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PLANT PRODUCTION AND SOIL MICROORGANISMS IN LATE-SUCCESSIONAL ECOSYSTEMS: A CONTINENTAL-SCALE STUDY[1]

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Abstract. Annual C inputs from plant production in terrestrial ecosystems only meet the maintenance energy requirements of soil microorganisms, allowing for little or no net annual increase in their biomass. Because microbial growth within soil is limited by C availability, we reasoned that plant production should, in part, control the biomass of soil microorganisms. We also reasoned that soil texture should further modify the influence of plant production on soil C availability because fine-textured soils typically support more microbial biomass than coarse-textured soils. To test these ideas, we quantified the relationship between aboveground net primary production (ANPP) and soil microbial biomass in late-successional ecosystems distributed along a continent-wide gradient in North America. We also measured labile pools of C and N within the soil because they represent potential substrate for microbial activity. Ecosystems ranged from a Douglas-fir forest in the western United States to the grasslands of the mid-continent to the hardwood forests in the eastern U.S. Estimates of ANPP obtained from the literature ranged from 82 to 1460 $g \cdot m^{-2} \cdot yr^{-1}$. Microbial biomass C and N were estimated by the fumigation–incubation technique. Labile soil pools of C and N and first-order rate constants for microbial respiration and net N mineralization were estimated using a long-term (32 wk) laboratory incubation. Regression analyses were used to relate ANPP and soil texture with microbial biomass and labile soil C and N pools.

Microbial biomass carbon ranged from 2 g/m^2 in the desert grassland to 134 g/m^2 in the tallgrass prairie; microbial N displayed a similar trend among ecosystems. Labile C pools, derived from a first-order rate equation, ranged from 115 g/m^2 in the desert grassland to 491 g/m^2 in the southern hardwood forest. First-order rate constants for microbial respiration (k) fell within a narrow range of values (0.180 to 0.357 wk^{-1}), suggesting that labile C pools were chemically similar among this diverse set of ecosystems. Potential net N mineralization rates over the 32-wk incubation were linear in most ecosystems with first-order responses only in the alpine tundra, tallgrass prairie, and forests. Microbial biomass C displayed a positive, linear relationship with ANPP ($r^2 = 0.51$), but was not significantly related to soil texture. Labile C also was linearly related to ANPP ($r^2 = 0.32$) and to soil texture ($r^2 = 0.33$). Results indicate that microbial biomass and labile organic matter pools change predictably across broad gradients of ANPP, supporting the idea that microbial growth in soil is constrained by C availability.

Key words: aboveground net primary production; carbon and nitrogen cycles; heterotrophic metabolism; labile organic matter; microbial respiration; net N mineralization; soil microbial biomass; soil microorganisms; soil texture; substrate-use efficiency.

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Introduction

On a global basis, soil microorganisms are thought to contain 1.5% of the C and 3.0% of the N stored within terrestrial ecosystems (Wardle 1992). Although these proportions are small, heterotrophic activity in soil is responsible for the mineralization of soil organic matter, which releases CO_2 to the atmosphere and NH_4^+ into soil solution. Recent attention has focused on these processes because climate change has the potential to alter the pattern in which C and N are cycled and stored within terrestrial ecosystems. The extent to which climate change may modify C and N cycles is, in part, contingent on the physiological response of soil microorganisms. However, few studies have systematically investigated the dynamics of soil microorganisms along broad spatial gradients of temperature, precipitation, and plant production (Myrold et al. 1989), controlling factors likely to be altered by changes in global climate (Melillo et al. 1993).

Because climate change could alter patterns of plant production at large spatial scales, it also may influence C inputs to soil and the amount of energy available for heterotrophic metabolism. Several analyses suggest that microbial growth in soil is constrained by C inputs from plant litter production and the efficiency at which organic substrates are used for biosynthesis (Babiuk and Paul 1970, Gray and Williams 1971). Smith and Paul (1990), for example, compared the maintenance requirements of soil microorganisms to plant C inputs over a range of ecosystems and concluded that the amount of C annually required to maintain soil microorganisms equaled that contained in the above- and belowground input of plant litter. Their analysis suggests that all labile C from plant litter and that stored in mineral soil should be metabolized on an annual basis, allowing for little or no net annual growth of soil microrganisms. If C inputs from plant production are only sufficient to maintain soil microorganisms, then annual rates of plant litter production should be well correlated with the microbial biomass content of soil. This relationship should be well expressed in late-successional ecosystems in which net primary production (NPP) is balanced by rates of organic matter decomposition (Rodin and Bazilevich 1967, Odum 1969, Vitousek and Reiners 1975, Bormann and Likens 1979). In these situations, NPP should be equivalent to the above- and belowground production of plant litter, which, in turn, provides the primary substrate for heterotrophic metabolism in soil.

Although numerous studies cite soil C availability as an important regulator of microbial metabolism, isolating its influence from that of soil texture is difficult. In the shortgrass prairie region of the central United States, for example, fine-textured soils typically contain greater quantities of organic matter and microbial biomass than coarse-textured soils (Schimel 1986, Burke 1989). Clay-sized particles are thought to protect organic matter through adsorption and aggregation (Jenkinson 1977, Paul 1984), shelter soil microorganisms from predation (Roper and Marshall 1974, Elliott et al. 1980), and increase substrate-use efficiency (Martin et al. 1976). As a consequence, plant litter production and soil texture should function in concert to influence the microbial biomass content of soil.

North America is traversed by a broad climatic gradient that gives rise to marked differences in plant production and the rate at which organic matter and associated nutrients are cycled within terrestrial ecosystems. Changes in plant production along such a gradient should directly influence organic matter additions to the soil and the amount of energy available to meet the maintenance requirements of soil microorganisms. Other things being equal (i.e., NPP), fine-textured soils should support more microbial biomass than coarse-textured soils. Our primary objectives were to determine: (a) how the biomass and substrate-use efficiency of soil microorganisms change along a continental-scale gradient of plant production and (b) how soil texture modifies those relationships. As a secondary objective we investigated changes in labile organic matter pools (i.e., C and N), because they represent substrate for heterotrophic metabolism and may be the pool of organic matter most influenced by climate change. We have assumed that late-successional ecosystems are near or at steady state with respect to C storage, and aboveground net primary production (ANPP) is directly proportional to total net primary production (Nadelhoffer et al. 1985).

Methods

Study sites and soil sampling

We studied a series of late-successional ecosystems representative of the broad vegetation patterns extending across the North American continent (Table 1). Most belong to the Long-Term Ecological Research (LTER) network, with the exception of the Manistee site in northwestern Lower Michigan. The ecosystems ranged from Douglas-fir forest in the western U.S. to the grasslands of the mid-continent to the eastern deciduous forests (Table 1). Many features of this gradient have been described, including spatial patterns of climate and ANPP (Whittaker 1975, Chabot and Mooney 1985, Greenland 1987). We studied sites for which published estimates of ANPP were available or where measurements were currently being undertaken (Table 2). Estimates were not available for the pinyon–juniper forest in New Mexico and the Lake States northern hardwood forest. In these cases, we used values from sites of similar species composition in the same geographic region (Table 2). Aboveground net primary production ranged from 82 $g \cdot m^{-2} \cdot yr^{-1}$ in the short-

TABLE 1. Summary of climatic characteristics for ten locations distributed across North America. Long-term (30-yr) mean monthly temperature and precipitation for Sevilleta, Manistee, and Hubbard Brook were gathered from the nearest weather station, and potential and actual evapotranspiration were calculated following Willmott (1977); long-term (30-yr) climatic variables for the remaining ecosystems were summarized from Greenland (1987).

