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Factors determining soil microbial biomass and nutrient immobilization in desert soils

ANTONIO GALLARDO[1] and WILLIAM H. SCHLESINGER[2]*
[1] *Departamento de Ecología, Universidad de Sevilla, Apdo. 1095, 41080 Sevilla, Spain;*
[2] *Departments of Botany and Geology, Duke University, Box 90340, Durham, NC 27708, USA; * Corresponding author: Department of Botany, Duke University, Durham, NC 27708-0340, USA*

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Abstract. We examined the 10-day response of soil microbial biomass-N to additions of carbon (dextrose) and nitrogen (NH_4NO_3) to water-amended soils in a factorial experiment in four plant communities of the Chihuahuan desert of New Mexico (U.S.A.). In each site, microbial biomass-N and soil carbohydrates increased and extractable soil N decreased in response to watering alone. Fertilization with N increased microbial biomass-N in grassland soils; whereas, fertilization with C increased microbial biomass-N and decreased extractable N and P in all communities dominated by shrubs, which have invaded large areas of grassland in the Chihuahuan desert during the last 100 years. Our results support the hypothesis that the control of soil microbial biomass shifts from N to C when the ratio of C to N decreases during desertification.

Introduction

Soil microorganisms play a critical role in the retention and release of nutrients in natural ecosystems. Soil microbial biomass acts as both a sink and a source of labile nutrients, capable of supplying a significant proportion of the nutrients used by plants (Jenkinson & Ladd 1981; Marumoto et al. 1982; Bonde et al. 1988). In many cases, the interaction between plants and soil microorganisms is both competitive and mutualistic (Harte & Kinzig 1993).

Plant production is often limited by low soil nutrients, particularly available nitrogen (Vitousek & Howarth 1991). In many areas, soil microbial biomass is strongly related to total soil nitrogen, implying a nitrogen-limitation of the heterotrophic community as well (Wardle 1992). In soils of the Chihuahuan desert of New Mexico (USA), Gallardo & Schlesinger (1992) found that microbial biomass was related to nitrogen in grassland soils with a high ratio of organic carbon-to-extractable nitrogen. They hypothesized that a shift from nitrogen to carbon limitation of microbial biomass occurs as soil organic matter is lost during desertification of semiarid grasslands. This paper reports on a field experiment to test this hypothesis by experimental manipulations of carbon and nitrogen in water-amended desert soils.

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 21 cm, with 53% of the precipitation occurring from July to September (Buffington & Herbel 1965).

Soil microbial biomass-N (MB-N), and soil extractable N and P were studied in four plant communities that dominate the Jornada Experimental Range: grasslands composed of black grama (*Bouteloua eriopoda*); and three types of shrublands, including tarbush (*Flourensia cernua*), mesquite dunes (*Prosopis glandulosa*), and creosotebush (*Larrea tridentata*). Soils in the grassland and creosotebush are derived from quartz monzonite alluvium from local mountains. Soils in the tarbush sites are derived from ancient floodplain alluvium of the Rio Grande. Mesquite shrubland is 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 1993. Along this transect, 16 24-cm diameter circular plots were chosen randomly including points both under and between shrub canopies in the shrubland sites. These plots were used in a factorial experiment with 4 replicates per site and the following treatments: addition of 1 liter of water, addition of 1 l of water with 12.5 g of dextrose, addition of 1 l of water with 2.5 g of NH_4NO_3, and addition of 1 l of water with both dextrose and NH_4NO_3. An equal number of samples between and under shrubs were assigned to each of the 4 treatments. Owing to the inefficiency of the fumigation-extraction method in dry soils (Sparling & West 1989), we found insignificant levels of soil microbial biomass in dry soils in our previous work in the Chihuahuan desert (Gallardo & Schlesinger 1992). Thus, in this paper we consider the watered soils as 'controls', against which we compare the effects of C and N treatments. Each of these treatments was applied on the first day of the experiment; subsequently pure water was applied at a rate of 1 liter/day to all plots for 10 days. At 1, 2, 3, 5, 8 and 10 days, two replicate samples of about 100 g of wet soil were removed from

the 0–10 cm layer, the zone of maximum microbial activity in desert soils (Skujins 1984). These samples were immediately taken to the laboratory for analysis.

