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Carbon and nitrogen limitations of soil microbial biomass in desert ecosystems

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Abstract. Microbial biomass nitrogen was measured in unamended (dry) and wetted soils in ten shrubland and grassland communities of the Chihuahuan desert, southern New Mexico, by the fumigation-extraction method. Microbial biomass-N in dry soils was undetectable. Average microbial biomass-N in wetted soils among all plant communities was 15.3 μg g^{-1} soil. Highest values were found in the communities with the lowest topographic positions, and the minimum values were detected in the spaces between shrubs. Microbial biomass was positively and significantly correlated to soil organic carbon and extractable nitrogen ($NH_4^+ + NO_3^-$). In a stepwise multiple regression, organic carbon and extractable nitrogen accounted for 40.9 and 5.6%, respectively, of the variance in microbial biomass-N among all the samples. Among communities, the soil microbial biomass was affected by the ratio of carbon to extractable nitrogen. Our results suggest a succession in the control of microbial biomass from nitrogen to carbon when the ratio of carbon to nitrogen decreases during desertification.

Introduction

The microbial community plays an essential role in the transformation and cycling of organic matter and plant nutrients in the soil. Because nitrogen (N) is usually the nutrient in greatest demand by plants, estimates of the amount of N in microbial biomass have received considerable attention. This pool, by forming part of the potentially mineralizable soil N, acts as both a sink and a source of labile nutrients, capable of supplying a significant proportion of the N used by plants (Jenkinson & Ladd 1981; Marumoto et al. 1982; Bonde et al. 1988). Vitousek & Matson (1984) concluded that microbial biomass, if conserved during forest management, retains N in harvested loblolly pine plantations. Competition between microbial biomass and plants for N is an important factor in controlling both the amount and form of N in the soil (Jackson et al. 1989). In arid

and semiarid ecosystems, nitrogen is an important factor limiting the productivity of perennial vegetation, since nitrogen amendments produce significant growth responses during the wet season (Fisher et al. 1987; Sharifi et al. 1988).

Discontinuous and stochastic rainfall is the dominant variable controlling plant growth in arid ecosystems. Many soil microorganisms are intolerant of low soil moisture, and changes in soil moisture status can result in rapid changes in the magnitude of microbial biomass (Harris 1981; Bottner 1985; Schnurer et al. 1986). In some cases, turnover of the microbial biomass is enhanced by soil drying-rewetting cycles (Ross 1987; Wardle & Parkinson 1990). In other cases, rewetting of dry soil may kill soil microbes through osmotic stress (Kieft et al. 1987).

Some authors suggest that the activity of soil microbes is less sensitive to soil water potential than is water uptake by plants and that a substantial amount of water is present at high tension during the dry season that is unavailable to plants but extractable by microbes (Calder 1957; Singh et al. 1989). In dry tropical ecosystems, Singh et al. (1989) found that microbial biomass accumulated and conserved nutrients in a biologically active form during the dry period and released them rapidly at the beginning of the wet season. Their findings suggest that in other ecosystems with frequent cycles of drying-rewetting, such as desert ecosystems, microbial biomass could play a similar role.

During the last 100 years, large areas of semiarid grasslands in the southwestern United States have been replaced by communities dominated by arid shrublands, especially creosotebush (*Larrea tridentata*) and mesquite (*Prosopis glandulosa*). This process has meant a shift from homogeneous to heterogeneous soil resource distribution (Schlesinger et al. 1990). Soil fertility in the new shrubland communities is relatively high at the base of shrubs, where soil is protected from erosion by wind and water. These changes affect abundance and distribution of N in desert soils, which determines plant productivity during the wet season (Fisher et al. 1988; Sharifi et al. 1988; Breman & de Witt 1983). The distribution of microbial biomass is also heterogeneous in desert shrublands, and its size and activity may affect the N availability in arid and semiarid ecosystems (Burke et al. 1989).

The objective of this study was to document the size and distribution of soil microbial biomass in different plant communities of the Chihuahuan desert, the factors that affect its abundance, and the changes in microbial biomass that occur during desertification.

Methods

Study sites

This study was conducted at the Jornada Experimental Range of southern New Mexico. The study area comprises 78,266 ha of the Chihuahuan Desert, which extends from the south-central United States to central Mexico. The climate of the area is characterized by an abundance of sunshine, a wide range between day and night temperatures, low relative humidity, an evaporation rate averaging 229 cm per year, and extremely variable precipitation. Mean annual temperature is 15.6 °C and mean annual precipitation is 210 mm, with 53% of the precipitation occurring from July to September (Buffington & Herbel 1965).