Location	Ecosystem	Latitude (N)	Longitude (W)	Elevation (m)	Mean annual temp. (°C)	Mean annual precip. (mm)	Evapotranspiration (mm)	
							Potential	Actual
H. J. Andrews (Oregon)	Old-growth Douglas-fir	44°14′	122°11′	1146	8.6	2290	593	552
Sevilleta (New Mexico)	Pinyon–Juniper	34°36′	106°69′	1975	10.5	329	696	311
	Desert grassland	34°37′	106°54′	1596	13.0	222	735	222
Jornada (New Mexico)	Desert grassland	32°30′	106°45′	1380	14.6	231	797	231
	Desert shrubland	32°30′	106°45′	1420	14.6	231	797	231
Niwot Ridge (Colorado)	Alpine tundra	40°03′	105°37′	3500	−3.7	930	306	257
Central Plains (Colorado)	Shortgrass steppe	40°48′	104°46′	1647	8.7	309	605	299
Konza Prairie (Kansas)	Tallgrass prairie	39°05′	96°35′	365	12.8	835	790	736
Cedar Creek (Minnesota)	Tallgrass prairie	45°35′	93°12′	280	5.5	726	597	586
	Upland pin oak forest	45°35′	93°12′	285	5.5	726	597	586
Manistee (Michigan)	Northern hardwood forest	44°48′	85°48′	325	7.2	810	576	575
Coweeta (North Carolina)	Southern hardwood forest	35°00′	83°30′	808	12.5	1847	702	702
Hubbard Brook (New Hampshire)	Northern hardwood forest	43°56′	71°45′	503	5.6	1395	542	532

grass steppe to 1460 $g \cdot m^{-2} \cdot yr^{-1}$ in the southern hardwood forest (Table 2).

In each ecosystem, we collected soil samples from 10 points systematically located along two 20-m transects. One transect was established by randomly locating a point to serve as a center and then measuring 10 m north and south from that point. A parallel 20-m transect was located 10 m to the west. Two soil samples were collected at each of five equally spaced intervals along each transect. Samples consisted of a 3.8-cm-diameter core that extended from immediately below the loose litter to a depth of 10 cm. Cores collected at each sample point were placed in a polyethylene bag, packed on ice, and shipped overnight to the University of Michigan. All soil samples were analyzed within 24 h of field collection.

Changes in edaphic properties along topographic gradients influence rates of C and N cycling in arid grassland ecosystems (Schimel et al. 1985*b*). Therefore, we located transects at top-, mid-, and bottom-slope positions in the rolling topography of the shortgrass steppe (Central Plains) and tallgrass prairie (Konza). Each transect was oriented perpendicular to the slope. Values for the shortgrass steppe and tallgrass prairie (Konza) are the mean of top-, mid-, and bottom-slope positions. Soil organic matter content and N availability also vary widely in semi-arid shrub-dominated ecosystems due to localized accumulations of organic matter beneath plant canopies (Charley and West 1977, Parker et al. 1984, Fisher et al. 1987, Burke 1989). To account for this source of variation, we stratified our sampling in the desert shrubland by collecting soil at each sample point and beneath the nearest shrub. Following soil sampling, visual estimates of shrub coverage were obtained for the entire transect area. Analytical values for soil collected beneath and between shrubs were weighted by their respective coverage to obtain areal estimates. Soil samples were collected from July to August 1989.

Soil analyses

The composite soil samples were weighed and thoroughly mixed. A 10-g subsample from each bag was dried at 105°C to determine soil water content. Soil bulk density was calculated as the ratio of oven-dried soil to combined core volume. Air-dried soil was used for analyses of texture, pH, organic C, and total N, whereas fresh field-moist soil was used to assay microbial biomass, microbial respiration, and net N mineralization. Soil texture was determined using the hydrometer method (Gee and Bauder 1986), and pH was measured in a 1:1 soil : deionized water paste. Soil organic C and total N were determined using a Carlo-Erba NA 1500 Analyzer. Carbonates in the Jornada and Sevilleta soils were removed with excess 5% H_2SO_3 (Nelson and Sommers 1982) prior to the analyses.

Soil microbial biomass was measured using the $CHCl_3$-fumigation–incubation procedure (Jenkinson and Powlson 1976, Voroney and Paul 1984). A 20-g soil subsample was fumigated for 18 h with CH_3CH_2OH-free $CHCl_3$ in a humid vacuum desiccator. A second 20-g subsample (a control) was treated in a similar manner, but $CHCl_3$ was not placed inside the desiccator. Following the fumigation, samples were inoculated with 0.3 g of fresh soil, placed in separate airtight glass jars, and incubated for 10 d at room temperature. A Tracor 540 gas chromatograph (Tracor Instruments, Austin, Texas, USA) equipped with a thermal conductivity detector was used to determine CO_2.

TABLE 2. Aboveground net primary production (ANPP) and dominant plant species for 13 ecosystems distributed along a climatic gradient in North America.

Location	Ecosystem	ANPP ($g \cdot m^{-2} \cdot yr^{-1}$)	Reference	Dominant species
H. J. Andrews	Old-growth Douglas-fir	800	Grier and Logan 1977	*Psuedotsuga menziesii* *Tsuga heterophylla* *Thuja placata*
Sevilleta	Pinyon–Juniper	212	Grier et al. 1992	*Pinus edulis* *Juniperus monosperma* *Bouteloua hirsuta*
	Desert grassland	185	D. Moore, 1993 *unpublished data*	*Bouteloua eriopoda* *Bouteloua gracilis* *Gutierrezia sarothrae*
Jornada	Desert grassland	225	W. Whitford, 1993 *unpublished data*	*Bouteloua eriopoda* *Gutierrezia sarothrae* *Yucca elata*
	Desert shrubland	171	W. Whitford, 1993 *unpublished data*	*Larrea tridentata* *Panicum obtusum* *Prosopis glandulosa*
Niwot Ridge	Alpine tundra	200	M. Walker, 1993 *unpublished data*	*Kobresia myosuroides* *Silene acaulis* *Sibbaldia procumbins*
Central Plains	Shortgrass steppe	82	D. Milchunas, 1993 *unpublished data*	*Bouteloua gracilis* *Sphaeralcea coccinea* *Opuntia polyacantha*
Konza Prairie	Tallgrass prairie	470	T. Seastedt, 1993 *unpublished data*	*Andropogon gerardii* *Sorghastrum nutans* *Schizachyrium scoparium*
Cedar Creek	Tallgrass prairie	93	Ovington et al. 1963, Reiners 1972	*Schizachyrium scoparium* *Artemisia ludoviciana* *Polygonum convolvulus*
	Upland pin oak forest	855	Ovington et al. 1963, Reiners 1972	*Quercus ellipsoidalis* *Corylus americana* *Carex muhlenbergii*
Manistee	Northern hardwood forest	950	Pastor et al. 1984	*Acer saccharum* *Tilia americana* *Ostrya virginiana*
Coweeta	Southern hardwood forest	1460	Monk and Day 1988	*Liriodendron tulipifera* *Quercus rubra* *Quercus coccinea*
Hubbard Brook	Northern hardwood forest	792	Marks 1974	*Acer saccharum* *Betula alleghaniensis* *Fagus grandifolia*