Laboratory procedures

Samples were sieved (<2 mm) in a field-moist condition. Soil MB-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. Subsamples, extracted with K_2SO_4 immediately after collection, served as controls for fumigated samples and indicated the amount of extractable N in each sample (NO_3^- and 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 the K_2SO_4 extracts was performed using a persulfate oxidation technique originally developed for the determination of total N in seawater (D'Elia et al. 1977). This method has proven to be a rapid and efficient way to measure total nitrogen in K_2SO_4 soil extracts (Cabrera & Beare 1993; Hossain et al. 1993). Nitrate in the digest was analyzed by the hydrazine reduction procedure with a Traacs 800 autoanalyzer (Bran & Luebbe 1986).

Subsamples of soil were oven-dried at 50 °C until constant weight and stored at room temperature for later analysis. Inorganic P in a 0.5-N-$NaHCO_3$ extract (Olsen et al. 1954) was analyzed in neutralized aliquots by the ammonium molybdate-ascorbic acid method (Murphy & Riley 1962) with a Traacs 800 autoanalyzer (Bran & Luebbe 1986). Soil carbohydrates were analyzed by the phenol-sulfuric acid procedures (Dubois et al. 1956) as outlined by Safarik & Santruckova (1992). This method quantifies soluble mono-, oligo- and polysaccharides as well as insoluble polysaccharides, such as cellulose. Soil carbohydrates were expressed in units of L-dextrose.

Statistical analysis

Balanced design ANOVA (type III sum of squares) was used to determine significant differences by treatments and sampling days. Multiple range comparisons between means for the different levels of each factor were performed using the Tukey's honest significant differences test (Neter et al. 1985). All analyses were performed using the statistical package Statgraphics (Statistical Graphics System 1991).

Table 1. Average microbial biomass-N, microbial biomass-P, extractable-N, extractable-P and total carbohydrates in watered (control) soils of four plant communities of the Chihuahuan desert during the entire 10-day experimental period. The table includes the ratios microbial biomass-N to microbial biomass-P, extractable-N to extractable-P, and total carbohydrates to extractable-N.

Community	MB-N	MB-P	EXT-N	EXT-P	MB(N:P)	EXT(N:P)
			(μg g^{-1} soil)			
Tarbush	16.7	8.5	6.7	13.4	1.9	0.5
Mesquite	11.3	4.6	7.5	12.7	2.5	0.6
Creosotebush	18.2	9.3	6.6	14.1	2.0	0.5
Grassland	10.7	6.8	4.0	16.1	1.6	0.2

Community	Carbohydrates (mg g^{-1} soil)	C:EXT-N
Tarbush	1.51	225.6
Mesquite	0.97	129.8
Creosotebush	1.39	210.5
Grassland	1.34	334.8

Results

Dynamics of soil microbial biomass and soil nutrients in watered soils

During the 10-day watering period mean values of soil MB-N in watered (i.e. control) samples ranged between 10.7 μg N g^{-1} soil for the grassland community and 18.2 μg N g^{-1} soil for the creosotebush community (Table 1). Among the 4 habitats MB-N reached a maximum value between day-2 (mesquite and creosotebush communities) and day-5 (tarbush community), decreasing to reach a minimum value on day-10 (Fig. 1a).

In control plots, mean values for soil carbohydrates ranged between 0.97 mg g^{-1} soil for the mesquite community and 1.51 mg g^{-1} soil for the tarbush community. The mean ratio of soil carbohydrates to extractable-N ranged between a maximum value of 334.8 for the grassland community and a minimum value of 129.8 for the mesquite community (Table 1). Carbohydrates increased to 125 to 146% of initial values in soils of all plant communities during the first 48 hours after watering (Fig. 1b).