Soil microbial biomass-N was studied in five plant communities that dominate the Jornada Experimental Range: grasslands composed of black grama (*Bouteloua eriopoda*); playas or low-lying areas with clay-textured soils dominated by tobosa (*Hilaria mutica*) and burrograss (*Scleropogon brevifolius*); and three types of shrublands, including tarbush stands (*Flourensia cernua*), mesquite dunes (*Prosopis glandulosa*), and creosote-bush (*Larrea tridentata*). To assess the potential range of microbial biomass in each community type, we selected subjectively two sites of each type that appeared to differ in plant biomass and productivity.

Soils in the grassland and most shrubland sites are derived from quartz monzonite alluvium from local mountains; soils in the playa are derived from ancestral Rio Grande river deposits with smaller amounts of alluvium. Mesquite shrublands are found on deposits of eolian sands. The soils have been more fully described by Wierenga et al. (1987) and Lajtha & Schlesinger (1988).

Field sampling

In each site, a 50-m transect was established in June 1991. In the shrubland communities, 40 soil samples were collected, 20 under shrubs and 20 between shrubs chosen at random points along the transect. In the grassland and playa communities, where plant cover is continuous, a total of 20 samples per transect were taken at random locations. In each site, half the samples were wetted 24 hours before sampling. For this purpose, a hollow cylinder 24 cm in diameter and 20 cm in height was inserted 10 cm into the soil at each sample location and 2 liters of water were added. After 24 hours, about 100 g of wet soil were taken from the 0—10 cm layer. The samples were taken to the laboratory and immediately processed.

Laboratory procedures

Samples were sieved (< 2 mm) in a field-moist condition. Subsamples were taken for analysis of water content (110 °C, 24 h) and pH (1 part soil in 2 parts 10 mM $CaCl_2$). On a randomly selected subset of 80 samples, total N and organic C were determined using a Perkin-Elmer CHN model 240 C analyzer. Total carbon (C) was determined before and after removal of $CaCO_3$ by treatment with 5% HCl, and the difference was taken as the $CaCO_3$ content in the soil.

Soil microbial biomass-N was analyzed by using the fumigation-extraction method as outlined by Brookes et al. (1985). We exposed the soils to chloroform for 5 days, extracted them with 100 ml of 0.5 M K_2SO_4, and filtered the extracts through 0.45-μ Millipore filters. Separate samples, extracted with K_2SO_4 immediately after collection, served as initial controls for the fumigated samples and indicated the amount of extractable N in each sample (NO_3^- plus NH_4^+). All results are expressed on the basis of oven-dried soil, determined by drying the samples after the extractions were complete. N in microbial biomass was calculated using a K_n of 0.69 (Brookes et al. 1985).

Nitrogen analysis of 0.5 M K_2SO_4 extracts was performed by using a persulfate oxidation technique originally developed for the determination of total N in seawater (D'Elia et al. 1977). This method recovered N from organic standards with greater than 90% efficiency (B. Thomas pers. comm.). Nitrate in the digest was analyzed by the hydrazine reduction procedure with a Traacs 800 autoanalyzer (Bran & Luebbe 1986).

Statistical analysis

For each shrubland community, we tested for significant differences in mean microbial biomass between samples taken under shrubs and samples taken in the shrub inter-space using the *t*-statistic. Because these differences were significant in most cases, reflecting a bimodal distribution of microbial biomass in shrublands, we used a non-parametric ANOVA (Kruskal-Wallis one way analysis by ranks) to test for differences between communities. Subsequently, the Kolmogorov-Smirnov test was used to examine the significance of differences between individual pairs of communities. Linear regressions between microbial biomass as a dependent variable and organic C, total N, extractable N, C:N ratio, C:extractable-N ratio, and pH as independent variables were performed for each site and for all sites. Because some independent variables were partially correlated, we used a forward stepwise multiple regression to select the variable or variables that best explained variation in microbial biomass for each site

and for all sites (Statistical Graphics System 1991). Outliers were removed using the Box and Whisker method (Statistical Graphics System 1991). They were found in the playa-college and mesquite site, where undecomposed plant materials were detected in 8 soil samples during the analytical procedure.