Following the CO_2 analysis, control and fumigated samples were extracted with a 2 mol/L KCl aqueous solution. Ammonium-N and NO_3^--N concentrations in filtrates were determined colorimetrically using an Alpkem RFA 300 (Alpkem, Clackamas, Oregon, USA). Microbial biomass C was calculated by dividing the flush of CO_2-C from fumigated samples by 0.41 (Voroney and Paul 1984). The N content of microbial biomass was calculated by dividing the flush of N (fumigated minus control) by a correction factor (k_n), determined from the equation of Voroney and Paul (1984): $k_n = -0.014(C_f/N_f) + 0.39$, where C_f and N_f are the flushes of C and N from fumigated samples, respectively.

Labile pools of C and N and rate constants for microbial respiration and net N mineralization were quantified using a long-term incubation technique (Nadelhoffer 1990). Thirty-gram soil subsamples were incubated in Falcon Filtration units (Model 7102, Becton Dickinson Labware, Lincoln Park, New Jersey, USA) that were modified by sealing each port with a rubber septum and replacing the original nitrocellulose filter with a glass-fiber filter (Whatman GF-A). Filtration units containing soil were made airtight by sealing the lid and seams with silicone rubber. After the silicone rubber had cured, 5 mL of air were injected, and pressure was measured using a transducer (Parkin et al. 1984) to ensure that each had an airtight seal. The septa were removed, and inorganic N was extracted from the soil with 100 mL of 0.01 mol/L $CaCl_2$ solution; extractions were followed by 20 mL of minus-N nutrient solution (Stanford and Smith 1972). The soil was

TABLE 3. Surface soil properties (0–10 cm) for 13 ecosystems distributed along a climatic gradient in North America.

Location	Ecosystem	Organic C (g/m^2)	Soil texture (%)			Soil pH	Bulk density (Mg/m^3)
			Sand	Silt	Clay		
H. J. Andrews	Old-growth Douglas-fir	6510	55.4	33.9	10.7	5.07	0.35
Sevilleta	Pinyon–Juniper	2330	40.0	43.9	16.1	8.33	1.17
	Desert grassland	390	74.0	14.5	11.5	7.37	1.20
Jornada	Desert grassland	675	81.6	8.0	10.5	7.58	1.26
	Desert shrubland	710	71.2	20.6	8.1	8.40	1.26
Niwot Ridge	Alpine tundra	7110	50.4	43.4	6.2	5.13	0.70
Central Plains	Shortgrass steppe	1592	57.3	19.2	23.5	6.21	1.36
Konza Prairie	Tallgrass prairie	4572	11.2	49.7	39.1	7.18	0.91
Cedar Creek	Tallgrass prairie	2050	85.8	11.0	3.2	5.60	1.29
	Upland pin oak forest	3010	89.1	6.9	4.0	4.51	1.30
Manistee	Northern hardwood forest	4150	86.6	8.9	4.6	6.30	0.68
Coweeta	Southern hardwood forest	3925	55.2	27.9	16.9	5.16	0.99
Hubbard Brook	Northern hardwood forest	8935	70.6	26.5	3.1	3.95	0.35

brought to field capacity (−0.03 MPa) using a hand-held vacuum pump, and the excess minus-N nutrient solution was discarded. The filtration units were then flushed with five air-space volumes of CO_2-free air and sealed airtight. An initial gas sample (0.4 mL) was removed and analyzed for CO_2 as described above. The filtration units were then incubated at 35°C in the dark for 32 wk. Additional gas samples were collected after week 1, after week 2, and at 2-wk intervals thereafter. Following each gas sampling, each filtration unit was flushed with five air-space volumes of CO_2-free air to replenish O_2 that had been consumed by microbial respiration. Inorganic N was extracted and minus-N nutrient solution was added at 1, 2, 4, 8, 16, and 32 wk. Each extraction was followed by the addition of CO_2-free air, and the filtration units were again sealed airtight. Carbon dioxide within the filtration units never exceeded 20 uL/mL (2%, vol./vol.).

Product accumulation curves for CO_2-C and inorganic-N were constructed for each filtration unit, and data were fit to a first-order [$y = a(1 - e^{-kt})$] equation. The equation estimates the pool of labile C or N (a) that could be potentially respired or mineralized, respectively, and the rate constant (k) for each process; t in the equation is time in weeks. Because soil temperature and moisture potential during the incubation are favorable for microbial activity, these processes should be limited by substrate (i.e., labile C or N) availability and not by environmental factors. We have assumed that the incubations estimate the pool of labile C and N contained in soil organic matter.

The relationship between basal respiration rate and microbial C content of soil (i.e., specific respiration rate) has been used to assess the substrate-use efficiency of microbial biomass; microorganisms efficient at converting substrate (i.e., C) into biomass have low specific respiration rates (Anderson and Domsch 1989, 1992). We used information from the long-term incubations to gain insight into changes in substrate-use efficiency of soil microorganisms among the 13 ecosystems. To calculate specific respiration rates, we divided microbial respiration rates over the first 10 d of laboratory incubation by the microbial biomass C content of each soil sample (Anderson and Domsch 1989). Values were expressed as milligrams of CO_2-C respired per gram of microbial C per hour.

Statistical analyses

An analysis of variance for a completely randomized design was used to test for significant differences among ecosystems, and means were compared using a Fisher's protected least-significant-difference (LSD) procedure. The first-order rate equation was fit to CO_2-C and inorganic N production for each filtration unit using nonlinear regression. Simple and multiple linear-regression analyses were used to relate ANPP and soil texture with microbial biomass and labile C and N pools (Wilkinson 1989). Significance for all statistical analyses was accepted at $\alpha = 0.05$.

RESULTS

Silt + clay ranged from 90% in the tallgrass prairie (Konza) to 11% in the glacially derived soils beneath the prairie and forests of the Lake States region (Table 3). The highest soil pH (8.40) was in the calcareous soils of the desert shrubland and lowest (3.95) in the northern hardwood forest at Hubbard Brook. Organic C ranged from 390 g/m^2 in the desert grassland (Sevilleta) to 8935 g/m^2 in the northern hardwood forest (Hubbard Brook; Fig. 1A, Table 3). Patterns of soil total N among ecosystems were similar to those of organic C (Fig. 1B).

