

MICROBIAL N AND BIOMASS, RESPIRATION AND N MINERALIZATION IN SOILS BENEATH TWO CHAPARRAL SPECIES ALONG A FIRE-INDUCED AGE GRADIENT

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Summary—A decline in available nutrients may contribute to the loss of vigor observed in older chaparral stands. We examined N mineralization and the storage of C and N in the microbial biomass of soil along a fire-induced chaparral chronosequence in San Diego County, Calif. Soil was collected under chamise (*Adenostoma fasciculatum* H. & A.) and ceanothus [*Ceanothus greggii* Gray var. *perplexans* (Trel.) Jeps] shrubs in stands burned 0, 2, 4, 11, 20, 54 and 80 yr prior to the study. Soil collected from the top 5 cm beneath chamise and ceanothus had similar microbial biomass patterns with stand aging. The amount of microbial C in soil remained relatively constant across the age gradient. Concentrations of microbial N and the amount of N mineralized fluctuated, with no significant trend across the stand-age gradient. For both chaparral species, NH_4^+ concentrations in soil were significantly higher in the recently burned stand (age = 0) than in stands burned from 2 to 80 yr earlier. Ammonium and nitrate concentrations in soil were not significantly different in most instances among soils from 2 to 80 yr-old stands. Soil collected under *A. fasciculatum* had significantly higher respiration rates, and higher concentrations of NH_4^+ and NO_3^- compared to *C. greggii*, suggesting that these chaparral species have differential influences on microbial processes in the soil around them.

INTRODUCTION

Recurring fire starts secondary plant succession in chaparral ecosystems. Plant species establishment is generally limited to the first several years after the fire (Horton and Kraebel, 1955). Species which will make up the mature community are present in the vegetation in the first post-fire year. Succession after this time consists of the sequential death of annuals, followed by short-lived perennials, and then longer-lived perennials (Hanes, 1971). Shrubs dominate the site at maturity. Eventually even the shrubs senesce, physiological activity decreases (Rundel and Parsons, 1980) and dead fuel accumulates (Hanes, 1971). The age at which senescence occurs is not the same for every site in spite of many shared species. However, stands older than 60 yr are often “decadent” (Hanes, 1971).

Stand senescence may be caused by nutrient shortages resulting from slow nutrient cycling, low input rates from precipitation or weathering of parent material, and sequestering of nutrients in standing biomass and in recalcitrant soil compounds. Long residence times of standing dead biomass (Christensen, 1973; Rundel and Parsons, 1980; Oechel and Reid,

1984; C. D. Winn, unpubl. thesis, California State University, Fullerton, 1977; Yeilding, 1977) or low decomposition rates are possible causes of slow nutrient cycling. Litter from many chaparral species is rich in allelopathic compounds which are known to reduce nutrient cycling process rates (Chou and Muller, 1972; Rice and Pancholy, 1972; Christensen, 1973; Kaminsky, 1981). Nutrients are lost from chaparral stands in leachate, runoff, sediment movement and in biogenic gas emissions (Mooney *et al.*, 1987); nutrient inputs include atmospheric deposition, biological fixation and rock weathering (Gray and Schlesinger, 1981).

It seems unlikely that nutrient accumulation in litter is the major factor causing nutrient deficiencies in older stands. N and P pools in litter in chaparral ecosystems are generally lower than in most temperate forest ecosystems, due to the lower productivity and accumulation of detrital material in chaparral stands (Gray and Schlesinger, 1981). The relationship between the rate of litter deposition and decomposition in chaparral in southern California is unclear, although in one study the two rates were similar over a wide range of stand ages (8–55 yr; Kittredge, 1955). Laboratory studies of chaparral litter decomposition also indicate that a thick litter layer would not accumulate, although between 15 and 54 yr litter decomposition rates decreased, presumably due to nutrient deficiencies; or allelopathic factors (C. D. Winn, *loc. cit.*).

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Our study was coordinated with a simultaneous investigation of potentially available N and P along a chaparral fire-cycle chronosequence in San Diego County, Calif. (Marion and Black, 1988). In their study, Marion and Black included the same chaparral sites that we sampled, except for our two youngest stands. Total soil N and potentially-mineralizable N increased with stand age up to 50–60 yr, after which total N and the available N fraction, decreased. Total P did not change with time, but available P decreased logarithmically with increasing age (Marion and Black, 1988). In our study we investigated N mineralization and the role of microbial biomass in the storage of C and N in chaparral stands ranging from 0 to 80 yr-old.

MATERIALS AND METHODS

Site description

Soil was collected on 6 February 1984, from the Sky Oaks Biological Preserve (0, 2 and 54 yr = old stands) and the adjoining Cleveland National Forest (4, 11, 20 and 80 yr-old stands) in San Diego County in southern California (Fig. 1). Stand ages refer to years since the last burn. Stand ages were based on ring counts of representative shrubs within each

stand and fire maps of San Diego County (Marion and Black, 1988). We sampled only sites with north aspects. The soils within the 0, 2 and 54 yr-old stands belong to the Tollhouse series, which is an Entic Haploxeroll (loamy, mixed, mesic, shallow). Soil in the 4, 11, 20 and 80 yr-old stands are of the Sheephead soil series, which is an Ultic Haploxeroll (loamy, mixed, mesic, shallow). All sites had chamise (*Adenostoma fasciculatum* H. & A.) and ceanothus [*Ceanothus greggii* Gray var. *perplexans* (Trel.) Jeps], except the 80 yr-old site which had little *C. greggii*. The major difference between the Sheephead and Tollhouse soils is that Sheephead is derived from micaceous schist and gneiss, and Tollhouse is derived from granodiorite (Marion and Black, 1988). Regression analysis of soil nutrient content versus soil series had not shown significant differences between the Sheephead and Tollhouse soils (Marion and Black, 1988). Marion and Black (1988) therefore dropped soil series as a variable in their subsequent data analyses.

