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REVIEW

CONTROLS OF TEMPORAL VARIABILITY OF THE SOIL MICROBIAL BIOMASS: A GLOBAL-SCALE SYNTHESIS

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Summary—The temporal variability of the soil microbial biomass is an important component of its turnover, and thus contributes to patterns of soil nutrient release and mineralization. I selected 58 previously published studies in which temporal data for soil microbial biomass C and N had been presented, and analyzed this data for underlying trends, by calculating coefficients of variation (standard deviation/mean) over time from each study as a measure of temporal variability. Contrary to expectations, there was no difference in temporal variability among forest, grassland and arable ecosystems, or between tilled and non-tilled arable systems, indicating that increasing disturbance levels does not have destabilizing effects on the microbial biomass. Correlation, partial correlation and stepwise multiple regression analyses between the coefficients of variation and selected soil and macroclimatic variables across the studies I considered showed that temporal variability of biomass C was most closely related to soil N content in forests, pH and latitude in arable ecosystems, and pH, latitude and soil C contents in grasslands. Relationships involving soil C, N and pH were negative; those involving latitude were positive. For the entire data set, temporal variability was best predicted by a three-component model incorporating pH, soil C and latitude. The effects of increasing latitude on increasing temporal variability of biomass C is interpreted in terms of higher latitudes having higher interseasonal variations in temperature, causing greater interseasonal flux of the biomass. The apparent effects of pH and soil C in reducing temporal variation indicates that alleviating stress on the microbial community has stabilizing effects. It is shown that those factors which stabilize the microbial biomass reduce its turnover, and this is likely to have important consequences for soil nutrient dynamics and ultimately plant growth and ecosystem productivity.

INTRODUCTION

The soil microbial biomass is the principle component of the decomposer subsystem regulating nutrient cycling, energy flow and ultimately plant and ecosystem productivity. While considerable research effort has been devoted to investigating the various factors responsible for determining the magnitude of the microbial biomass, few general principles exist about the patterns of its temporal variability, or which factors are the most important in regulating this variation. The soil microbial biomass is not a static entity (although it is sometimes treated as such), and its temporal dynamics are likely to be extremely important in determining the extent of release of immobilized labile nutrients, and the availability of these nutrients for other components of the ecosystem (Robertson *et al.*, 1993; Bauhus and Barthel, 1995; Diaz-Ravina *et al.*, 1995) including primary producers (Singh *et al.*, 1989).

The temporal variability of a given group of organisms is a measure of its lack of "stability" (Pimm, 1991; Bengtsson, 1994; Tilman, 1996), partly because if organisms are more resistant to disturbance, they will tend to fluctuate less in response to changes in environmental conditions. The factors which enhance stability of the soil microbial biomass are therefore more likely to enhance nutrient conservation in the soil (Wardle and Nicholson, 1996), and will contribute to reduced turnover of microbial tissue, leading to reduced release rates of immobilized nutrients; this release is additional to that released by steady-state turnover. Several studies have measured microbial biomass at various intervals over a set time course for given locations in the field (e.g. Kinsbursky and Steinberger, 1989; Luizao *et al.*, 1992; Maxwell and Coleman, 1995) and many of these have attempted to interpret the trends observed in relation to external environmental factors (e.g. Van Gestel *et al.*, 1992; Garcia and Rice, 1994; Joergensen *et al.*, 1994) but there has been no serious attempt to determine whether general patterns exist across different studies in relation to these trends.

In this study, I compiled data from several published studies for which temporal data for soil microbial biomass C and N had been presented, so as to determine whether temporal variability (and thus instability) could be statistically related to external factors including land-use type, and macroclimatic and soil properties. This was made possible by the fact that several studies presenting temporal microbial biomass data have been published since the literature synthesis of microbial biomass data by Wardle (1992) was conducted, in which patterns of temporal variability could only be assessed qualitatively. The ultimate goal was to determine which factors had a consistent role in promoting instability of the microbial biomass, and interpret the outcome in terms of possible consequences for microbial turnover and thus ecosystem function.

THE APPROACH

For the present study, I utilized a comparative approach in which data from several published studies conducted in vastly differing situations around the world were collated and statistically analyzed for underlying trends (Wardle, 1992). Fifty-eight studies were chosen for which microbial biomass C or N values had been determined repeatedly at the same location; I preferentially selected studies with four or more repeat measurements over time, and which encompassed most or all seasons throughout the year (Table 1). This selection is intended to be representative, not exhaustive. The index of temporal variability I used was the coefficient of variation (CV), or the "standard deviation/mean" of the microbial biomass C or N over the duration of the study, with each sampling time representing an independent data value. This measure is one of the most popular indices of temporal variability (Pimm, 1991) and has been successfully used for evaluating temporal variability of plant biomass (Tilman, 1996); this measure has the attraction that it is independent of sample size, so would not be biased by different studies containing different numbers of sampling events. This index was calculated from temporal biomass C and N data presented in each study. When temporal data for several plots or treatments were presented, only control treatments were considered, and for studies in which control plots or treatments were non-definable (or when several treatments could qualify equally as controls), CVs were determined separately for each plot or treatment and all the CVs were averaged to provide one value per study. However, when data were presented for clearly different locations or ecosystem types within the same study, the different CVs were kept separate.