Soil microbial C was 2 g/m^2 in the sandy, organic-matter-poor soil of the desert grassland (Sevilleta), the lowest value measured in any ecosystem (Fig. 1C). The largest microbial C pool (134 g/m^2) occurred in the fine-textured, organic-matter-rich soil of the tallgrass prairie (Konza). Microbial C in the tallgrass prairie (Konza) was almost 50 times greater than that of the shortgrass steppe (3 g/m^2). Topographic position with-

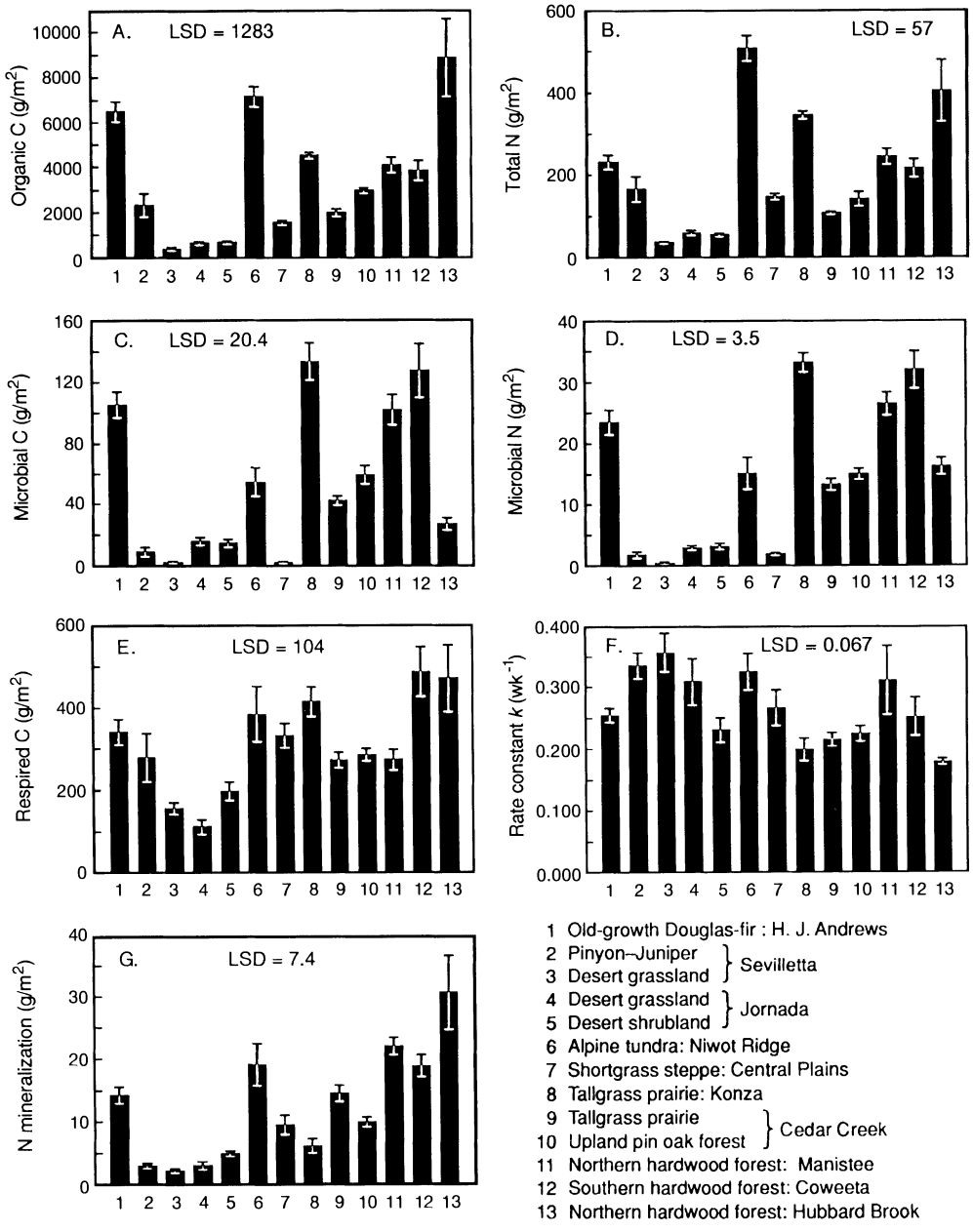

FIG. 1. Soil organic C (A), soil total N (B), microbial C (C), microbial N (D), respired C (E), rate constants for microbial respiration (F), and potential net N mineralization (G) in 13 late-successional ecosystems distributed across North America. Ecosystem values = means ± 1 SE.

in these grassland ecosystems had little influence on microbial C, and contents were similar along each catenary sequence (Appendix). In the forested ecosystems, the smallest pool of microbial C occurred in the pinyon–juniper forest (9 g/m^2), whereas the largest pool (128 g/m^2) occurred in the southern hardwood forest (Fig. 1C). Microbial C was 0.2% of soil organic C in the shortgrass steppe and was 6.4% in the tallgrass prairie of Minnesota; values in the other ecosystems were intermediate (Table 4). Differences in microbial N among ecosystems were similar to those for microbial C (Fig. 1D).

Microbial C displayed a positive, linear relationship with ANPP that accounted for 51% of the variation in microbial biomass among the 13 ecosystems (Table 5, Fig. 2A). However, microbial C was not significantly related to either soil silt + clay (Fig. 2B) or clay content. Microbial C also was linearly related to organic C (r^2 = 0.201, P = 0.035) and mean annual precipitation (r^2 = 0.481, P = 0.001). Microbial N displayed a signifi-

TABLE 4. The percentage (means ± 1 SE) of soil organic C present as microbial biomass C and respired C in the soil of 13 late-successional ecosystems in North America. Specific respiration rate for microbial biomass and the ratio of respired C to mineralized N also are summarized.

Location	Ecosystem	Microbial C as % of organic C	Respired C as % of organic C	Specific respiration* ($mg \cdot g^{-1} \cdot h^{-1}$)	Respired C: Mineralized N (mg/mg)
H. J. Andrews	Old-growth Douglas-fir	1.6 ± 0.09	5.2 ± 0.24	4.2 ± 0.42	24 ± 2.0
Sevilleta	Pinyon–Juniper	0.4 ± 0.10	12.4 ± 0.85	85.2 ± 31.53	98 ± 15.6
	Desert grassland	0.6 ± 0.14	42.2 ± 4.89	140.6 ± 33.61	77 ± 7.4
Jornada	Desert grassland	0.6 ± 0.48	18.2 ± 3.40	11.4 ± 1.18	48 ± 10.5
	Desert shrubland	0.7 ± 0.34	30.0 ± 2.91	19.9 ± 2.59	48 ± 10.3
Niwot Ridge	Alpine tundra	0.8 ± 0.13	5.2 ± 0.74	25.3 ± 13.9	21 ± 2.7
Central Plains	Shortgrass steppe	0.2 ± 0.01	21.0 ± 1.07	173.6 ± 20.06	42 ± 4.3
Konza Prairie	Tallgrass prairie	3.0 ± 0.16	9.2 ± 0.43	3.9 ± 0.83	125 ± 25.4
Cedar Creek	Tallgrass prairie	6.4 ± 0.49	31.2 ± 2.27	5.8 ± 0.55	29 ± 2.0
	Upland pin oak forest	4.9 ± 0.34	33.0 ± 2.63	7.6 ± 0.91	20 ± 3.0
Manistee	Northern hardwood forest	2.5 ± 0.23	6.7 ± 0.62	4.6 ± 1.06	12 ± 0.9
Coweeta	Southern hardwood forest	3.3 ± 0.32	11.7 ± 1.14	5.6 ± 1.61	28 ± 3.9
Hubbard Brook	Northern hardwood forest	0.7 ± 0.29	5.2 ± 0.50	19.5 ± 3.93	25 ± 8.8

* Units are milligrams of CO_2-carbon per gram of microbial carbon per hour.

cant linear relationship with ANPP (Table 5), but was not related to either soil silt + clay or clay content. Aboveground net primary production and percentage of silt + clay were not significantly related.