Results

In all dry soils, mean microbial biomass-N was $-0.57\ \mu g\ g^{-1} \pm 3.45$ SD. This mean was not significantly different from 0 ($t = -1.26$; $p = 0.21$), and further data analysis was performed only with samples taken from wetted soils.

When averaged over all sites, soil microbial biomass-N was $15.3\ \mu g\ g^{-1}$ (± 14.7 SD). ANOVA showed the different plant communities to be a significant source of variation in microbial biomass ($p < 0.001$). Tarbush (under shrubs) and playa communities had the highest microbial biomass-N (Fig. 1). The lowest levels of microbial biomass were found in the samples taken between shrubs in all the shrubland sites. Statistical differences between microbial biomass-N under and between shrubs were significant (*t*-student, $p < 0.01$) in all shrublands except for one creosotebush community (CT). Differences between the two creosotebush sites (Kolmogorov-Smirnov test) and between the two grassland sites (*t*-student) were not significant and data were pooled in regression analysis. Proportion of the total organic N contained in microbial biomass ranged from 3.6% in samples taken under shrubs in one of the tarbush communities (tarbush-east), to 0.2% in the spaces between shrubs in the mesquite-well community (Fig. 1). The communities with highest values in microbial biomass-N (tarbush and playa) showed the highest proportion of total N in microbial biomass (Fig. 1).

Although there was a large amount of variation, microbial biomass was positively and significantly related to soil organic C, total N, extractable N ($NH_4^+ + NO_3^-$), and the C:N ratio over all sites (Fig. 2). In contrast, microbial biomass showed no significant relationship to $CaCO_3$ content, pH, and C-to-extractable N ratio. The samples from one of the playas (PC) averaged 1.99% organic C and were removed from Fig. 2 as outliers, even though their inclusion would have improved the regression ($r = 0.78$, $p < 0.001$) with microbial biomass. Using a stepwise multiple regression to predict microbial biomass, only organic C and extractable N were included in the model as independent variables, accounting for 40.9% and 5.6% of the variance, respectively (Table 1).

The relationship of microbial biomass to organic C and extractable N

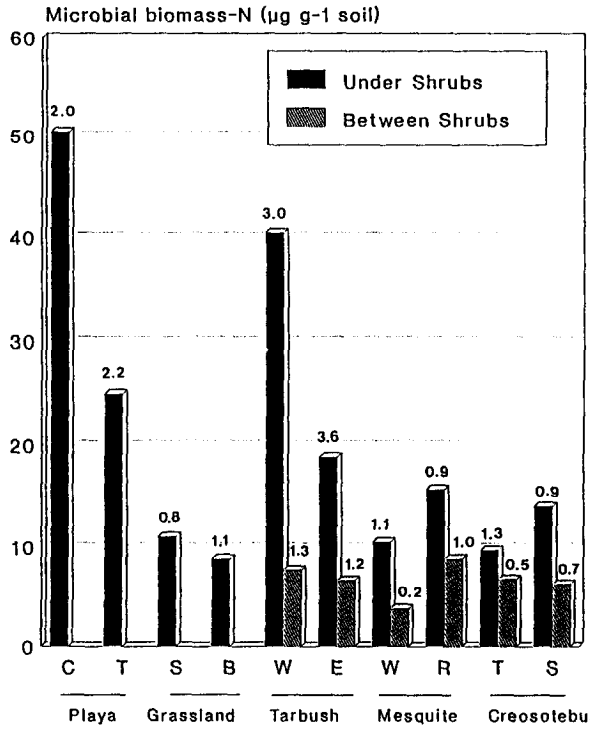

Fig. 1. Microbial biomass-N in ten communities of the Chihuahuan desert as absolute values (bars) and as a percent of total soil nitrogen (numbers on bars). Symbols are as follow: W, tarbush-west; E, tarbush-east; C, playa-college; T, playa-tabosa; S, grassland-sand; B, grassland-basin; W, mesquite-well; R, mesquite-rabbit; T, creosotebush-termite; S, creosotebush sand.

was different in the different plant communities. All tarbush and mesquite sites and one playa site (PT) showed a positive and significant correlation between microbial biomass and both organic C and extractable N. Using a stepwise multiple regression, only C was significant in these sites (Table 2). Microbial biomass was also significantly related to organic C in the other playa site. Creosotebush and grassland sites showed a positive and significant correlation with extractable N, but not with organic C.