It is relevant that the different studies I considered used different methodologies and variants of methodologies. For the microbial C values used in the analysis, 52.1% were obtained using fumigation incubation (FI), 33.3% using fumigation extraction (FE), 12.5% using substrate-induced respiration (SIR) and 2.1% using direct microscopy. For microbial N, 39.3% used FI and 60.7% used FE. It is assumed that selection of methodology did not influence the values of CV obtained, since one-way ANOVA analyses testing for differences in CV between FI, FE and SIR for biomass C, or between FI and FE for biomass N were clearly non-significant (biomass C: $F_{2,73}=0.16$, $P = 0.857$; biomass N: $F_{1,33}=0.11$, $P = 0.746$). In terms of variation within method, determination of CV values were observed to be less when FI values without controls were used rather than FI values with controls (e.g. data of Srivastava and Singh, 1989, Franzluebbers *et al.*, 1994, 1995). However, when data was presented in a given publication for both approaches, the values with controls subtracted, or (when presented) with controls measured between 10 d and 20 d of incubation subtracted, were normally used so as to provide greater uniformity across different studies since the majority only presented results for which controls had been subtracted.

In addition to calculation of the CVs, soil pH, organic C, total N, clay content and total microbial C and N data were also extracted from each study when presented. The latitude, mean total annual rainfall and mean annual temperature were also determined for each study, either by using values presented by the authors, or estimated through the use of climate maps when this data was not presented (Wardle, 1992). To determine which of these factors (or combination of factors) was important in regulating the CV (and thus the temporal variability) of microbial biomass C and N across the studies presented in Table 1, correlation analysis, partial correlation analysis and stepwise multiple regression were employed.

TEMPORAL TRENDS – QUALITATIVE ASSESSMENT

In an earlier (qualitative) literature synthesis of temporal microbial biomass data (Wardle, 1992), I concluded that the trends which had been identified were often contradictory, with different studies reporting peaks in different seasons, and reporting both positive and negative responses to temporal patterns of both soil moisture and plant productivity. The much larger body of data published since 1991 reinforces this conclusion, as is apparent in Table 1. However, around half of the studies that I considered from temperate ecosystems indicated maximal microbial biomass in spring or summer, and several showed a significant decline in the winter, indicating that differences in temperature between summer and winter may be important in determining temporal variability at higher latitudes. In this context, it is relevant that out of all the studies presented in Table 1, the one which had been conducted at the most northerly latitude (i.e. Cochran *et al.* (1989) in northern Alaska) also showed the highest temporal variability for both

Table 1. Summary of studies considering seasonal dynamics of microbial biomass C and N