Respired C pools ranged from 115 g/m^2 in the desert grassland (Jornada) to 491 g/m^2 in the southern hardwood forest (Fig. 1E). Although the pool of respired C was greatest in the forested ecosystems and least in the arid ecosystems, the opposite trend was present when respired C was expressed as a percentage of soil organic C (Table 4). For example, respired C ranged from ≈5% of soil organic C in the old-growth Douglas-fir, alpine tundra, and northern hardwood (Hubbard Brook) ecosystems to 42% in the desert grassland (Sevilleta). Respired C displayed a significant positive relationship with ANPP and percentage of silt + clay (Table 5, Fig. 2C and D). A multiple-regression model incorporating both variables accounted for 65% of the variation among ecosystems (Table 5). Respired C also was significantly related to organic C ($r^2 = 0.591$, $P = 0.002$), microbial C ($r^2 = 0.324$, $P = 0.042$), and actual evapotransporation, AET ($r^2 = 0.411$, $P = 0.018$).

Rate constants (k) for microbial respiration, determined by nonlinear fits to the first-order model, differed significantly among ecosystems. However, most values fell within a relatively narrow range (0.159–0.357/wk^{-1}; Fig. 1F). As a consequence, pool turnover ($1/k$ at 35°C) varied from 2.8 wk in desert grassland (Sevilleta) to 6.3 wk in the tallgrass prairie (Konza).

The specific respiration rates for microbial biomass C varied from 3.9 $mg \cdot g^{-1} \cdot h^{-1}$ in the tallgrass prairie (Konza) to 173.6 $mg \cdot g^{-1} \cdot h^{-1}$ in the shortgrass steppe. Values were low in the northern (Manistee) and southern hardwood forests, tallgrass prairie (Cedar Creek), and old-growth Douglas-fir ecosystems (Table 4). In contrast, specific respiration rates were high in the desert ecosystems, alpine tundra, and one northern hardwood forest (Hubbard Brook). There was a significant, negative linear relationship between specific respiration rates and AET ($r^2 = 0.332$, $P = 0.043$). However, specific respiration rates were not significantly related to ANPP, soil texture, or other climatic variables.

Net mineral N production exhibited a linear increase through time (i.e., zero-order kinetics) in most ecosystems. First-order responses were present in the alpine tundra, tallgrass prairie (Cedar Creek), and forested ecosystems (see Appendix). Therefore, we used net mineral N production during the 32-wk incubation as an index of potential net N mineralization. The desert ecosystems with their low soil organic C contents also mineralized the lowest quantities of N under laboratory conditions (Fig. 1G). In contrast, potential net N mineralization was relatively high in the forested ecosystems and alpine tundra (Fig. 1G). We found equivalent values in the shortgrass steppe and the tallgrass prairie (Konza), even though organic C was much greater in the tallgrass prairie. The ratio of respired C to mineralized N differed by an order of magnitude among ecosystems, with the lowest ratio (12) measured in the

TABLE 5. Regression equations predicting microbial biomass and labile organic C per unit area (in g/m^2) from aboveground net primary production (g/m^2) and soil silt + clay (% of dry mass). Relationships were constructed using 13 late-succesional ecosystems distributed across North America.

	r^2	Root MSE	P
Soil microbial biomass			
C = 13.91 + 0.080(ANPP)	0.512	35.27	0.006
N = 4.10 + 0.020(ANPP)	0.561	8.16	0.003
Respired C			
C = 236.45 + 0.149(ANPP)	0.318	98.29	0.044
C = 200.74 + 2.948(silt + clay)	0.327	97.68	0.041
C = 123.43 + 0.152(ANPP) + 2.989(silt + clay)	0.655	73.38	0.005

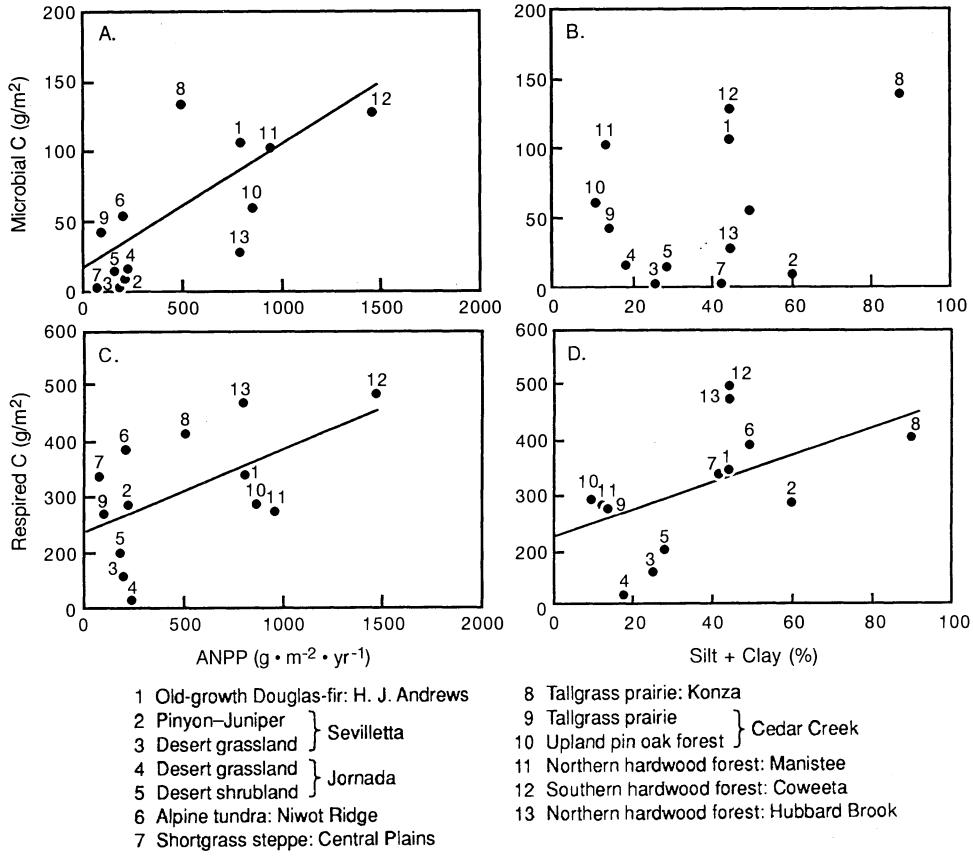

FIG. 2. The relationship of aboveground net primary production (ANPP) and soil texture with soil microbial C and with respired C in a series of late-successional ecosystems distributed along a climatic gradient in North America.