Levels of extractable-N in soil decreased in all plant communities from the first day to the last day of the experiment in water-amended (control) samples (Fig. 2). However, changes in extractable-P showed an irregular pattern,

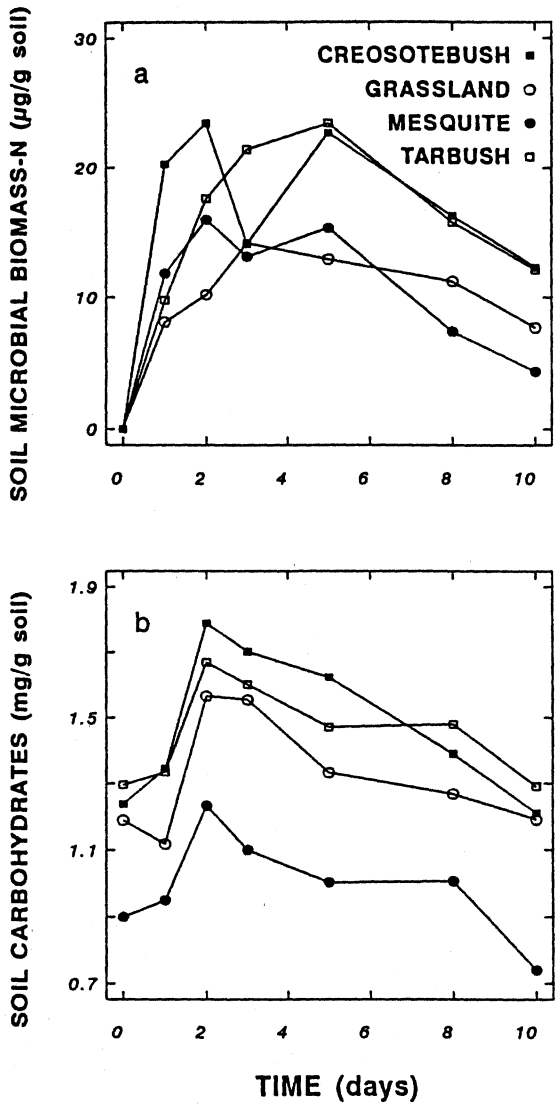

Fig. 1. Changes in soil microbial biomass-N (a) and total soil carbohydrates (b) after daily watering of the soil in four plant communities of the Chihuahuan desert.

with amounts of extractable-P at the end of the experiment not significantly different than the initial values.

Table 2. Analysis of variance for the dependent variables of soil microbial biomass-N with carbon amendment, nitrogen fertilization and time since the beginning of the experiment in shrubland and grassland communities at the Chihuahuan desert.

Source of variation	Sum of squares	DF	*F*-ratio	Probability >*F*
		Tarbush community		
Main effects				
A: Carbon	658.2	1	14.8	0.0002
B: Nitrogen	7.8	1	0.2	0.6807
C: Time	3197.9	5	14.5	0.0000
Interactions				
AB	62.2	1	1.4	0.2398
AC	188.3	5	0.8	0.5185
BC	79.9	5	0.4	0.8736
ABC	203.6	5	0.9	0.4732
		Mesquite community		
Main effects				
A: Carbon	174.5	1	4.1	0.0477
B: Nitrogen	750.3	1	17.5	0.0001
C: Time	3236.9	5	15.1	0.0000
Interactions				
AB	0.4	1	0.0	0.9266
AC	218.5	5	1.0	0.4146
BC	556.2	5	2.6	0.0329
ABC	189.5	5	0.9	0.4980
		Creosotebush community		
Main effects				
A: Carbon	1372.2	1	40.3	0.0000
B: Nitrogen	46.3	1	1.4	0.2474
C: Time	532.4	5	3.1	0.0131
Interactions				
AB	0.7	1	0.0	0.8890
AC	276.2	5	1.6	0.1651
BC	780.1	5	4.6	0.0011
ABC	148.5	5	0.9	0.5038

Table 2. (continued)

Source of variation	Sum of squares	DF	*F*-ratio	Probability >*F*
		Grassland community		
Main effects				
A: Carbon	359.7	1	13.6	0.0004
B: Nitrogen	789.4	1	29.9	0.0000
C: Time	1270.1	5	9.6	0.0000
Interactions				
AB	445.2	1	16.9	0.0001
AC	440.9	5	3.3	0.0090
BC	422.6	5	3.2	0.0115
ABC	428.0	5	3.2	0.0107