The selection of C or N as a variable that explains microbial biomass seems related to the ratio of C to extractable N in each site (Table 2). To test this hypothesis, we plotted microbial biomass-N versus organic C in samples separated into three different ranges of the C-to-extractable N ratio (Fig. 3). Samples with C-to-extractable N ratio below 0.06 and between 0.06 and 0.12 showed a highly significant relationship, but the slope decreased from 65 in the first group to 46 in the second group. Samples with a C-to-extractable N ratio above 0.12 did not show a significant statistical relationship between microbial biomass-N and organic C.

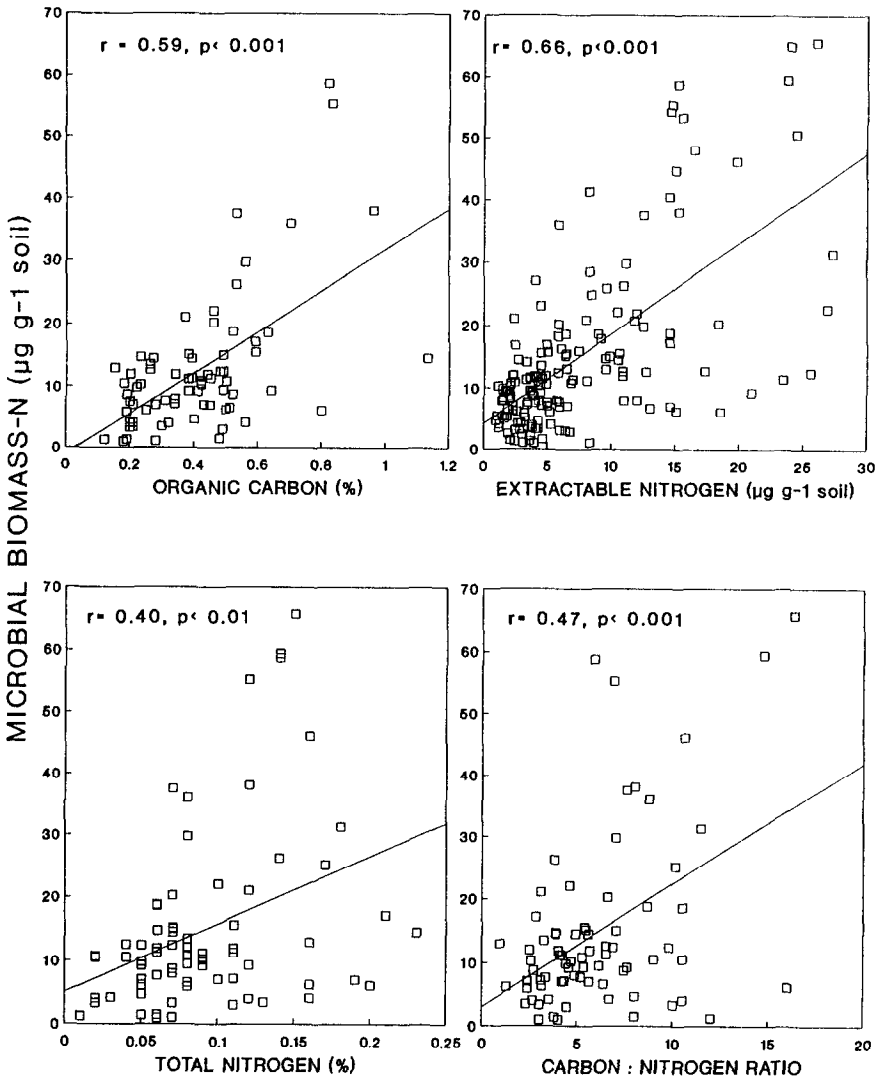

Fig. 2. Microbial biomass-N versus organic C, extractable N, total N and C-to-N ratio for all the samples in the ten sites.

Transformations of soil N upon wetting dry soils in the different communities are presented in Table 3. In the soils of creosotebush, grasslands, and playa-college communities, a significant decrease of extractable N was observed, indicating net uptake of inorganic-N by microbial biomass in the 24-h interval. However, in each case the uptake of N by microbial biomass in wet soils exceeded the initial levels of extractable N, indicating that some N that is mineralized from soil organic matter is also taken up by microbes in the 24-h interval after wetting.