Lake States northern hardwood forest and the highest (125) in the tallgrass prairie (Table 4). Laboratory estimates of net N mineralization displayed a significant positive relationship with ANPP ($r^2 = 0.311, P = 0.047$), organic C ($r^2 = 0.641$, $P = 0.001$) and total N ($r^2 = 0.443, P = 0.013$). Net N mineralization, N_{min}, in grams per square metre, also was significantly inversely related to the ratio of respired C to mineralized N $\{N_{min} = 46.68 - 21.902$ [log (respired C/mineralized N)], $r^2 = 0.545$, $P = 0.004\}$.

DISCUSSION

The biomass of soil microorganisms is thought to reflect long-term C additions to soil from NPP (Anderson and Domsch 1986, McGill et al. 1986), a pattern that could be further modified by soil texture (van Veen et al. 1985). We have argued that such a relationship should be well expressed in late-successional ecosystems where C storage represents an equilibrium between NPP and organic matter decomposition (Vitousek and Reiners 1975). Because soil C storage also is near steady state, NPP in late-successional ecosystems should equal the amount of C entering the soil from above- and belowground plant production. It should, therefore, represent the amount of C available to meet the annual maintenance requirements of microbial populations. In the late-successional ecosystems we studied, ANPP (aboveground NPP) was significantly related to labile organic C pools and microbial biomass, supporting the idea that substrate availability constrains the biomass of soil microorganisms at large spatial scales. Although soil texture was significantly related to respired C pools, we have no evidence to suggest that it influences the microbial biomass content of soil at large spatial scales.

The relationship we found between ANPP and soil microbial biomass also has been observed by Myrold et al. (1989) in a series of relatively late-successional coniferous forests. Aboveground net primary production ranged from 30 to 1400 $g \cdot m^{-2} \cdot yr^{-1}$ among those ecosystems and accounted for 67% of the variation in microbial C. Myrold et al. (1989) also found ANPP was well correlated ($r = 0.96$) with mean annual microbial respiration, similar to the relationship we found between ANPP and respired C. It is important to note that our results and those of Myrold et al. (1989) are correlative, and causation can only be inferred. How-

ever, both studies strongly suggest that microbial populations in soil are tightly controlled by spatial patterns of autotrophic C fixation and organic matter addition to soil.

Patterns of root production and mortality undoubtedly influence soil C availability and the metabolic activities of soil microorganisms. However, we were unable to account for belowground production for several reasons. Few studies have focused on this process, and where data do exist, measurements are of uncertain accuracy. Several studies have evaluated C allocation in forest ecosystems, but a generalized pattern between above- and belowground production has not emerged. For example, Nadelhoffer et al. (1985) proposed that ANPP increases in direct proportion to belowground production. Others have suggested an inverse relationship wherein belowground production on poor sites increases at the expense of aboveground production (Keyes and Grier 1981, Persson 1981, Linder 1987). We are unaware of any generalized relationship between above- and belowground plant production that can be applied to the ecosystems we studied. Consequently, we could only assume that ANPP was proportional to the total amount of C entering the soil from net primary production; such an assumption has obvious limitations. Clearly, estimates of belowground production are needed before a definitive conclusion can be drawn regarding the influence of plant production on soil C availability and microbial populations. Nevertheless, our results support the contention that microbial populations in soil are linked to spatial patterns of plant growth.

Insam et al. (1989) found a significant, but weak, correlation ($r^2 = 0.02$) between soil texture (e.g., clay content) and microbial biomass in temperate agricultural soils. The soils in the aforementioned study ranged from 13% to 39% clay, a range of values similar to that in our study (3–44% clay). We used two measures of soil texture (silt + clay and clay content), but found no relationship between those variables and microbial C. Although several studies have demonstrated that soil texture has a significant influence on soil microbial biomass (van Veen et al. 1985), this relationship may only be of importance within a particular climatic regime. At relatively large spatial scales, factors other than soil texture seem to be more important constraints on the biomass of soil microorganisms.

In many agricultural ecosystems the ratio of microbial biomass C to soil organic C is thought to be relatively constant (Beck 1984, Anderson and Domsch 1986, 1989, Insam et al. 1989). Although microbial biomass was significantly related to organic C, we have no evidence to support a consistent ratio between these C pools. In our study the proportion of soil organic C present as microbial C varied by an order of magnitude (from 0.3 to 3.3%). These results are not unexpected in light of the broad differences in litter production and chemistry among the ecosystems we studied. One would expect to find a small proportion of microbial C in ecosystems where soil organic matter was dominated by a large pool of recalcitrant material or where environmental conditions limit microbial activity. Our results suggest that a fixed relationship between microbial biomass and soil organic matter may only occur in situations where plant litter inputs display little variation (e.g., temperate agricultural soils under similar management practices).

Our data indicate that labile C pools within soil change predictably across broad spatial gradients of ANPP and soil texture. We found that respired C pools were small in ecosystems with low ANPP and sandy-textured soils. Nevertheless, respired C accounted for much different proportions of soil organic C in the forests, prairie, and desert ecosystems. For example, labile C ranged from 5 to 12% of soil organic C in the forests, suggesting that the majority of organic matter in these ecosystems was relatively recalcitrant. In contrast, respired C averaged 30% of soil organic C in the desert ecosystems, and was 21% in the shortgrass steppe. The relatively large proportion of labile C in these arid ecosystems suggests that physical factors, e.g., soil water potential, likely limit its in situ metabolism. Because labile C represents a relatively large proportion of organic C in arid ecosystems, a change in climate that favors microbial activity has the potential to rapidly influence soil C storage.

Although respired C pools varied substantially among ecosystems, rate constants (k) fell within a relatively narrow range. Turnover times ($1/k$) for respired C ranged from 3 to 6 wk, a relatively short period of time in comparison to more stabilized forms of soil organic matter (e.g., 9 yr for active soil organic matter and 3500 yr for old organic matter; van Veen et al. 1984). Paul and Clark (1989) suggested that microbial biosynthesis can significantly influence rate constants, with corrections for microbial growth efficiency generally increasing the value of k. The soils we studied varied in organic matter chemistry (i.e., C:N ratio; see *Appendix*) and probably differed in the species composition of the microbial community, two factors known to influence growth efficiency (Adu and Oades 1978, Holland and Coleman 1987, Schimel 1988). However, correcting our data for microbial biosynthesis would only decrease turnover times, further suggesting that respired C was derived from a relatively labile C substrate. As a consequence, in situ differences in microbial respiration among ecosystems are likely driven by variation in environmental conditions and labile C pool size and not by differences in substrate chemistry, as reflected by k.