		Coefficient of variation (%)		
Reference	Location	biomass C	biomass N	Observed trend
	Arable			
Basu and Behera (1993)	Orissa, India	12.7		no clear trends
Buchanan and King (1992)	N. Carolina, U.S.A.	32.8		spring/summer max.
Burton and McGill (1992)	Edmonton, Canada	17.7	16.3	midsummer max.
Chang and Juma (1996)	Edmonton, Canada	40.0	17.4	linked to crop dynamics
Chatigny *et al.* (1996)	Quebéc, Canada	45.5		spring/summer max.
Cochran *et al.* (1989)	Central Alaska	90.6		summer max.
Collins *et al.* (1992)	Ohio, U.S.A.	16.1	49.2	generally early spring max.
De Luca and Keeney (1994)	Iowa, U.S.A.	38.4		peak in late winter
Engels *et al.* (1993)	Bonn, Germany	34.5		no clear trends
Franzluebbers *et al.* (1994)	Texas, U.S.A.	9.5		related to crop inputs
Franzluebbers *et al.* (1995)	Texas, U.S.A.	10.4		related to crop inputs
Ghoshal and Singh (1995)	Varasni, India	13.8	7.9	summer max.
Granatstein *et al.* (1987)	Idaho, U.S.A.	18.9		summer drop/autumn max.
Haines and Uren (1990)	Victoria, Australia	14.6		spring and autumn max.
Joergensen *et al.* (1994)	near Göttingen, Germany	15.8	14.5	no obvious trends
Kaiser *et al.* (1995)	Braunchweig, Germany	18.3		winter min./summer max.
Kandeler and Bohm (1996)	Lower Austria	32.3		related to moisture levels
Kirchner *et al.* (1993)	N. Carolina, U.S.A.	35.0		summer max./winter min.
Lynch and Panting (1982)	Oxfordshire, U.K.	49.3		moisture related
McGill *et al.* (1986)	Alberta, Canada	47.7		summer/early winter max.
Mueller *et al.* (1996)	near Göttingen, Germany	13.6		autumn max./winter min.
Ocio *et al.* (1991)	Rothamsted, U.K.	7.5	12.4	no consistent trends
Patra *et al.* (1995)	Lucknow, India	22.2	10.8	summer maximum
Robertson and Morgan (1996)	Victoria, Australia	10.5	15.7	generally little pattern
Robertson *et al.* (1993)	Queensland, Australia	19.3		no obvious trends
Roder *et al.* (1988)	Nebraska, U.S.A.	11.1		autumn max.
Santruckova (1992)	Chelice, Czech Rep.	40.1		related to moisture
Santruckova and Vrany (1990)	Czech Rep.	32.7		no clear trends
Srivastava and Lal (1994)	Varasni, India	7.6	37.9	min. in late rainy season
Srivastava and Singh (1989)	Uttar Pradesh, India	22.2	25.6	summer maximum
Van Gestel *et al.* (1992)	Kapunda, S. Aust.	22.5		winter max./summer min.
Wardle *et al.* (1993)	Hamilton, New Zealand	13.2		no clear trends
	Grassland (incl. savannas)			
Basu and Behera (1993)	Orissa, India	7.8		no clear trends
Bristow and Jarvis (1991)	Hurley, England	24.7		follows fine root growth
Chatigny *et al.* (1996)	Quebéc, Canada	45.8		no clear trends
Collins *et al.* (1992)	Ohio, U.S.A.	27.2	24.5	general max. in early spring
De Luca and Keeney (1994)	Iowa, U.S.A.	32.0		peak in late winter
Garcia and Rice (1994)	Kansas, U.S.A.	14.6	15.5	inversely with plant growth
Kandeler and Eder (1993)	Gumpenstein, Austria	16.8		early summer max.
Lovell *et al.* (1995)	Devon, U.K.	21.8	21.7	no obvious trends
Luizao *et al.* (1992)	Amazonia, Brazil	23.3		no consistent trends
Raghubanshi (1994)	Uttar Pradesh, India	33.3	32.1	summer max.
Robertson and Morgan (1996)	Victoria, Australia	26.5	21.5	generally little pattern
Robertson *et al.* (1993)	Queensland, Australia	25.8		no obvious trends
Ross (1990)	North I., New Zealand	8.9		summer and autumn max.
Ross *et al.* (1981)	Otago, New Zealand	20.3	11.3	no consistent trends
Ross *et al.* (1995a)	Manawatu, New Zealand	8.0	4.8	no consistent effects
Ross *et al.* (1995b)	Manawatu, New Zealand	9.0	8.4	little consistent effect
Santruckova (1992)	Chelcice, Czech Rep.	38.2		related to moisture
Singh *et al.* (1991)	Uttar Pradesh, India	32.5	21.5	summer maximum
Tate *et al.* (1991)	North I., New Zealand	28.9	13.0	autumn maximum
	Forest (mineral soil)			
Basu and Behera (1993)	Orissa, India	4.0		no clear trends
Bauhus and Barthel (1995)	Solling, Germany	10.9	11.9	no clear trends
Cochran *et al.* (1989)	Central Alaska	53.9		summer maximum
Diaz-Ravina *et al.* (1995)	Galicia, Spain	25.5	25.6	spring and winter max.
Gallardo and Schlesinger (1994)	North Carolina, U.S.A.		12.0	winter min./summer max.
Holmes and Zak (1994)	Michigan, U.S.A.	15.8	9.2	autumn max./summer min.
Hossain *et al.* (1995)	near Canberra, Australia		15.2	spring max.
Luizao *et al.* (1992)	Amazonia, Brazil	28.4		no consistent trends
Maithoni *et al.* (1996)	Meghaloya, India	30.0	34.7	winter maximum
Maxwell and Coleman (1995)	Sthn. Appalacians, U.S.A.	19.6	32.7	autumn max./spring min.
Raghubanshi (1991)	Uttar Pradesh, India	27.4	26.2	summer maximum
Santruckova (1992)	Chelice, Czech Rep.	37.0		related to moisture
Srivastava and Singh (1989)	Uttar Pradesh, India	28.1	28.1	summer max.
Von Lützow *et al.* (1992)	Augsburg, Germany		20.9	no obvious trends
Yavitt *et al.* (1993)	Panama Canal zone		37.9	no obvious trends
	Forest (humus)			
Pietikäinen and Fritze (1993)	Evo, Finland	11.5	10.0	no clear trends
Santruckova (1992)	Chelice, Czech Rep.	43.5		related to moisture
Scholle *et al.* (1992)	Solling, Germany	38.9		spring max.
Von Lützow *et al.* (1992)	Augsberg, Germany		16.1	no obvious trends
	Desert shrubland			
Kinsbursky and Steinberger (1989)	Israel	30.4		rainy season max.
Sarig and Steinberger (1994)	Israel	49.8		summer and autumn max.