Table 1. Analyses of variance for the stepwise multiple regression of microbial biomass-N as the dependent variable and organic C and extractable nitrogen as the independent variables.

Factor	Sum of squares	Df	F-ratio	% variation	Probability > F
Organic C	3523.9	1	52.2	40.9	< 0.001
Extractable N	481.5	1	7.1	5.6	< 0.01
Total	4005.5	2	29.6	46.4	< 0.001
Error	4459.1	66			
Total corrected	8464.6	68			

Discussion

Our samples from the Chihuahuan desert showed the lowest levels of microbial biomass-N found in the literature (Fig. 4). Microbial biomass-N in desert ecosystems is only 37% of the pool of microbial biomass-N in warm-temperate forest and 20% of the pool reported in tropical forests. In each of these studies, the microbial biomass was measured by fumigation-extraction using the recovery coefficient ($k_n = 0.69$) proposed by Brookes et al. (1985). By watering the soil, we created optimal conditions for the rapid growth of microbial biomass. During most of the year desert soils are dry, and both microbial biomass and activity are likely to be even lower than our values. Bamforth (1984), studying groups of microbes in Arizona deserts and woodlands by direct microscopy, found that the maximum abundance of any microbial group in deserts was only 10—30% of that found in forest habitats. Insam et al. (1989) reported that soil microbial biomass per g of organic C in different climatic regimes was significantly related to the ratio of precipitation to evaporation at the sites, and Insam (1990) reported a negative relationship between microbial biomass and temperature in several soils from different climatic regions. In all cases, soils from deserts had low microbial biomass.

The microbial biomass-N in the tarbush community accounted for more than 3% of total nitrogen in soil (Fig. 1). That value is considered normal for agricultural soils (Stevenson 1986), and is also very similar to the percentage reported in a warm-temperate forest (3.3%, Gallardo & Schlesinger 1990). However, in most of the other desert communities, microbial biomass-N accounted for less than 2% of the total soil nitrogen, being as low as 0.2% in the mesquite-well community, and $\leqslant 1\%$ in creosotebush, grassland and mesquite-rabbit communities (Fig. 1). In

Table 2. Correlation coefficients between microbial biomass-N as the dependent variable and organic C and extractable N as the independent variables in the 0—10 cm depth of soils at eight different sites in the Chihuahuan desert of New Mexico. When both C and N are significantly correlated, the accepted variable has been selected by a stepwise multiple regression. Average organic C, $CaCO_3$, total N, the C:N ratio, extractable N, and the C-to-extractable N ratio for each site is included. Extractable N is the sum of NH_4-N and NO_3-N, both expressed as mg/l, in the initial soil extractions from each site.

Site	Soil variable	Correlation coefficient	Probability	Accepted variable	Organic C (%)	Total N (%)	C-to-total N	Extractable N ($\mu g\ g^{-1}$)	C-to-extractable N	$CaCO_3$ (%)
Tarbush-west	C	0.83	<0.01	C	0.57	0.09	6.1	10.3	0.054	0.14
	N	0.64	<0.01							
Tarbush-east	C	0.88	<0.01	C	0.41	0.07	7.2	7.6	0.054	0.63
	N	0.64	<0.01							
Mesquite-rabbit	C	0.67	<0.05	C	0.25	0.08	4.9	8.79	0.047	0.12
	N	0.50	<0.05							
Mesquite-well	C	0.77	<0.01	C	0.37	0.09	5.4	8.82	0.046	0.15
	N	0.83	<0.01							
Playa-college	C	0.90	<0.05	C	1.99	0.16	12.6	26.4	0.072	0.28
	N	0.55	NS							
Playa-tabosa	C	0.95	<0.05	C	0.61	0.08	8.0	7.41	0.082	1.26
	N	0.72	<0.05							
Creosotebush	C	−0.22	NS	N	0.39	0.10	4.2	3.71	0.11	0.02
	N	0.38	<0.05							
Grassland	C	−0.16	NS	N	0.33	0.07	5.6	2.61	0.13	0.03
	N	0.49	<0.05							

