.0	77.9	8.1	30.1	2.6	0.5	Singh et al. (1991)
26	Forest	2583.3	221.4	12.5	64.8	4.6	0.9	Singh et al. (2001)
68	Other	34250.0	–	–	2500.0	178.6	11.6	Sjursen et al. (2005)
41	Forest	5000.0	150.0	27.4	29.3	4.4	6.2	Sparling et al. (1994)
41	Other	6000.0	328.6	37.1	28.5	7.1	10.9	Sparling et al. (1994)
–	Grassland	750.0	87.9	9.4	22.6	–	0.6	Srivastava and Singh (1988)
–	Other	1333.3	155.0	17.1	48.8	–	1.0	Srivastava and Singh (1988)
24	Forest	1816.7	159.7	11.6	50.8	4.6	0.8	Srivastava and Singh (1991)
24	Other	1004.2	76.1	4.8	33.1	2.7	0.6	Srivastava and Singh (1991)
24	Forest	1933.3	210.7	11.3	31.1	1.6	0.5	Srivastava (1998)
24	Forest	1700.0	168.6	11.9	35.8	1.9	0.5	Srivastava (1998)
24	Other	1000.0	77.9	8.1	17.8	1.7	0.3	Srivastava (1998)
24	Other	1033.3	80.0	6.5	18.8	1.0	0.4	Srivastava (1998)
70	Other	–	–	–	616.7	25.6	1.4	Stark and Grellmann (2002)
70	Other	–	–	–	–	25.0	0.9	Stark et al. (2002)
71	Other	–	–	–	–	8.3	2.3	Stark et al. (2002)
68	Other	–	–	–	–	35.5	0.9	Stark et al. (2002)
–	Grassland	3250.0	214.3	25.8	34.3	4.1	1.0	Turner et al. (2001)
–	Grassland	2583.3	214.3	32.3	43.4	7.5	1.3	Turner et al. (2001)
–	Grassland	3916.7	357.1	41.9	58.2	9.2	2.2	Turner et al. (2001)
–	Grassland	2583.3	214.3	25.8	60.3	8.5	2.6	Turner et al. (2001)
–	Grassland	2750.0	285.7	29.0	68.2	9.9	2.5	Turner et al. (2001)
–	Grassland	4166.7	357.1	19.4	71.0	4.3	2.1	Turner et al. (2001)
–	Grassland	3333.3	214.3	12.9	75.0	6.2	2.2	Turner et al. (2001)
–	Grassland	2500.0	214.3	16.1	76.9	8.4	2.5	Turner et al. (2001)
–	Grassland	2416.7	285.7	32.3	78.4	9.5	3.1	Turner et al. (2001)
–	Grassland	4666.7	428.6	32.3	80.4	11.4	1.8	Turner et al. (2001)
–	Grassland	3666.7	357.1	32.3	88.2	11.4	2.6	Turner et al. (2001)
–	Grassland	5000.0	357.1	35.5	93.0	13.6	2.2	Turner et al. (2001)
–	Grassland	3333.3	285.7	19.4	101.7	14.0	3.1	Turner et al. (2001)

Appendix A continued

Latitude	Vegetation type ^a	Soil nutrients (mmol kg ⁻¹ soil)			Microbial biomass (μmol kg ⁻¹ soil)			Citations
		Carbon	Nitrogen	Phosphorus	Carbon	Nitrogen	Phosphorus	
–	Grassland	3750.0	285.7	41.9	103.2	10.9	2.5	Turner et al. (2001)
–	Grassland	4000.0	357.1	29.0	103.6	14.9	2.4	Turner et al. (2001)
–	Grassland	3833.3	357.1	35.5	104.0	12.6	3.6	Turner et al. (2001)
–	Grassland	4000.0	357.1	25.8	108.3	11.6	4.7	Turner et al. (2001)
–	Grassland	4916.7	428.6	48.4	118.9	17.5	3.8	Turner et al. (2001)
–	Grassland	3750.0	285.7	19.4	119.1	7.6	3.3	Turner et al. (2001)
–	Grassland	3500.0	285.7	25.8	129.4	12.9	3.8	Turner et al. (2001)
–	Grassland	3083.3	285.7	19.4	132.9	12.1	3.9	Turner et al. (2001)
–	Grassland	5666.7	571.4	32.3	148.2	18.9	4.3	Turner et al. (2001)
–	Grassland	3916.7	357.1	29.0	151.8	18.1	3.5	Turner et al. (2001)
–	Grassland	4000.0	357.1	32.3	159.0	15.6	4.5	Turner et al. (2001)
–	Grassland	5750.0	500.0	32.3	169.8	17.5	5.3	Turner et al. (2001)
–	Grassland	3666.7	357.1	32.3	173.4	16.4	4.1	Turner et al. (2001)
–	Grassland	5500.0	500.0	29.0	185.3	17.4	5.1	Turner et al. (2001)
–	Grassland	5333.3	500.0	25.8	185.7	16.2	4.0	Turner et al. (2001)
–	Grassland	6666.7	642.9	64.5	284.3	24.7	7.7	Turner et al. (2001)
24	Forest	1047.5	–	–	11.1	2.4	0.4	Wang et al. (2004)
–	Grassland	–	–	–	81.4	7.4	1.5	West et al. (1986)
–	Grassland	–	–	–	42.4	7.9	2.3	West et al. (1986)
35	Forest	8316.7	–	–	56.3	7.9	0.6	Wright and Coleman (2000)
35	Forest	8316.7	–	–	45.8	6.6	0.5	Wright and Coleman (2000)
35	Forest	8316.7	–	–	68.8	9.8	0.5	Wright and Coleman (2000)
42	Forest	9358.3	–	–	57.5	5.6	0.7	Wright and Coleman (2000)
42	Forest	9358.3	–	–	81.7	10.9	0.3	Wright and Coleman (2000)
43	Forest	8575.0	–	–	45.8	5.7	1.0	Wright and Coleman (2000)
43	Forest	8575.0	–	–	91.7	12.7	0.9	Wright and Coleman (2000)
43	Forest	8575.0	–	–	55.0	7.3	0.5	Wright and Coleman (2000)
10	Forest	3666.7	250.0	20.6		10.0	1.2	Yavitt et al. (1993)
45	Forest	–	–	–	1328.4	271.6	186.0	Yeates and Saggarr (1998)
45	Grassland	–	–	–	932.4	217.0	108.5	Yeates and Saggarr (1998)

Cases where specific data were not available are denoted by (–)

^a Vegetation types besides grassland and forest were ignored for the vegetation analysis

^b Data obtained from litter layer

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