arable and forest ecosystems. Another apparent control of temporal variability was moisture dynamics; the microbial biomass in some situations shows a positive relationship with soil moisture (e.g. Santruckova, 1992; Kandeler and Bohm, 1996) but others reveal negative relationships, probably as a result of enhanced plant competition for nutrients under superior moisture regimes (e.g. Raghubanshi, 1991). Similarly, plant root growth has the potential to induce both stimulatory effects (e.g. Bristow and Jarvis, 1991) and negative effects (e.g. Garcia and Rice, 1994), reflective of the dual effects of plants on soil microbes, on one hand stimulating them through C addition and on the other hand suppressing them through resource competition (Van Veen *et al.*, 1989). In cropping systems, the temporal pattern of crop residue return and related aspects of cropping practice also emerge as important controls of the microbial biomass (e.g. Franzluebbers *et al.*, 1994, 1995; Kaiser *et al.*, 1995). Finally, it is apparent, particularly with studies in tropical and warmer temporal habitats (i.e. areas where the ground does not freeze over winter) that the microbial biomass often shows no consistent temporal trends — over a quarter of the studies listed in Table 1 failed to find consistent, seasonally-determined temporal patterns of microbial biomass change.

TEMPORAL TRENDS – QUANTITATIVE ASSESSMENT

Effects of ecosystem "type" and disturbance

Populations or biomasses of organisms subjected to significant amounts of disturbance may be expected to be less resistant (though more resilient) to external perturbations than those in less disturbed situations and therefore could be expected to be less stable (Richards, 1987; Pimm, 1991). Therefore we would expect microbial biomass to show less temporal variability in a system in which there is inherently less disturbance. However, when the data presented in Table 1 is quantitatively analyzed, it is apparent that this is not the case — although the more persistent and less disturbed ecosystem types (forest and grassland) have higher microbial biomass C and N

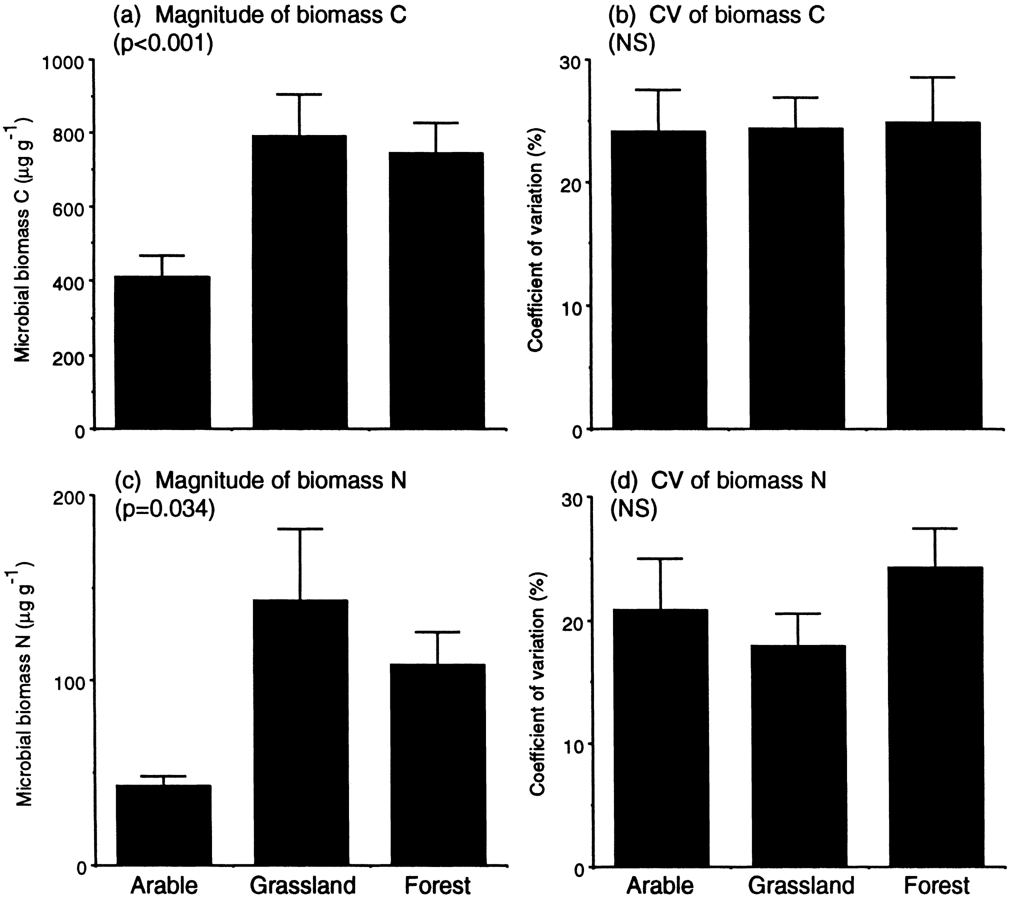

Fig. 1. Microbial biomass C and N, and the coefficient of variation of biomass C and N, for the studies listed in Table 1, categorized as according to ecosystem "type". The P-values for sub-graphs (a) and (c) represent the probabilities of the three ecosystem types not being different (one-way ANOVA); NS = no significant difference between the three ecosystem types.