Sample preparation

Soils were sampled by scraping away the litter layer and taking three subsamples from the 0 to 5 cm layer from each of the four geographic quadrants under

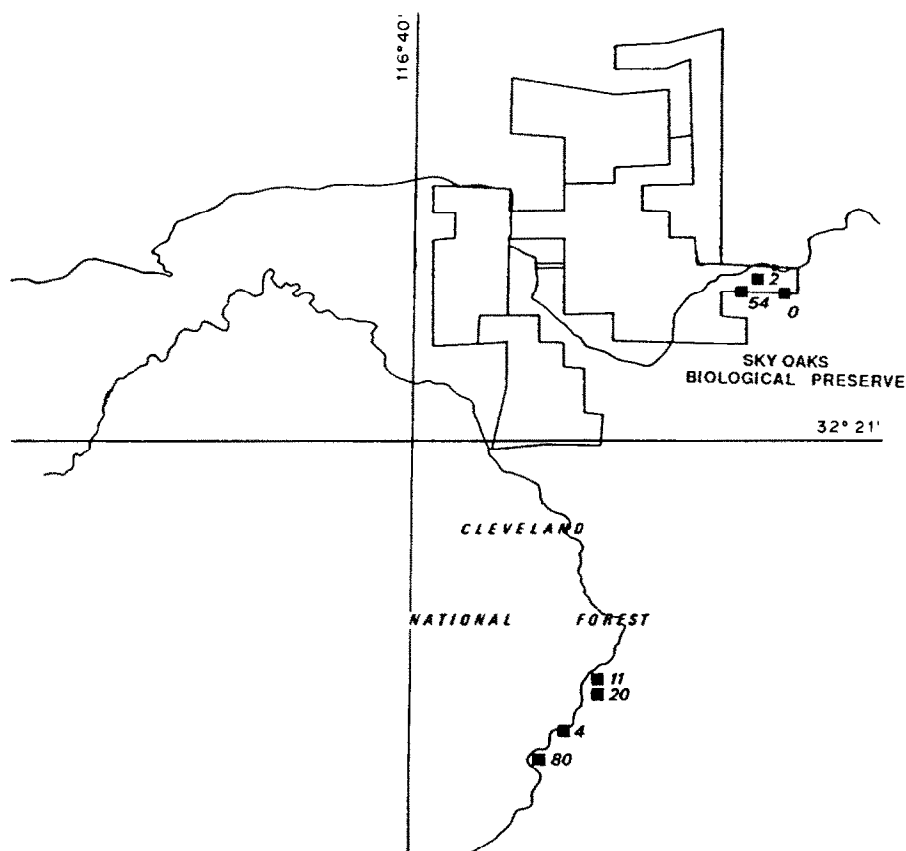


Fig. 1. Location of the different aged chaparral stands used in this study. Modified from Oechel and Reid (1984).

each shrub canopy. Within each quadrant a subsample was taken near the trunk, midway out to the drip line and at the drip line. All 12 subsamples taken from beneath each shrub were combined into one composite sample per shrub. We collected soil beneath three randomly-selected replicate shrubs for each stand age and shrub species combination; a 7 (age) \times 2 (species) factorial design. The samples were kept at ambient temperature during the day of sampling. The samples were sieved (<2 mm) on the second day. On day 3 each sample was divided for microbial biomass and N mineralization determinations.

Microbial biomass and soil respiration

Microbial biomass was measured in two ways. The potential microbial biomass of the soil was measured using the substrate induced respiration method of Anderson and Domsch (1978). Soil samples were moistened to approximately one-half field capacity and maintained in beakers covered with saran wrap for 10 days. A glucose-talc mixture, as a fine powder, was then added to 20-g subsamples of soil to obtain 1 mg glucose g⁻¹ soil. No glucose was added to the control soils. The soil samples were then placed into plexiglass tubes (2.5 cm i.d. \times 12.7 cm). The soil was secured at each end with a screen and an "O" ring. Air was pumped through the tubes at a rate of 20 ml min⁻¹. The concentration of CO₂ in the air before and after passage through the tubes was measured with an infrared gas analyzer. CO₂ production of soil was determined from the difference in CO₂ concentration in air before and after passage through the tubes. Basal soil respiration rates were determined in the same manner for moistened control soil without glucose amendment.

The second method used to measure microbial biomass was the fumigation-incubation technique of Jenkinson and Powelson (1976) and Parkinson and Paul (1982). A K_C value of 0.41 was used to determine microbial C. Soil (200 g per sample) was moistened to field capacity and fumigated with CHCl₃ for 24 h to kill soil microorganisms, after which the CHCl₃ was removed, and the soil was reinoculated with 1.0 g of the original soil. The soil was kept in a sealed enclosure along with a beaker of NaOH to trap CO₂. After 10 days the NaOH was titrated with acid to determine the amount of CO₂ evolved from the soil. By comparing CO₂ evolution from fumigated soils to unfumigated controls, the microbial biomass at the time of fumigation was calculated.