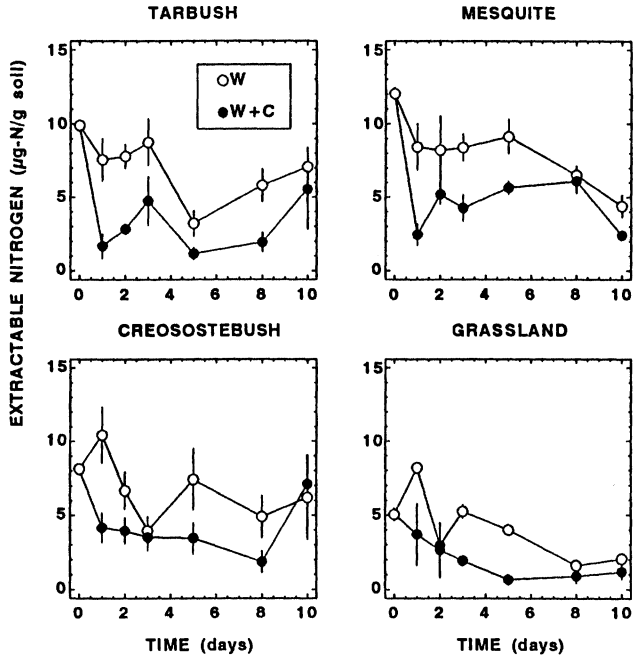

Fig. 2. Changes in extractable-N with time after daily watering of soils and amendment with C in four plant communities of the Chihuahuan desert.

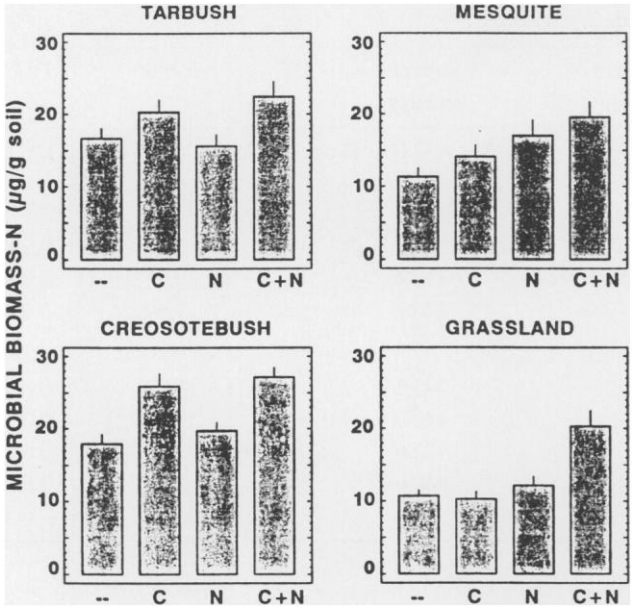

Fig. 3. Responses of soil microbial biomass-N to C and N amendments in four plant communities of the Chihuahuan desert. Bars are means over all days following application of the experimental treatment.

Responses of soil microbial biomass to C and N additions

Fertilization with N and C caused different responses of MB-N in each community (Fig. 3). In the tarbush community, addition of carbon to the soil caused significant increases of MB-N. Nitrogen fertilization did not show any significant effect on MB-N (Table 2, Fig. 3), and the interaction of C and N was not statistically significant (Table 2). Similar results were found for the creosotebush community, with significant increases of MB-N with C amendment, but not with N fertilization (Table 2). In the mesquite community, there was a significant response of MB-N to both C and N additions to the soil, but the interaction between these two factors was not significant. As in the mesquite community, we found a significant increase of MB-N with C and N additions to the soil of the grassland community (Table 2). However, the interaction between these factors was statistically significant, indicating that MB-N responded to C additions only when N was simultaneously supplied to the soil (Fig. 3). There was also a significant interaction between C, N and sampling dates (Table 2).

In tarbush and creosotebush communities, MB-N in C-amended samples showed significantly higher values than in N-fertilized samples throughout