values than the most disturbed type (arable), the temporal variability of all three types is remarkably similar (Fig. 1). This means that the temporal variability of the microbial biomass is apparently independent of even large differences in vegetation and land-use type, and also implies little linkage between above-ground and below-ground stability. It also means that a relatively undisturbed ecosystem such as a forest affords no greater buffering against such factors as climatic variation than

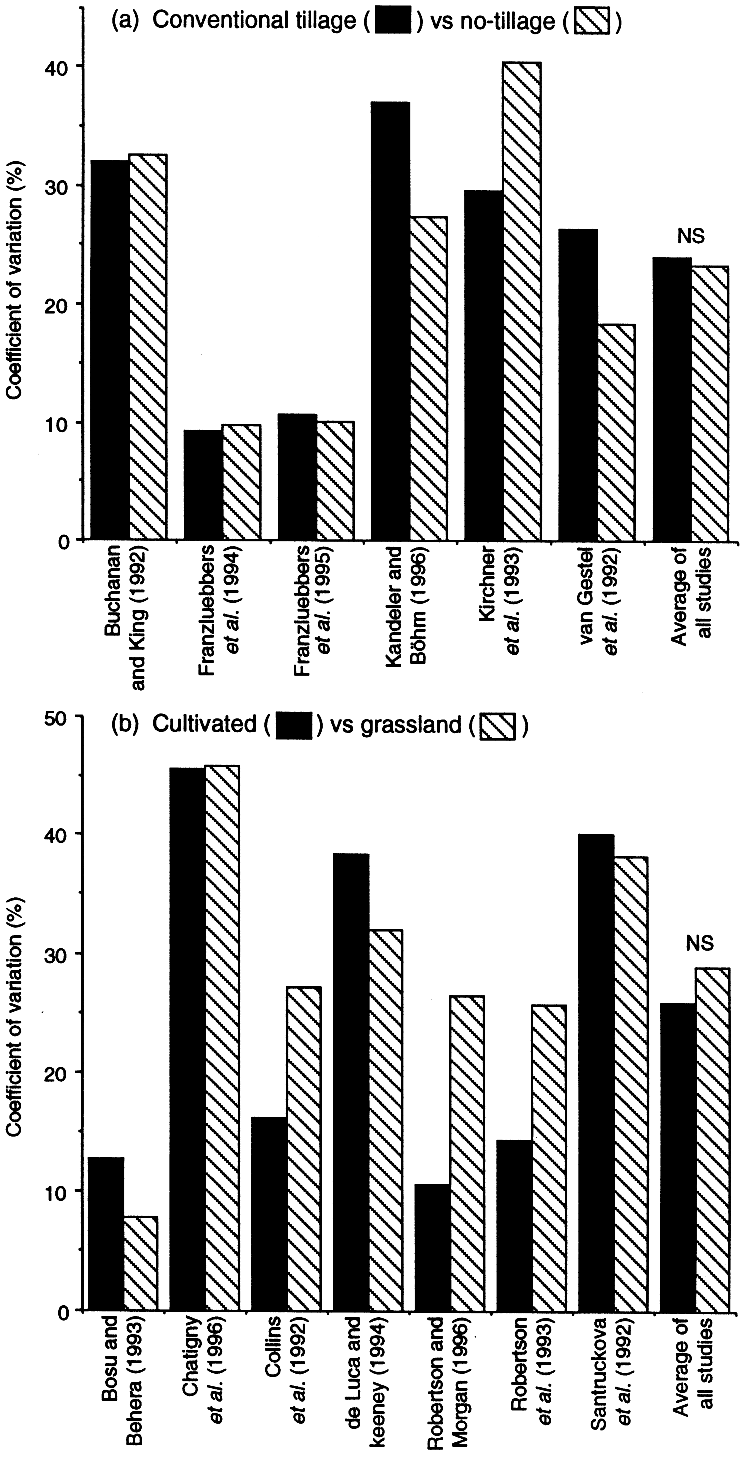

Fig. 2. Effects of tillage or cultivation on the coefficient of variation of biomass C for a selection of previous studies. NS = no significant difference for overall data (two-way ANOVA with each study serving as a replicate block).

does a regularly disturbed and intensively-managed ecosystem.