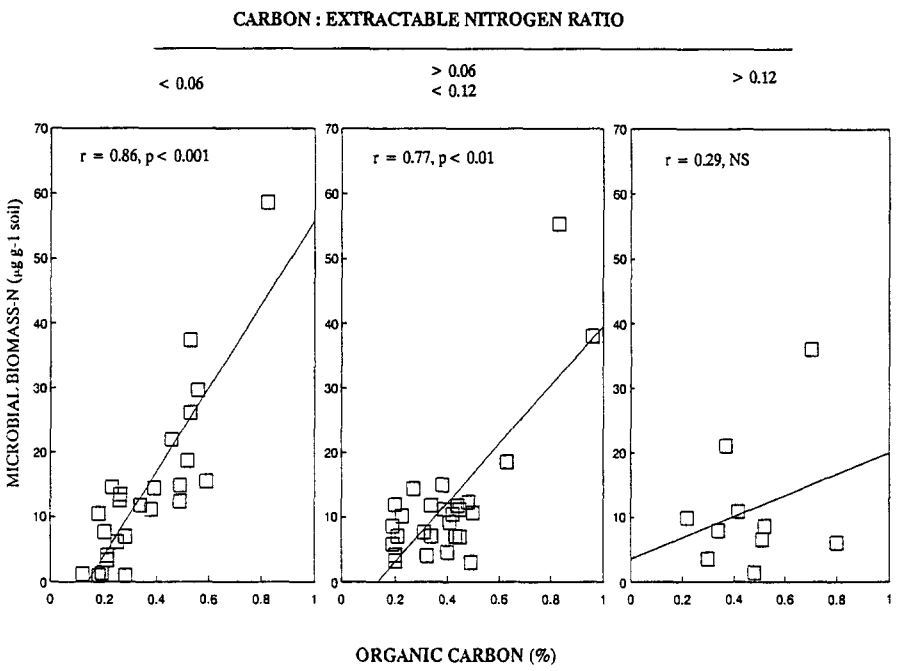

Fig. 3. Microbial biomass-N versus organic C at three different ranges of C-to-extractable-N ratios for all the samples from the ten sites. Extractable N is the sum of NH_4-N and NO_3-N, both expressed as mg/l, in the initial soil extractions from each site.

Table 3. Extractable nitrogen in dry soils and wet soils (24 h after watering), and microbial biomass-N in wet soils, in shrubland and grassland communities in the Chihuahuan desert. A minimum estimate of N-mineralization was calculated as the sum of microbial biomass-N and the change in the pool of extractable N. (NS) = Values are not significantly different from 0 (*t*-test). (*) Values are significantly different from 0, $p < 0.05$ (*t*-test). (1) Undershrub values.

	μg N g^{-1} soil				
Site	Dry soil extractable N	Wet soil extractable N	Difference	Microbial biomass N	Estimated 24-h mineralization rate
Tarbush-west (1)	12.4	13.2	+0.8 (NS)	40.4	41.2
Tarbush-east (1)	9.2	10.7	+1.5 (NS)	18.8	20.3
Mesquite-rabbit (1)	21.4	13.8	−7.6 (NS)	15.7	8.1
Mesquite-well (1)	12.8	14.9	+2.3 (NS)	10.5	12.8
Playa-college	36.1	26.4	−9.7 (*)	50.4	40.7
Playa-tabosa	11.8	7.4	−4.4 (NS)	24.9	20.5
Creosotebush (1)	9.8	5.4	−4.4 (*)	11.4	7.0
Grassland	3.5	2.6	−0.9 (*)	9.9	9.0

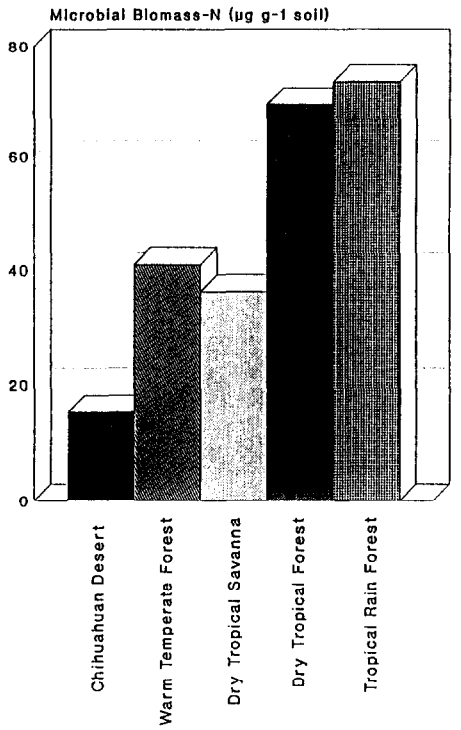

Fig. 4. Overall microbial biomass-N in five different ecosystems. The Chihuahuan desert average is derived from this study. Warm-temperate forest average was taken from Gallardo and Schlesinger (1990). Dry tropical savanna and dry tropical forest average was calculated from the range reported by Singh et al. (1989). Tropical rain forest average was calculated from the range reported by Livingston et al. (1988).

shrubland communities the proportion of N held in microbial biomass tends to be lower in samples taken between shrubs vs under shrubs. A low ratio of microbial biomass-N to total N could indicate a low potential mineralization rate in these soils.