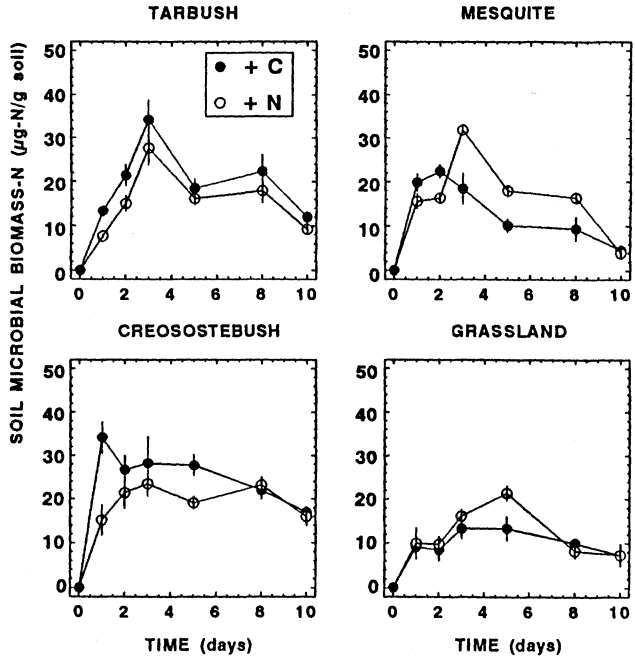

Fig. 4. Changes in the soil microbial biomass-N with time after daily watering of the soil and amendment with C or N in four plant communities of the Chihuahuan desert.

the experiment (Fig. 4, $p < 0.05$, tukey multiple range test). In the mesquite community, values of MB-N in C-amended samples were only significantly higher than in N-fertilized samples until day-2 of the experiment, and lower or not significantly different thereafter. In the grassland community, N-fertilized samples showed higher microbial biomass values than in C-amended samples during days 2–5 of the experiment (Fig. 4).

N and P immobilization

We found significantly lower values of extractable-N in the C-amended samples than in water-amended (control) samples for all plant communities ($p < 0.01$; Fig. 2). In the tarbush community, extractable-N declined from 9.9 μg N g^{-1} soil to 7.7 μg N g^{-1} soil 24 hours after watering the soil, and to 1.7 μg N g^{-1} when C was added to the soil. After 10 days extractable-N was still lower in C-amended than in control soils, but differences were not significant. Similar tendencies were observed in mesquite, creosotebush and grassland communities (Fig. 2). Using the mean for all sampling dates, the extractable-N in C-amended soil samples accounted for 55%, 41%, 35% and

50% of the extractable-N in water-amended samples in the tarbush, mesquite, creosotebush and grassland communities, respectively.

As for extractable-N, differences between values of extractable-P in water and C-amended soil samples were significant ($p < 0.01$), with lowest values of extractable-P in C-amended samples for all plant communities. Addition of C to the soil caused a decrease in extractable-P of 24%, 33%, 10% and 16% in the tarbush, mesquite, creosotebush and grassland communities, respectively.

Discussion

The response of soil microbial biomass in water-amended (i.e. control) soils may be analogous to that which occurs in New Mexico each year, as late-summer rainstorms end the dry period of early summer. Many workers have found that abrupt changes in soil moisture stimulate the turnover of microbial biomass in soils (Ross 1987; Wardle & Parkinson 1990). Rewetting of dry soil may kill soil microbes through osmotic stress (Kieft et al. 1987). Many workers report increased carbon and nitrogen mineralization when dry soils are remoistened, with a large portion of the carbon mineralization derived from dead organic matter (Van Gestel et al. 1991, 1993).

MB-N values in this study were in the same range as those reported in a previous paper for the same community types in the Chihuahuan desert (Gallardo & Schlesinger 1992). Generally the maximum values of microbial biomass were found 2 to 3 days after watering; in the tarbush community we observed the maximum MB-N on day 5 (Fig. 1a). This variation may be explained by differences in soil texture. Tarbush communities are typically situated in low-lying areas with clay-textured soils. Clay content is an important factor controlling the biomass and dynamics of microbial biomass, since organic matter is more protected and growth of the microbial community is slow in clay-rich soils (Van Veen et al. 1989; Gregorich et al. 1991). In addition, clay soils may hold more moisture between daily waterings.

During the increase in MB-N, there was also a net increase of soil carbohydrates (Fig. 1b). An increase in soil carbohydrates during a drying-wetting cycle in desert soils has not been described previously, but is likely to be caused by the decomposition of the organic matter accumulated during the dry period. The rapid flush of decomposition after wetting the soils may be due to a persistent pool of enzymes capable of tolerating extended periods of desiccation, as shown by Peterjohn (1991) for denitrifying enzymes.