The absence of effects of disturbance on temporal variability is also apparent when CVs are calculated for both tilled and non-tilled treatments in each of several studies (Fig. 2). Despite the apparently destabilizing effects often attributable to tillage (Hendrix *et al.*, 1986; Wardle, 1995), it is apparent that the stability of the microbial biomass is largely unaffected. A similar pattern appears to apply for those studies which have investigated the effects of removing tropical forests — calculation of CVs for three studies in which temporal microbial biomass data were presented for intact forest and adjacent cleared areas (Srivastava and Singh, 1989; Luizao *et al.*, 1992; Basu and Behera, 1993) provides no evidence for enhanced temporal variability after clearing. Whatever adverse effects soil disturbance has on soil biological properties, destabilization of the microbial biomass is not one of them. This means that greater nutrient loss from disturbed ecosystems is not likely to be attributable to enhanced turnover of the microbial biomass resulting from greater temporal variability.

It is unclear as to why stability of the microbial biomass is so unresponsive to large-scale disturbance regimes. One possibility is that the soil microflora is regulated by disturbance regimes which operate at the microscopic spatial scale, and that differences in disturbance regimes between ecosystem types might be less at microscopic scales than at the landscape scales. Another possibility is that other factors may be more important in regulating temporal variability; this is explored below.

Effects of soil properties and macroclimatic factors

Correlation studies performed on the various studies listed in Table 1 (but with those involving humus, or those conducted in "outlier" habitats (central Alaska, Israeli deserts) excluded) revealed that certain soil chemical factors, and latitude (related to macroclimate) were sometimes significantly correlated with CV values for biomass C. Specifically, CV values were significantly related to pH and latitude in arable ecosystems; organic C, pH and latitude in grasslands; and total soil N concentration in forests (Table 2). It is apparent that the controls of temporal variability differed between the three ecosystem "types", and in particular, CVs in forested ecosystems were related to different factors than were the other two types. The significance of soil N as a control in forests may be linked to N being more important in forests than in other ecosystems as a determinant of microbial biomass (Wardle, 1992). Organic C, pH and latitude were all important determinants of biomass C values when all the data were considered collectively. Partial correlation analysis (Table 2) and stepwise multiple regression (Table 3) indicated that all three factors operated separately as controls of temporal variability of the microbial biomass, since each of the factors explained a different component of the overall variance for the CV data.

It would be reasonable to expect latitude to serve as a control of CV of biomass C, since at increasing latitudes the difference between summer and winter temperatures becomes more extreme, and at cooler temperate latitudes winter freezing significantly reduces microbial biomass (Cochran *et al.*, 1989), with rapid microbial growth during spring thaw (De Luca and Keeney, 1994). The role of total organic C in reducing temporal variability is curious. Firstly, organic C is also an important control of the magnitude of the microbial biomass. In the present study, biomass C and the CV of biomass C were both correlated with organic C, but not with each other. This means that organic C both enhances microbial C and reduces its temporal

Table 2. Correlation coefficients among temporal coefficients of variation (CV) for microbial biomass C and N, and soil chemical and macroclimatic factors on a global scale

Variable	CV for biomass C arable (n = 38)	 grassland (n = 20)	 forest (n = 14)	 all studies (n = 72)	CV for biomass N all studies (n = 35)
		Pearson's correlation coefficients			
Biomass C	0.198	–0.412†	–0.484†	–0.126	–0.274
Biomass C-to-total C	–0.223	0.209	–0.083	–0.103	–0.033
Organic C	0.020	–0.560‡	–0.383	–0.197	–0.158
Total N	–0.027	–0.527*	–0.590*	–0.268	–0.187
Soil C-to-N ratio	0.148	–0.164	0.042	0.050	–0.047
pH	–0.524§	–0.207	0.036	–0.286*	–0.079
Clay content	0.028	ND[1]	ND	0.183	ND
Annual rainfall	–0.045	–0.430†	–0.173	–0.144	0.192
Mean annual temp.	–0.240	–0.267	0.054	–0.196†	0.293†
Latitude	0.445§	0.173	0.254	0.304	–0.219
		Partial correlation coefficients[2]			
Organic C (pH, latitude)	–0.327†	–0.780§	–0.462†	–0.451§	–0.187
pH (organic C, latitude)	–0.594§	–0.652‡	–0.200	–0.534§	–0.163
Latitude (pH, organic C)	0.373*	0.565*	0.305	0.381‡	–0.140

†, *, ‡, § = correlation coefficient is significantly different to 0 at P = 0.10, 0.05, 0.01 and 0.001, respectively.

[1] ND = not determined due to insufficient data points.

[2] Variables controlled for with each partial coefficient are in brackets.