Microbial N, ammonification and nitrification

The fumigated samples were used to calculate N and P in the microbial biomass. The amount of microbial N in soil was calculated by subtracting the amount of NH₄⁺ extracted with KCl from fumigated, reinoculated soil after 10 days of incubation, from the amount of NH₄⁺ extracted from soil immediately after fumigation with CHCl₃ (Jenkinson, 1976; Voroney and Paul, 1984). A K_N value of 0.3 was

used to determine microbial N. We also assayed for microbial P, but due to technical difficulties in P analysis no reliable data are available on microbial P.

Subsamples of the soil used for microbial biomass studies were collected for assaying NH₄⁺ and NO₃⁻ production. For each shrub sampled, 200 g of soil were placed in a beaker and moistened to field capacity. The beakers were covered with saran wrap and kept at room temperature for 8 weeks. Every 7 days 5 g of soil were collected and extracted with 2 N KCl from each of three replicate beakers per stand-shrub species combination. The concentrations of N as NH₄⁺ and as NO₃⁻ in the soil extracts were determined with a Technicon autoanalyzer. Concentrations of NH₄⁺ and NO₃⁻ were calculated on a soil dry weight basis.

Statistical analyses

Differences between soil from around the two chaparral species in microbial biomass, ammonification, nitrification and soil respiration rates were determined by analysis of variance with stands as blocks. An α level of 0.05 was chosen for determining significant differences between treatments. In comparing N mineralization between stands or between the two chaparral species, we used the means of the highest concentrations measured in soil incubations—after 1 week for NH₄⁺ and after 8 weeks for NO₃⁻. Means of NH₄⁺ and NO₃⁻ concentrations in soil among the different stands were tested for significant differences by one-way ANOVA's performed separately for the two chaparral species, followed by Tukey's test from means comparison. Trends across the chronosequence in microbial C and N, soil respiration, microbial C to N ratios and net N mineralization (NO₃⁻ plus NH₄⁺ from week 8 minus week 1, both species combined) were determined by simple linear regressions on stand age, followed by ANOVA hypothesis testing for zero slope. Trends were also tested by curvilinear regression using a model equation with the form of a power curve with a non-zero intercept as follows: $y = a + bx^c$, where y is the dependent variable and x equals stand age.

RESULTS

Microbial biomass and soil respiration

There was no significant trend (from linear regression analysis) for microbial biomass ($P = 0.10$ – 0.69) with increasing stand age, nor with soil respiration ($P = 0.42$ – 0.68 ; Fig. 2). Evidence for trend by fitting the power function was no greater than simple regression. Patterns of the amount of microbial biomass in soil across the chronosequence were similar for both the glucose-addition technique and the fumigation-incubation method. However, absolute values determined for microbial biomass with the glucose-addition technique averaged 51% higher than values obtained with the fumigation-incubation method (Fig. 2).