Specific respiration rates have been used to assess the substrate-use efficiency of soil microorganisms (Anderson and Domsch 1989). Microbial populations exhibiting low rates are thought to allocate proportionately more C to biosynthesis and less to cell maintenance. In our study, specific respiration rates varied

by a factor of 35 among ecosystems, less than that reported by Santruckova and Straskraba (1991) among agricultural, old field, pasture, and forest ecosystems. Although rates varied widely among ecosystems, we found no evidence to suggest that soil texture influences the substrate-use efficiency of microbial biomass. The highest rates we measured occurred in ecosystems in which microbial C represented a small proportion of soil organic C (i.e., desert ecosystems, pinyon–juniper forest, shortgrass steppe, alpine tundra, and northern hardwood forest; Table 4). One could conclude that microbial populations in these ecosystems are inefficient at using C for biosynthesis, or that soil organic matter was dominated by compounds not readily metabolized for biosynthesis. The latter is likely in the alpine tundra, pinyon–juniper, and northern hardwood forests (Hubbard Brook) in which labile C pools were small. In the desert ecosystems and shortgrass steppe, however, respired C ranged from 18 to 42% of soil organic C, suggesting that soil organic matter was not dominated by material resistant to microbial degradation. High specific respiration rates in those ecosystems resulted from a large initial CO_2 flush when these previously dry soils (3% H_2O w/w) were brought to field capacity. Soulides and Allison (1963) suggested large releases of CO_2 following the wetting of dry soil result from the metabolism of labile C derived from dead microbial cells. Relatively large pools of labile C, in combination with low microbial C contents and high specific respiration rates, suggest that environmental factors (e.g., low water potentials) exert an important influence on soil C availability and microbial activity in arid ecosystems. The inverse relationship between specific respiration rates and actual evapotranspiration (AET) provides further support for this contention.

One could argue that a single point sample in time may not be adequate to assess the substrate-use efficiency and biomass of soil microorganisms. Seasonal variation in controlling factors, like soil temperature, water potential, and substrate input, could give rise to marked variation in heterotrophic activity as well as biomass. However, data regarding seasonal patterns of microbial substrate use and biomass are not available for the ecosystems we studied. Wardle (1992) summarized seasonal changes for a different set of desert, pasture, savanna, and forest ecosystems, and concluded that microbial biomass reaches a seasonal peak in temperate ecosystems during midsummer, or during seasons when rainfall is high. In our study soil temperatures reach a seasonal maximum during midsummer in all ecosystems, but seasonal patterns of precipitation are more variable (Greenland 1987). Most ecosystems are characterized by ample summer precipitation; however, midsummer drought is characteristic of the Douglas-fir ecosystem (Greenland 1987). Nonetheless, our sampling occurred when microbial biomass should be near or at a seasonal maximum, a period of time when its size should be limited by substrate availability. Clearly, sequential sampling over time would provide further insight into the dynamics of labile soil organic matter and the biomass of soil microorganisms.

Net N mineralization is a process strongly conforming to first-order kinetics (Stanford and Smith 1972, Talpaz et al. 1981, Juma et al. 1984). Such a response assumes that NH_4^+ production occurs as a constant proportion of some organic substrate pool(s). The alpine tundra, tallgrass prairie (Cedar Creek), and the forested ecosystems all displayed first-order kinetics, but rate constants ranged more widely than those for respired C (see *Appendix*). Although first-order responses have been reported for desert soils (Fisher et al. 1987), we found that net N mineralization was linear in arid ecosystems. Klopatek (1987) also found linear increases in net N mineralization for several pinyon–juniper forests in the southwestern U.S. The kinetic responses we observed could be explained by two alternatives. Different kinetics (i.e., zero-order vs. first-order) could apply to net N mineralization in the ecosystems we studied. However, this seems unlikely given the large number of studies documenting a first-order response. A more plausible explanation is that first-order rate constants vary widely among these ecosystems. If N was mineralized from stable forms of soil organic matter, then low rate constants could produce a relatively linear response even after 32 wk of incubation. Studies centered on quantifying changes in substrate quality in the ecosystems we studied could provide insight into the exact mechanism(s) responsible for these kinetic responses.

The inverse relationship we observed between the respired C : mineralized N ratio and potential net N mineralization suggests that labile C pool size influences the balance between gross rates of mineralization and microbial immobilization. Schimel et al. (1985*a*) reported a similar relationship for prairie and agricultural ecosystems co-occurring on the same soil, wherein the prairie soils had high respired C : mineralized N ratios and low rates of potential net N mineralization. The ratios we report for tallgrass prairie (Cedar Creek), alpine tundra, and forest ecosystems are similar to those of Schimel et al. (1985*a*), but ratios in the other ecosystems are much greater. Zak et al. (1993) found respired C : mineralized N ratios varied from 12 to 19 for a series of Lake States forests. In that study, respired C : mineralized N ratios were also significantly related to net N mineralization ($r = -0.989$, $P = 0.001$; $n = 5$; calculated from Zak et al. 1993). In combination, these results indirectly suggest that greater amounts of N are immobilized when labile C pools are large.

Numerous studies have used climatic and edaphic factors to predict spatial patterns of plant production. For example, global patterns of ANPP and plant litter production can be described using actual evapotranspiration (AET), an integrated measure of temperature, precipitation, and soil water-holding capacity (Rosenzweig 1968, Lieth 1973, Meentemeyer et al. 1982). In

temperate North American forests, N availability is thought to limit plant production because ANPP is often well correlated with rates of net N mineralization (Pastor et al. 1984, Zak et al. 1989). In the diverse ecosystems we studied ANPP was better correlated with AET ($r = 0.708$, $P = 0.005$) than N availability, suggesting that climatic factors impose a greater constraint on plant production at the scale of our study; such a result is not surprising. Nevertheless, our laboratory incubation may not have accurately portrayed relative differences in N availability among ecosystems, which could, in part, contribute to the poor correlation we observed. Laboratory conditions of temperature and soil water potential differed greatly from those in situ. This effect was greatest in the arid ecosystems and alpine tundra, where laboratory estimates probably least reflect in situ rates. As such, our relative estimates of net N mineralization are high for these ecosystems. Additional variation was undoubtedly introduced into the relationship between ANPP and net N mineralization, because we did not directly measure ANPP in each ecosystem. Direct measurements of ANPP together with in situ estimates of net N mineralization are needed before generalizations can be made regarding the influence of N availability on plant productivity at the spatial scale of our study.

In summary, our results suggest that plant production influences labile soil C pools and microbial biomass at broad spatial scales. Although soil texture was significantly related to respired C, we have no indication that it constrains the biomass or C-use efficiency of soil microorganisms at the spatial scale of our study. Climate directly influences soil microorganisms by affecting soil temperature and moisture regimes, which regulate the rate of physiological processes. Climate also indirectly regulates microbial populations by influencing rates of plant production and the subsequent input of substrate both above- and belowground. Regional patterns of plant production and the cycling of C and N have been predicted using climatic and edaphic factors as driving variables (Pastor and Post 1986, Parton et al. 1988). Our work suggests that plant production holds promise in predicting patterns of labile organic matter pools and microbial biomass at much larger spatial scales. Moreover, changes in global climate that alter spatial patterns of plant production also have the potential to modify soil C availability and the biomass of soil microorganisms.