Table 3. Stepwise linear multiple regression relationships for predicting temporal coefficients of variation (CV) (in %) of soil microbial biomassfrom soil chemical and macroclimatic factors

Ecosystem "type"	Regression equation[1]	Standard errors of variables	Correlation coeff.
Arable	CV = 70.1 – 6.95(pH)	pH: 1.91‡	0.524‡
	CV = 47.2 – 5.98(pH) + 0.422(LAT)	pH: 1.91‡; LAT: 0.190*	0.608‡
Grassland	CV = 36.9 – 3.57(C)	C: 1.25†	0.559†
	CV = 82.5 – 4.96(C) – 6.71(pH)	C: 1.42†; pH: 3.26 (p = 0.060)	0.711†
	CV = 81.3 – 5.31(C) – 8.71(pH) + 0.381(LAT)	C: 1.22‡; pH: 2.92*; LAT: 0.161*	0.814‡
Forest	CV = 40.8 – 37.0(N)	N: 16.8*	0.591*
All studies	CV = 12.2 + 0.321(LAT)	LAT: 0.120†	0.304†
	CV = 34.4 + 0.389(LAT) – 3.92(pH)	LAT: 0.120†; pH: 1.22†	0.462‡
	CV = 58.5 + 0.342(LAT) – 6.56(pH) – 2.33(C)	LAT: 0.177†; pH: 1.39‡; C: 0.619‡	0.597‡

*, †, ‡ = standard error or correlation coefficient is significantly different from 0 at $P = 0.05$, 0.01 or 0.001, respectively.

[1] C = soil organic C (%), N = total soil N (%), LAT = latitude (deg.).

variability, but probably not through the same mechanism. Secondly, the finding that increasing organic C enhances stability of the microbial biomass is consistent with theoretical predictions (De Angelis, 1992) that donor-controlled, detritus-based food webs are inherently more stable than non detritus-based webs. The present study shows that increasing amounts of resources (organic C), which are of detrital origin, have stabilizing effects on the soil microbial biomass. Stabilizing effects of detritus have been shown in aquatic systems (Closs and Lake, 1994) and may help to explain the resistance of soil food webs to disturbance in general (Wardle, 1995). Finally, the significance of increasing pH in reducing temporal variability indicates the stabilizing effect of less stressful conditions in the soil subsystem, although the precise mechanism is not clear. Perhaps alleviation of "stress", rather than "disturbance" (*sensu* Grime, 1979) is more important in enhancing stability of the microbial biomass.

It is also apparent that some factors which clearly regulate the magnitude and activity of the microbial biomass, and contribute to nutrient conservation in the soil, do not emerge as controls of temporal variability. Soil C-to-N ratios, which are indicative of resource quality of the soil, and which help regulate the microbial biomass and certain soil processes, shows no relationship with temporal variability (Table 2). Further, although clay particles clearly protect microorganisms against predation and thus reduce turnover of microbial biomass at microscopic spatial scales (Insam *et al*., 1991), there is no evidence of increasing soil clay content having stabilizing effects in the present study. Further, both the magnitude of the microbial biomass and the biomass C-to-organic C ratio show no relationship with temporal variability, indicating that a high content of microbial biomass, or an increment of biomass, is not likely to enhance its stability.

While I have identified three factors which control temporal variability, it is clear from Table 3 that a significant proportion of the total global variation of the CV for biomass C is still unaccounted for. This may be partly because the site upon which each study is based has its own controlling factors which operate at the within-site spatial scale, and some controls may be site specific. However, the possibility exists that other controls exist which operate at spatial scales but which were not possible to quantify in the present study, for example temporal variability of rainfall pattern (especially between seasons). This latter factor is probably important given the role of moisture dynamics in regulating the microbial biomass (Bottner, 1985; Sparling *et al*., 1986), and two examples from Table 1 should help to reinforce this. Firstly, those studies conducted in the Uttar Pradesh area of India (e.g. Srivastava and Singh, 1989; Raghubanshi, 1991, 1994; Singh *et al*., 1991) show a greater temporal variability than expected for tropical latitudes. In this region there are clear and very distinct rainy and hot dry seasons. Secondly, studies conducted in the North Island of New Zealand sometimes show temporal variability of less than expected (e.g. Wardle *et al*., 1993; Ross *et al*., 1995a,b). Such studies are located in areas with rainfall levels of over 1200 mm y^{-1}, and this rainfall is often distributed comparatively equitably throughout the year.

Although I was able to identify controls of temporal variability of biomass C, any attempt to do this for biomass N was unsuccessful. This is possibly at least in part because a high proportion of the studies considering temporal variability of biomass N have been conducted for forest soils while the majority of those for biomass C have been done for grassland and arable soils. It appears that the controls identified for temporal variability of biomass C are less likely to be applicable to forest than other ecosystems, so a data set more heavily weighted to forests (such as for the biomass N data) is more likely to yield non-significant results. Unfortunately, not enough studies have been carried out on temporal variability of biomass N to date to perform separate analyses for each ecosystem type.