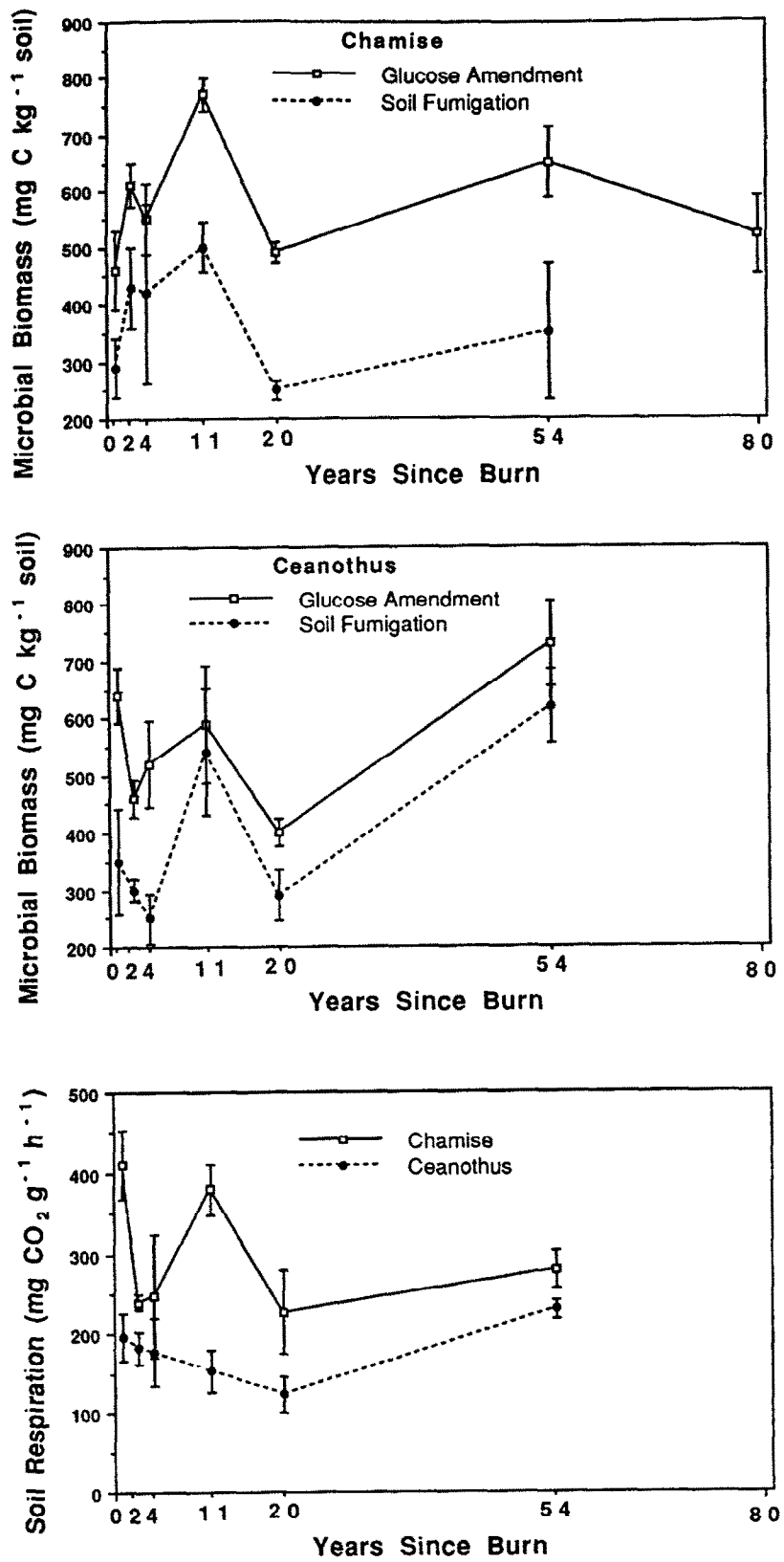


Fig. 2. Microbial biomass and respiration rates in soil from beneath *A. fasciculatum* and *C. greggii* along a fire-induced age gradient. Each data point and error bar represent the mean and standard error for three replicate shrubs within a stand. Since only one stand of each age was sampled, error bars refer only to estimates for those particular stands, but not to estimates for the specified ages.

Table 1. Microbial C and N, net N mineralization and microbial C:N ratio in the soil of a chaparral chronosequence*

Stand age (yr)	mg kg ⁻¹			
	Microbial C†	Microbial N	Net N mineralization‡	Microbial C:N
0	550 (58)	79	42 (4.1)	7:1
2	536 (36)	54	42 (4.0)	10:1
4	534 (70)	47	37 (2.4)	11:1
11	680 (66)	78	62 (4.5)	9:1
20	444 (21)	41	35 (2.8)	11:1
54	687 (70)	21	72 (4.5)	33:1
80	519 (69)	41	55 (4.1)	13:1

*Data for stands 0–54 yr-old are averages of combined data for soil beneath chamise and ceanothus. Data for the 80 yr-old stand are for soil beneath chamise only. Numbers in parentheses are standard errors.

†Determined by the glucose-addition method.

‡Nitrogen (NH₄⁺ and NO₃⁻) extracted from soil after 8 weeks of incubation minus N extracted after 1 week of incubation.

Average values for microbial C (all stand ages combined) ranged from 560 to 590 mg kg⁻¹ soil for the two chaparral species, using the glucose-addition method. Corresponding values for microbial C according to the fumigation–incubation method were 380 mg kg⁻¹ soil for both plant species.

The microbial biomass of soils under *A. fasciculatum* and *C. greggii* were not significantly different based on the glucose-addition technique ($P = 0.38$) or the fumigation–incubation method ($P = 0.97$). Basal soil respiration rates as measured by CO₂ evolution were significantly higher ($P < 0.001$) for soil collected under *A. fasciculatum* (297 µg CO₂ g⁻¹ h⁻¹) than soil collected under *C. greggii* (177 µg CO₂ g⁻¹ h⁻¹) (Fig. 2).

Microbial N and C

Because concentrations of microbial C and N were not significantly different in soil for the two chaparral species, data on microbial C and N for chamise and ceanothus were combined. The amount of microbial N in soil fluctuated, but with no statistically significant trend with stand age (based on linear and curvilinear regression analysis; Table 1). The C:N ratio of the microbial biomass in the chaparral soils ranged from 7 to 13 (excluding the 54 yr-old stand which had an abnormally high ratio of 33). Although the microbial C:N ratio tended to increase with stand age, the trend was not significant ($P = 0.13$).

Ammonification and nitrification

In the recently-burned stands (age = 0) NH₄⁺ concentration in soil was greatest after 1 week of incubation. In the following weeks NH₄⁺ production declined rapidly, and by week 4 or 5 was at baseline level (Figs 3 and 4). In 2 yr-old stands and older NH₄⁺ concentrations in soil were near baseline amounts for the entire 8 weeks of incubation. Nitrate on the other hand, tended to increase each successive week, and was usually at the highest after 8 weeks.

Since the amount of NH₄⁺ in soil was highest after 1 week of incubation, concentrations of NH₄⁺ after the first week were compared for soils of the

two chaparral species and from different stands. Ammonium concentrations in soil from chamise were not significantly different between stands 2–80 yr-old (Fig. 3), nor in soil from ceanothus in stands 2–54 yr-old (Fig. 4). Ammonium concentrations (0–54 yr-old stands) averaged 15.4 mg kg⁻¹ in soils from chamise and 10.2 mg kg⁻¹ for soil beneath ceanothus after 1 week of incubation (Figs 3 and 4). Ammonium concentrations in soil beneath the two species were significantly different at $P = 0.10$ (data from stands 0 to 54 yr-old combined). After 1 week of incubation, NH₄⁺ concentrations in soils of the recently-burned sites (age = 0) were 4–14 times as high as in stands 2–80 yr-old (Figs 3 and 4).