Three communities showed a significant increase in microbial biomass with C amendments (tarbush, creosotebush and mesquite), and only two (mesquite and grassland) with N fertilization. Gallardo & Schlesinger (1992) postulated that microbial biomass limitation by C or N depends on the ratio of C-to-extractable-N in the soils of the Chihuahuan desert. In agreement with

these results, the soil of the grassland community showed the highest ratio of carbohydrates-to-extractable-N (Table 1), and C amendments had no effect on microbial biomass in this community. Our earlier work suggested that soil microbial biomass would be limited by nitrogen in areas of creosotebush. We found that the ratio of organic-C-to-extractable-N was relatively high (0.11) in creosotebush soils, and soil microbial biomass was weakly correlated to soil N (r = 0.38) (Gallardo & Schlesinger 1992). However, in the present study we found no response of microbial biomass to added N in these areas. Soil microbial biomass in areas of creosotebush, like the other shrublands, responded to additions of organic carbon. We have no explanation for the discrepancy between the correlation that we observed in prior work and our current experimental results. The response of soil microbial biomass to C additions in all shrublands supports the hypothesis that the control of microbial biomass shifts from N to C when the ratio of C to N decreases during desertification (Schlesinger et al. 1990).

Phosphorus levels did not play a significant role in the limitation of soil microbial biomass in these plant communities of the Chihuahuan desert. The ratio of extractable-N to -P was very low relative to typical values in soil microbial biomass (Brookes et al. 1984, 1985; Raghubanshi 1991), and phosphorus, unlike nitrogen, was not immobilized when water was added to dry soil. Thus, competition between plants and microbes for P is unlikely, and plants should have a high P availability in this ecosystem, in agreement with the findings of Lajtha & Schlesinger (1988).

With additions of C to soils, we observed a significant immobilization of both N and P. Even when C in amended soils returned to its initial levels after 2–3 days (Fig. 5), significant immobilization of N and P remained for most of the experiment, indicating that when the extra C is exhausted only a fraction of the immobilized N and P is returned to the soil. The remainder is held in microbial biomass and recycled during the death of soil microbes. These results support previous work by Parker et al. (1984) and Gutierrez & Whitford (1987). They found that a wet year stimulated the growth of the herbaceous vegetation in the Chihuahuan desert. When this material subsequently died, the large input of organic carbon to the soil immobilized N, causing a N-limitation to the growth of shrubs. Our results also support the hypothesis of Fisher et al. (1987) that high moisture availability reduces N availability in the Chihuahuan desert.

Although our study focuses on the short-term response of the soil microbial biomass to additions of water, C and N, our results may indicate potential changes in arid ecosystems as a result of global change. If higher precipitation or atmospheric CO_2 increases the net primary production in arid lands, greater inputs of plant litter of high C/N ratio may exacerbate N immobilization by

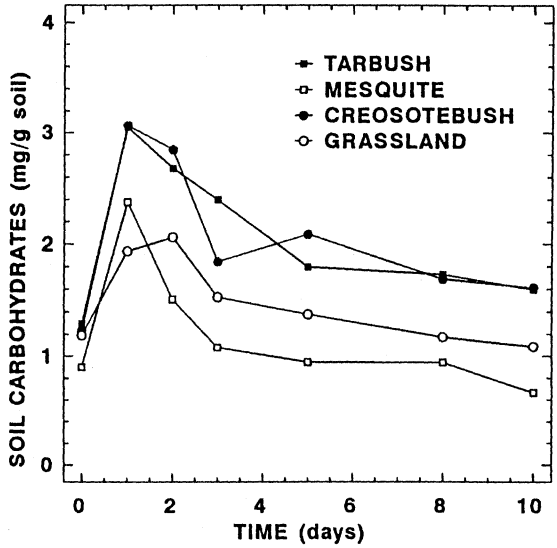

Fig. 5. Changes in total soil carbohydrates with time in C-amended plots in four plant communities of the Chihuahuan desert.

soil microbes and nitrogen limitation of desert ecosystems. Greater water-use efficiency by arid-land plants growing under higher CO_2 may yield the same result, but changes in nitrogen-use efficiency might negate it (Lajtha & Whitford 1989). We recommended whole-system experiments to examine the effects of changes in precipitation and increasing atmospheric CO_2 on soil nitrogen balance in desert ecosystems.

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