Predicting microbial turnover

Increasing temporal variation of the microbial biomass makes an important contribution to increasing turnover of the microbial biomass since temporal dynamics are associated with alternating periods of net microbial death and net growth of new tissue. This turnover has important consequences for soil nutrient dynamics, particularly in terms of mineralization of nutrients from labile microbial tissue following death, and immobilization of nutrients during periods of growth (Singh *et al.*, 1989), and makes an additional contribution over and above that induced by turnover of microbial biomass under steady state conditions (cf. Jenkinson and Ladd, 1981). The relationships derived in Table 3 can be used to demonstrate how factors controlling temporal variability of the microbial biomass can increase turnover through the use of a hypothetical example of an ecosystem with four seasons per year. In the first season, the microbial biomass has a magnitude of X units and in the second season this increases by Y units. By the third season it declines to X units again and in the fourth season it declines a further Y units, before increasing back to X units by the first season of the following year. In this situation, the rate of microbial turnover through temporal dynamics will be linearly related to CV of the biomass as follows: turnover rate (y^{-1}) = $2.45 \times$ CV (since a turnover rate of 1.0 corresponds to a CV of 0.408). For this example, I have determined the predicted microbial turnover rate and time using the relationship for determining CV of the microbial biomass (Table 3, last equation) for a range of conditions, i.e. varied latitude (pH and soil C held constant), varied pH (latitude and soil C constant) and varied soil C (latitude and pH constant) (Fig. 3). It is clear from Fig. 3 that increasing latitude has important effects on increasing biomass turnover through enhancing temporal variability. This is in direct contrast to prediction by modelling approaches (Jenkinson and Ladd, 1981) which suggest a greater turnover rate in warmer latitudes through greater microbial metabolic activity. However, it is apparent that turnover has two components, i.e. that determined by microbial activity (which includes cryptic growth and which occurs even if biomass remains unchanged over time) which could not be estimated in my study, and that regulated by temporal dynamics, which is not included in the approach of Jenkinson and Ladd (1981). The two components respond in opposite directions to increases in latitude.

It is also apparent from Fig. 3 that increasing soil pH, and (to a lesser extent) enhancing soil C, could also be expected to reduce the rate of microbial turnover, which may have important consequences for reducing mineralization of nutrients immobilized in the microbial biomass, and enhancing conservation of nutrients in the soil. This implies that alleviation of stress in the soil sub-system may have important ecological consequences through stabilizing the soil microbial biomass.

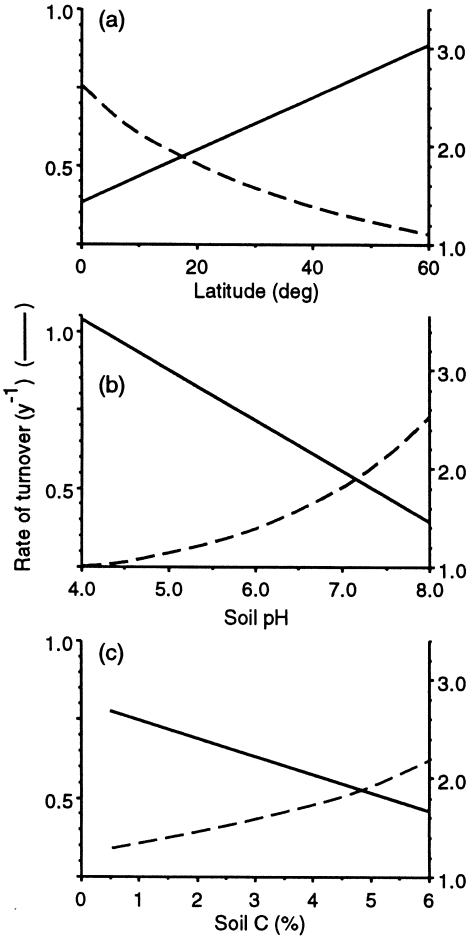

Fig. 3. Rate of turnover, and turnover time of microbial biomass C, for a hypothetical example (see text), using the last equation listed in Table 3. (a) latitude varied, organic C = 1.5%, pH = 6.0; (b) soil pH varied, organic C = 1.5%, latitude = 45°; (c) organic C varied, C = 1.5%, latitude = 45°.

CONCLUSIONS

While temporal variability of the microbial biomass undoubtedly has a critical role in determining microbial turnover, this variable has received rather less attention than other microbial properties, and the factors responsible for regulating it are still poorly understood. However, it is clear that both macroclimatic and soil quality factors have important roles in regulating the degree of temporal variability. The effect of macroclimatic temporal variability on determining microbial temporal variability is relatively predictable. But the stabilizing effects of increasing soil organic C and pH have also been demonstrated in this study; both of these factors contribute to alleviation of stress on the microbial community. Contrary to expectations, factors indicative of varying disturbance (e.g. tillage regime, vegetative cover) had no detectable effect on temporal variability, suggesting that intensity and degree of disturbance does not have destabilizing effects on the microbial biomass. Since temporal variability of the microbial biomass is directly linked to the turnover of nutrients, nutrient availability and ultimately ecosystem productivity, a better understanding of the controls of microbial temporal variability should greatly assist our understanding of how ecosystems function.

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