Because NO₃⁻ concentrations were nearly always highest after 8 weeks, concentrations for soils of *A. fasciculatum* and *C. greggii* were compared after 8 weeks of incubation. Nitrate concentrations in soil from chamise stands from 2 to 80 yr-old were not significantly different (Fig. 3). Nitrate concentrations in soil from ceanothus shrubs in the different-aged stands were not significantly different, except in the case of the 54 yr-old stand, which had higher NO₃⁻ concentrations than the 4 and 20 yr-old stands (Fig. 4). Nitrate concentrations after 8 weeks of incubation were significantly higher ($P < 0.04$; data from stands 0 to 54 yr-old combined) in chamise soil (68.4 mg kg⁻¹) compared to soil beneath ceanothus shrubs (56.6 mg kg⁻¹).

DISCUSSION

We found no evidence that N stored in microbial biomass of the chaparral soils is involved in nutrient deficiencies in older chaparral stands. However, gross flux of N through the microbial biomass, turnover rates of the microbial biomass and the amounts and types of microbial products generated could vary across the chronosequence. The amount of microbial N and of N mineralized in the chaparral soils was highly similar across the age gradient. The C:N ratio of the microbial biomass in our chaparral soils (7–13) was typical of microbial biomass C:N ratios (Paul and Voroney, 1980). Soil microbial biomass is considered a relatively labile fraction of the soil organic matter. Assuming that microbial N is a major fraction of the mineralizable N pool, the small size of the microbial biomass may belie its importance as a labile reservoir and transforming agent of soil nutrients.

It should be emphasized that our data is based on soil collected from only the top 5 cm of the mineral soil. Nevertheless, in a study of various 20–25 yr-old chaparral stands throughout California, more than three times as much N was stored in the top 5 cm of soil under chamise than in foliage, stems, roots and litter combined. Under ceanothus, N storage in the top 5 cm of soil was 30% greater than in plant biomass and litter combined (Zinke, 1981). 33% of the fine roots of *C. greggii* and 43% of *A. fasciculatum* were found within the top 20 cm of soil from a