Using independent samples taken in June—September, 1990, D. R. Zak (pers. comm. 1992) found microbial biomass-N of 3.0 g m^{-2} in grasslands and 5.1 and 1.6 g m^{-2} under shrubs and between shrubs, respectively, at the Jornada Experimental Range using the fumigation-incubation method. Our 1991 values for the same communities and the same soil profile depth (0—10 cm) expressed on a surface area basis are lower (1.13 g m^{-2} for grasslands, 1.41 g m^{-2} under shrubs and 0.62 g m^{-2} between shrubs). However, Zak used a recovery coefficient (k_n) of 0.326, calculated from the equation of Voroney & Paul (1984). If we had used the same k_n, our values would be very similar to his values (2.39 g m^{-2} in grasslands, 2.98 g m^{-2} under shrubs and 1.31 g m^{-2} between shrubs).

Mazzarino et al. (1991) studied soil microbial biomass-N in a semiarid

woodland under individuals of *Larrea* spp. in northwestern Argentina and found values ranging between 10 μg g^{-1} in the dry season to 43 μg g^{-1} in the wet season. (We have recalculated their values using a recovery coefficient [k_n] of 0.69 to conform to our study). Higher values were reported under the canopy of *Prosopis flexuosa*, a leguminous tree (between 34 and 60 μg g^{-1}). These higher values compared with shrubland values in the Chihuahuan desert may be explained by the higher precipitation and plant biomass in the semiarid woodlands of Argentina.

Differences in microbial biomass under and between shrubs were also reported by Mazzarino et al. (1991). In the shrub interspaces, microbial biomass-N ranged from 14.5 to 29 μg g^{-1} (again, using $k_n = 0.69$), which is significantly higher than the range found in the Chihuahuan desert (3.7 to 8.8 μg g^{-1}).

Our sampling scheme in shrublands consisted of 10 random samples taken from underneath and 10 taken between shrubs, and we did not measure the proportional cover of shrubs in these communities. The coefficient of variation associated with mean microbial biomass-N is higher in shrubland communities ($n = 20$) than in the grasslands ($n = 10$) (Fig. 5). Recognizing that the shrubland and grassland communities were

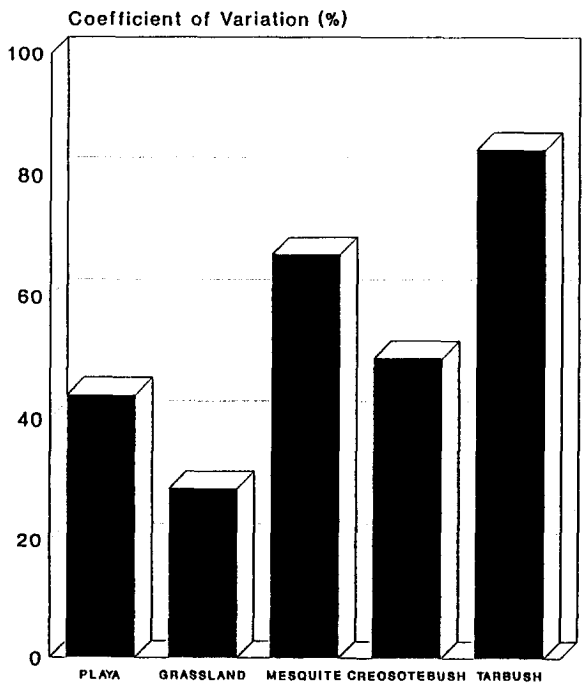

Fig. 5. Coefficient of variation for microbial biomass in five different communities in the Chihuahuan desert.

sampled somewhat differently, we suggest that increasing heterogeneity of soil fertility develops as shrubland communities replace grasslands during desertification (Schlesinger et al. 1990; Hook et al. 1991). It is likely that erosion by wind and water leads to losses of soil organic matter and nutrients in the spaces between shrubs and to lower microbial biomass.