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APPENDIX

Summary of data (means ± 1 SE) for ecosystems distributed across North America.

Location	Ecosystem	Organic C $(g/m)^2$	Total N $(g/m)^2$	C:N	Extractable NH_4^+ (mg/m^2)
H. J. Andrews	Old-growth Douglas-fir	6510.6 ± 443.24	231.4 ± 16.13	28.4 ± 1.13	86.7 ± 71.4
Sevilleta	Pinyon–Juniper	2331.4 ± 512.50	167.5 ± 28.80	13.2 ± 0.60	17.9 ± 10.5
	Desert grassland	391.8 ± 15.70	37.7 ± 1.23	10.4 ± 0.23	4.6 ± 4.6
Jornada	Desert grassland	675.7 ± 65.18	60.5 ± 5.56	11.1 ± 0.30	37.9 ± 15.7
	Desert shrubland				
	Under shrub	836.2 ± 57.11	73.9 ± 4.85	11.5 ± 0.80	70.1 ± 16.1
	Between shrub	579.5 ± 82.24	40.8 ± 2.61	13.9 ± 1.38	107.3 ± 68.0
Niwot Ridge	Alpine tundra	7206.1 ± 447.34	507.6 ± 30.81	14.2 ± 0.18	116.4 ± 26.1
Central Plains	Shortgrass steppe				
	Bottom slope	1753.1 ± 132.14	158.7 ± 8.83	10.9 ± 0.28	46.6 ± 25.3
	Middle slope	1562.4 ± 109.55	147.7 ± 7.18	10.5 ± 0.26	22.0 ± 9.6
	Top slope	1460.4 ± 55.37	140.1 ± 4.23	10.4 ± 0.19	94.8 ± 22.1
Konza Prairie	Tallgrass prairie				
	Bottom slope	3972.0 ± 96.88	306.9 ± 7.54	12.9 ± 0.19	8.7 ± 5.7
	Middle slope	4915.8 ± 159.01	392.8 ± 11.91	12.5 ± 0.32	5.6 ± 1.9
	Top slope	4828.3 ± 122.90	345.0 ± 7.23	14.0 ± 0.50	40.0 ± 6.6
Cedar Creek	Tallgrass prairie	2047.1 ± 162.7	109.2 ± 3.31	18.7 ± 0.48	18.5 ± 7.0
	Upland pin oak forest	3012.0 ± 97.3	142.0 ± 16.2	21.0 ± 0.27	163.2 ± 69.7
Manistee	Northern hardwood forest	4148.0 ± 350.50	244.7 ± 18.32	17.5 ± 0.63	108.5 ± 18.5
Coweeta	Southern hardwood forest	3925.7 ± 421.98	217.5 ± 21.80	18.0 ± 0.56	240.0 ± 25.6
Hubbard Brook	Northern hardwood forest	8935.3 ± 1696.44	404.9 ± 75.82	21.7 ± 0.88	415.7 ± 172.5

* Ecosystem displayed linear increases in mineral N produced over the 32-wk incubation.

APPENDIX. Continued.

Extractable NO^-_3 (mg/m^2)	Microbial biomass C (g/m^2)	Microbial biomass N (g/m^2)	Respired C (g/m^2)	Rate constant, k (wk^{-1})	N mineralization (g/m^2)	Mineralized N (g/m^2)	Rate constant, k (wk^{-1})
6.2 ± 4.2	105.8 ± 8.12	23.6 ± 1.91	342.2 ± 31.26	0.255 ± 0.0117	14.4 ± 1.24	14.7 ± 1.08	0.099 ± 0.0124
61.9 ± 35.6	9.2 ± 2.78	1.9 ± 0.46	281.4 ± 57.50	0.336 ± 0.0216	3.0 ± 0.39	*	*
7.4 ± 6.5	2.5 ± 0.61	0.6 ± 0.08	159.3 ± 12.52	0.357 ± 0.0315	2.3 ± 0.22	*	*
89.2 ± 46.4	16.2 ± 2.35	3.0 ± 0.38	115.1 ± 16.18	0.310 ± 0.0378	3.1 ± 0.72	*	*
189.1 ± 96.2	21.1 ± 4.25	5.1 ± 0.86	273.6 ± 30.77	0.285 ± 0.0215	6.4 ± 0.39	*	*
233.1 ± 188.2	8.8 ± 1.39	1.6 ± 0.16	125.2 ± 14.13	0.178 ± 0.0171	4.1 ± 0.29	*	*
238.1 ± 64.1	55.1 ± 9.49	15.2 ± 2.63	387.3 ± 65.74	0.326 ± 0.0299	19.3 ± 3.37	23.1 ± 2.74	0.078 ± 0.0113
253.9 ± 138.7	3.1 ± 0.33	2.5 ± 0.24	365.2 ± 42.19	0.204 ± 0.0267	12.7 ± 2.86	*	*
58.8 ± 27.9	2.5 ± 0.34	1.8 ± 0.23	301.9 ± 27.31	0.280 ± 0.0296	7.3 ± 0.66	*	*
150.3 ± 39.9	3.0 ± 0.28	1.6 ± 0.14	336.4 ± 19.93	0.320 ± 0.0278	9.2 ± 1.28	*	*
413.3 ± 61.9	129.3 ± 6.26	32.8 ± 1.32	371.9 ± 21.18	0.159 ± 0.0078	10.2 ± 1.52	*	*
822.5 ± 143.4	137.6 ± 19.11	34.9 ± 1.95	466.7 ± 43.34	0.254 ± 0.0285	5.5 ± 1.40	*	*
881.8 ± 216.4	135.7 ± 10.04	32.4 ± 0.95	415.9 ± 41.89	0.184 ± 0.0197	3.6 ± 0.57	*	*
193.9 ± 76.5	43.0 ± 2.88	13.4 ± 0.98	275.5 ± 17.31	0.216 ± 0.0107	10.3 ± 0.72	11.5 ± 0.54	0.059 ± 0.0080
28.1 ± 23.1	59.9 ± 5.88	15.1 ± 0.82	288.5 ± 14.54	0.225 ± 0.0125	14.9 ± 1.20	14.8 ± 1.47	0.186 ± 0.0208
696.7 ± 134.3	102.9 ± 9.91	26.6 ± 1.91	276.9 ± 24.39	0.313 ± 0.0555	22.3 ± 1.43	21.8 ± 1.56	0.112 ± 0.0107
22.2 ± 9.6	128.1 ± 17.40	32.1 ± 2.99	491.0 ± 60.49	0.253 ± 0.0309	19.2 ± 1.78	21.4 ± 2.30	0.059 ± 0.0065
235.9 ± 139.1	28.1 ± 3.93	16.4 ± 1.30	475.5 ± 81.21	0.180 ± 0.0044	31.0 ± 5.93	31.9 ± 5.21	0.154 ± 0.0123