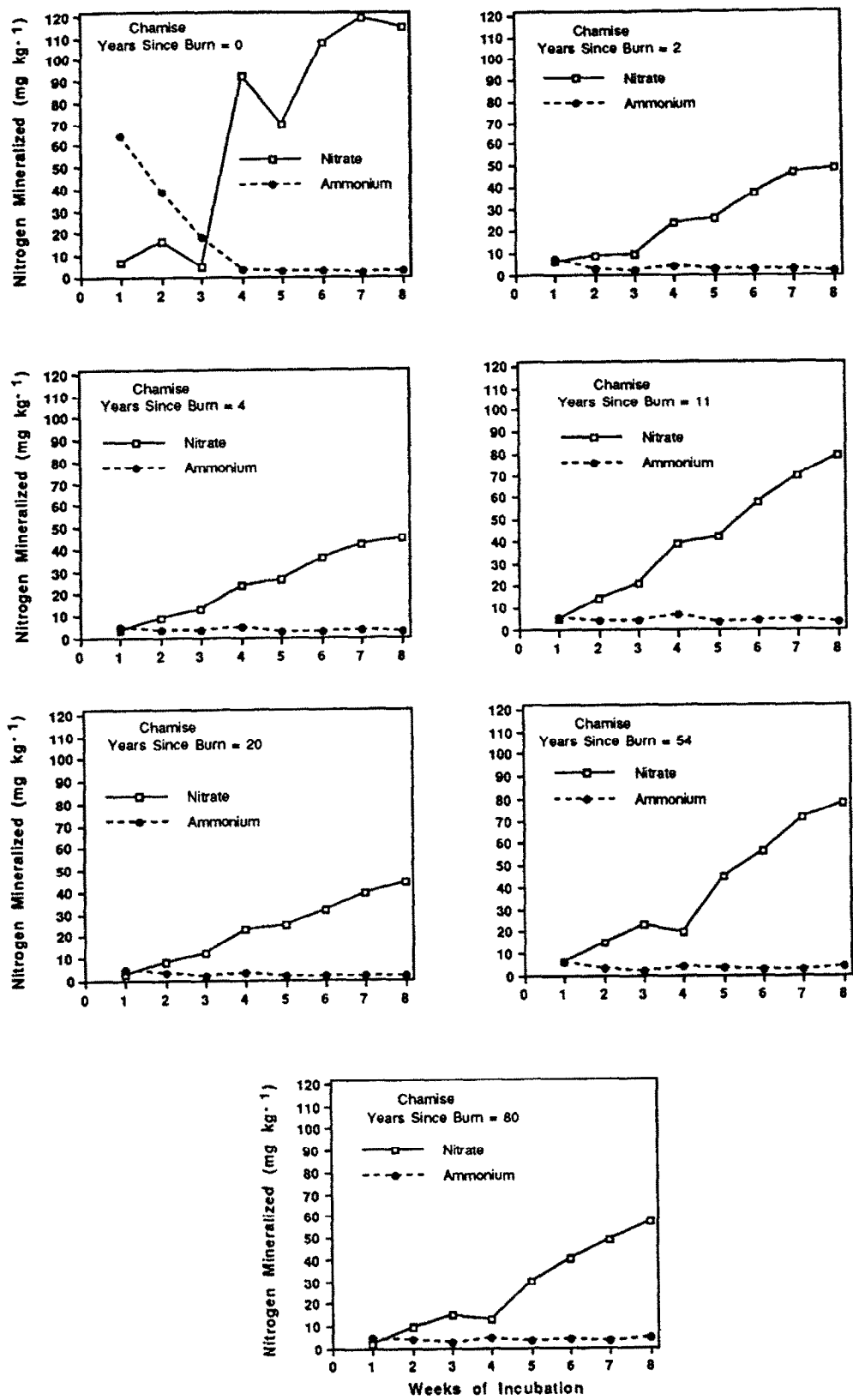


Fig. 3. Nitrogen mineralization for soils collected beneath *A. fasciculatum* along a fire-induced age gradient. Soil was assayed for extractable NH_4^+ and NO_3^- once a week for 8 weeks.

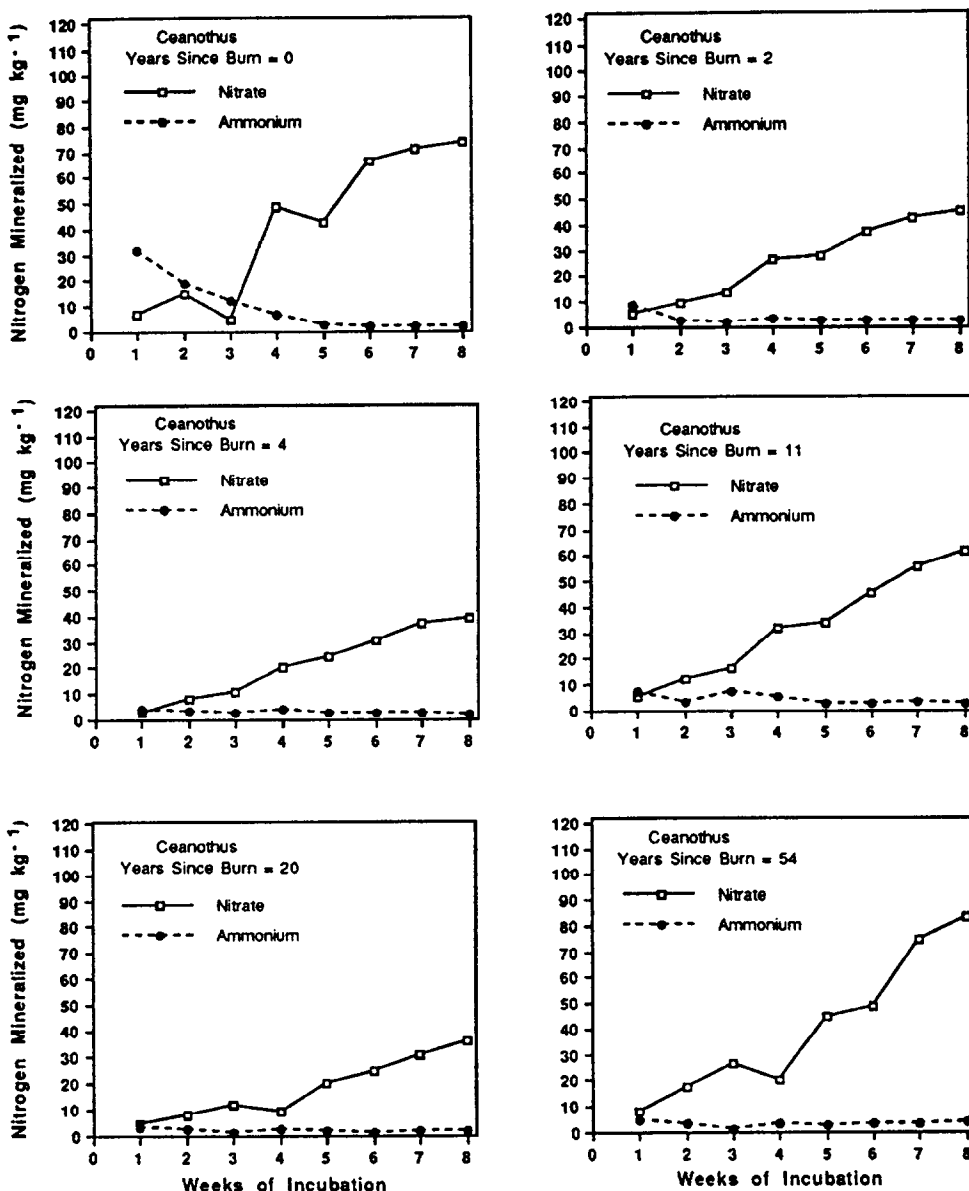


Fig. 4. Nitrogen mineralization for soils collected beneath *C. greggii* along a fire-induced age gradient. Soil was assayed for extractable NH_4^+ and NO_3^- once a week for 8 weeks.

north-facing chaparral plot in San Diego County near the site of our study (Kummerow *et al.*, 1977).