We found the highest values of microbial biomass in playa and tarbush, the communities with lowest topographic positions in the landscape. These communities receive soil materials and nutrients from the higher elevations, dominated by shrublands, due to erosion of soils from intershrub areas. The bare soils in shrublands yield a greater horizontal transport of runoff resulting in accumulations of fine-textured soils in basin depressions with higher carbon, nutrient, and moisture content (Schlesinger et al. 1990; Rostagno 1989). As an additional indication of this process, $CaCO_3$ concentration in the 0—10 cm depth of soil profile appeared to be significantly higher in playa and tarbush communities (low elevations) than in shrubland and grassland communities (high elevations) (Table 2).

Burke et al. (1989) found a similar distribution of microbial biomass in sagebrush ecosystems of Wyoming, where the highest values were found in topographic depressions. The accumulation of clay in the low topographic communities may have a direct effect on microbial biomass. Soils with higher clay content have the capacity to preserve or protect microbial biomass, which may allow more efficient transfer of nutrients to succeeding generations of microorganisms (van Veen et al. 1984; Gregorich et al. 1991).

Microbial biomass-N appears to be related to organic C and extractable N in all the communities. Scheu (1990) studied a secondary succession from field to beechwood in Germany and reported C limitations in the first stage followed by N and P limitation in the later stages of the succession. Limitation of microbial biomass by organic C has also been found in a warm temperate forest (Gallardo & Schlesinger 1990) and in several ecosystems along a gradient of climate and plant production (D. R. Zak, pers. comm. 1992).

We found that different sizes of microbial biomass in desert soils do not depend on the absolute values of C and extractable N in the soil, but on the ratio between them. For instance, in playa-college, the community with the highest level of soil C, microbial biomass appeared to be affected by levels of C because of the high soil N content. On the other hand, microbial biomass in creosotebush shrublands and grasslands, the communities with the highest topographic positions, was correlated with extractable N, which could indicate limited nutrients in these sites due to erosion. Control by C in both mesquite communities, with the lowest C contents and a relatively high N content, may be related to the fact that

mesquite is a symbiotic N fixer and competition between microbial biomass and plant roots for extractable N is unlikely. Part of the N fixed by mesquite may accumulate near the soil surface as litter, increasing the N availability in this community (Virginia & Jarrell 1983; Lajtha & Schlesinger 1986).

The slope of the relationship between organic C and microbial biomass-N decreases when the ratio of C-to-extractable N increases. The difference in slope suggests a shift in the control of microbial biomass from C to N. Thus, as soil organic matter declines when desert shrublands, such as mesquite, replace grasslands, the landscape may shift from a control by N to an overall control by C. In many cases, greater losses of organic matter than of organic N are seen upon soil disturbances, such as cultivation (Tiessen et al. 1982). Even if C control is prevailing, increments in soil C would result in different increments of microbial biomass depending on soil N availability.

Extractable N significantly decreased in the soil of three communities during a 24-h period after wetting when the microbial biomass increased. Assuming that no significant leaching occurred, this decrease in extractable-N could be explained by uptake by microbial biomass. Creosotebush communities experienced the highest decrease, as the final extractable-N value was 44.6% lower than the initial value, while in playa and grassland communities this decrease accounted for 26% of the initial pool of soil N. These results suggest that in these communities soil wetting produced a net decrease in available-N for plant uptake. This hypothesis is supported by the results of Fisher et al. (1987) in a creosotebush community, where N availability was reduced during wet weather.

In the creosotebush communities, the net uptake of inorganic-N accounted for 39% of the total microbial biomass-N after 24 h of wetting the soils, while in grassland and playa communities the uptake of net inorganic-N accounted for 9.3% and 19.2% of the pool of N in microbial biomass, respectively. In each case, the growth of the microbial community during the 24-h period after soil wetting also depended on N mineralized from soil organic matter and immobilized in microbes. Uptake of mineralized N was lower in the creosotebush communities (7 μg N g^{-1} soil) than in the grassland communities (9 μg N g^{-1} soil). Because extractable-N was only measured in samples taken under shrubs, differences in the overall mineralization of organic-N in shrubland and grassland ecosystems could be even higher than indicated by these results. Our results support the idea that the replacement of grasslands by shrublands leads to losses of soil fertility.

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