Soils at the Sky Oaks sites (0, 2 and 54 yr-old) are of a different series than the soils at the Cleveland National Forest sites (4, 11, 20 and 80 yr-old). Marion and Black (1988) did not find significant differences in the nutrient content of these soils. Nonetheless, differences between these soils could influence our results, and cannot be ruled out as a confounding factor. Furthermore, the presence or absence of significant trends with stand age in this study must be viewed with caution, considering the lack of replication for stand age.

Results of our N mineralization assays indicate that all of the soils across the chaparral chronosequence

contain significant quantities of mineralizable N. The soil microbial biomass can function as a net source (mineralization) or sink (immobilization) of available N (Smith and Paul, 1990) depending on factors such as the C:N ratio of microbial substrates and the growth rate and N demand of the microbial biomass. The C:N ratio of these soils (14:1 to 19:1; Marion and Black, 1988) and the results of our N mineralization assays, indicate that more N was mineralized than immobilized by the microbial biomass of the soils along the chronosequence. Immobilization may dominate over N mineralization in these soils under different conditions, e.g. during periods of rapid fine-root turnover or in microsites favoring N immobilization due to fast microbial growth.

Total soil C increased with stand age in a larger study including most of the chaparral stands we sampled (Marion and Black, 1988). Microbial C, at least in the top 5 cm, did not show significant trend with stand age in our study, suggesting a possible shift in organic matter composition as the stands aged. The increase in total soil C with stand age (Marion and Black, 1988) is probably due to the accumulation of plant-derived organic matter and microbial products. Paul and Voroney (1980) reported that during extended soil incubations the buildup of microbial products nearly equalled microbial biomass.

The distribution of N among the different soil fractions, and the amount of N sequestered in microbial and plant residues of varying degrees of recalcitrance, may change as the chaparral stands age. **In a contemporary study which included most of our chaparral stands, soils accumulated N with increasing stand age up to 50–60 yr, after which total N and potentially available N (PMN) declined (Marion and Black 1988);** presumably with greater proportions of N in the more recalcitrant residues. **Even so, total soil N and PMN were higher in 80- and 85 yr-old stands than in 11 yr-old stands (Marion and Black, 1988).** Marion and Black suggested that sequestering of N and P in recalcitrant soil compounds, plant biomass and litter in older chaparral stands may contribute to stand senescence; but they also stated that their data did not conclusively show that nutrient sequestering is the dominant mechanism controlling the availability of N and P in the older chaparral stands. Further studies are needed on the dynamics of organic matter fractionation with stand aging before we can understand to what extent nutrient sequestering in soil organic matter may influence chaparral senescence.

Concentrations of N mineralized in short-term soil incubations did not exhibit a decreasing trend in stands aging from 2 to 80 yr in our study. **This suggests that N cycling is not diminished sufficiently in soil of older stands to contribute to N deficiency or stand senescence.** We extracted NH_4^+ and NO_3^- weekly with 2 N KCl for 8 weeks, whereas Marion and Black (1988) extracted NH_4^+ and NO_3^- from soil every 2 weeks for 11 weeks with 10 mM CaCl_2 , followed by further leaching with a nutrient solution. Discrepancies between results of the two studies may be due to the different methods employed. The possibility that available soil N or P may be limiting in older chaparral stands and contributing to stand senescence remains an open question.

Ammonium concentrations in soil were higher in the recently-burned stand (0 yr-old) than in stands 2–80 yr-old; presumably due to the well-known phenomenon of fire-induced nutrient release from burned biomass (Christensen and Muller, 1975; Dunn *et al.*, 1979). Burning also reduces the populations of nitrifier bacteria in chaparral ecosystems (Dunn *et al.*, 1979). During the 8 weeks of soil incubation, NH_4^+ concentrations of soil from the recently-burned stand dropped rapidly as NO_3^- concentrations steadily

increased. In stands 2 yr old or older, NH_4^+ concentrations were near baseline quantities during the entire 8 weeks, whereas NO_3^- concentrations steadily increased with each additional week of incubation. Apparently mineralized NH_4^+ was continuously oxidized to NO_3^- , resulting in fairly low but constant concentrations of NH_4^+ in soil, and increasing concentrations of NO_3^- during the 8 weeks of incubation.

Microbial respiration, NO_3^- concentrations, and to a lesser degree, NH_4^+ concentrations, were higher in surface soil collected under *A. fasciculatum* than in soil collected under *C. greggii*. These two chaparral species may differentially affect soil microbial activity because of differences in: (1) the rate of fine root litter production, litter nutrient content and decomposability of litter; (2) partitioning of site nutrients between below and aboveground biomass and soil; and (3) the composition and physiological activity of the soil microbial community; e.g. because of plant influence on site micro-climate, or because of differences in root exudates or other biologically-active substances produced by the two chaparral species.

Although we do not have data on total N concentrations in soil under *A. fasciculatum* and *C. greggii*, Zinke (1981) found that in chaparral stands throughout California chamise stored a higher proportion of total site N (including biomass and litter) within the top 5 cm of soil than ceanothus. If higher concentrations of N also occur in the surface soil under *A. fasciculatum* in our sites, this may be a factor in the greater microbial activity in soil under *A. fasciculatum* compared to *C. greggii*.

Ceanothus species are nodulated nitrogen-fixing shrubs (Kummerow *et al.*, 1978b). Plausible explanations as to why presumptive N fixation under *C. greggii* did not result in higher microbial activity in soil (due to higher N concentrations in soil or detritus) include: (1) *C. greggii* fixes N at very low rates in southern California (Kummerow *et al.*, 1978b); (2) nodules on *C. greggii* roots occur at depths > 5 cm (Kummerow *et al.*, 1978b); and (3) a higher proportion of N is allocated to aboveground plant biomass in *C. greggii* compared to *A. fasciculatum* (Marion and Black, 1988; Zinke, 1981), thereby reducing the amount of N available to the soil microbial biomass under *C. greggii*. Kummerow *et al.* (1978b) conservatively estimated an annual N fixation rate of 0.1 kg ha⁻¹ yr⁻¹ for *C. greggii* in southern California. Root nodule density of *C. greggii* was much lower than in Ceanothus species in northern California (Delwiche *et al.*, 1965), presumably due to the more arid conditions in southern California chaparral ecosystems (Gray and Schlesinger, 1981).

The roots of *A. fasciculatum* tended to be more superficial than those from *C. greggii* within a 70 m² area in the Echo Valley area, about 45 km east of San Diego, California according to Kummerow *et al.* (1977); even though *A. fasciculatum* is generally considered to be deep-rooted and *C. greggii* to be a shallow-rooted species (Miller and Ng, 1977;

Kummerow *et al.*, 1977). In another study in the Echo Valley area, all the roots of two *C. greggii* shrubs and one *A. fasciculatum* shrub were within the top 30 cm of soil, whereas c 50% of the roots of three additional *A. fasciculatum* shrubs were within the top 30 cm (Miller and Ng, 1977). Both of these studies are based on a small number of plants due to the difficulty of excavating roots *in situ*; and it is therefore difficult to make general conclusions in comparing the rooting patterns of these two chaparral species. It does seem clear however that *C. greggii* and *A. fasciculatum* often have root biomasses concentrated near the soil surface (Miller and Ng, 1977; Kummerow *et al.*, 1977). Differences in fine root density, root litter quality or root exudates in the surface soil may contribute to the greater microbial activity we measured in the top 5 cm of soil from *A. fasciculatum* compared to *C. greggii*. Kummerow *et al.* (1978) found evidence of considerable fine-root turnover in mixed chaparral dominated by *A. fasciculatum* and *C. greggii* in San Diego County. The major period of root decomposition in this Mediterranean climate appears to begin with the fall rainy period (Kummerow *et al.*, 1978a). We collected soil in early February, well into the cool wet season, and probably after the initial period of rapid decomposition of root litter.

Graham and Wood (1991) studied soil formation in large unconfined lysimeters which in 1937 had been filled with homogenous soil material, allowed to stabilize for 9 yr and then planted with monocultures of chaparral species native to southern California. 41 yr after planting, significantly greater earthworm activity and darker more clay-enriched A horizons were found under *C. crassifolia* Torr. compared to *A. fasciculatum* (Graham and Wood, 1991). Clay has long been known to slow the decomposition of organic matter (Jenkinson and Ladd, 1981). If higher clay content occurs in the A horizon of soils under ceanothus than under chamise, this may result in stabilization of organic matter, and lower turnover rates and microbial activity in ceanothus soils.

Although soil microbial biomass probably depends more on root and mycorrhizal litter and root exudates than on aboveground litter, most available information on chaparral decomposition focuses on foliage and aboveground woody detritus. Litter bag studies have shown that the decomposability of leaf litter from *A. fasciculatum* and *C. greggii* is very similar (Yeilding, 1977). When comparing the overall decomposition rate of foliage and woody materials in several size classes, Yeilding (1977) reported that litter from *C. greggii* decomposed slightly faster than litter from *A. fasciculatum*. In any case, soil around *A. fasciculatum* exhibited higher microbial activity than soil from *C. greggii* in our study, which is the reverse of the relative litter decomposition rates for these two species reported by Yeilding (1977). Unpublished results (by P. H. Dunn) of studies conducted throughout California on soil fungal de-

composer populations around these two shrub genera indicate that the fungal communities are similar. More subtle differences in the composition of microbial communities, or differences in the influence of these chaparral plants on biological activity in soil (e.g. differences in root exudates, root litter quantity or quality or earthworm populations) may result in the higher respiratory and N-cycling activity of microorganisms in soil associated with *A. fasciculatum* compared to *C. greggii*.

In summary, we found no significant trends in the amount of microbial biomass C and N or of net N mineralization in the surface soils of seven chaparral stands ranging from 0 to 80 yr-old. Our data suggest that N in the microbial biomass of the top 5 cm of soil is not a major N storage pool contributing to N deficiencies in older stands. However, we have no data on turnover rates of the microbial biomass or of the amounts and types of microbial products in soil of the different-aged stands. Soil collected under *A. fasciculatum* respired at a higher rate and mineralized more N than soil under *C. greggii*. Characteristics of *A. fasciculatum* and *C. greggii* which could contribute to higher microbial activity of surface soils under *A. fasciculatum* include: (1) higher N storage in soil under *A. fasciculatum*, possibly related to a greater allocation of N to aboveground biomass in *C. greggii*; (2) higher clay content in the surface soil of *C. greggii* (caused by higher earthworm activity) with resultant clay-induced stabilization of organic matter and slower decomposition rates, and (3) differences in fine root density, root litter quality or quantity, or plant exudates between these two chaparral species.

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