

Biogeochemical Cycling of Calcium and Magnesium by Ceanothus and Chamise

S. A. Quideau,* R. C. Graham, O. A. Chadwick, and H. B. Wood

ABSTRACT

Vegetation has long been recognized as a fundamental factor in soil formation, but vegetation and soils commonly covary in response to other environmental factors, confounding the specific effects of vegetation on soil properties. The lysimeter installation at the San Dimas Experimental Forest in southern California offers a rarely found opportunity for quantifying cation-cycling processes in a setting where all factors except vegetation are kept constant. The lysimeters were filled in 1937 with homogenized, fine sandy loam and planted in 1946 with chamise (*Adenostoma fasciculatum* Hook. and Arn.) and ceanothus (*Ceanothus crassifolius* Torr.). Comparison of the chamise and ceanothus lysimeters was best achieved by using the Ca/Mg ratio of the different cation pools and fluxes as an index. In 1987, the ceanothus exchangeable soil pool contained proportionally more Ca than Mg compared with chamise; that is, the Ca/Mg ratio in the ceanothus exchangeable soil pool was higher than that in chamise. Strong evidence supports vegetation influence on intra-system fluxes (weathering and biocycling) as the basis for these differences. First, more Ca than Mg was released by weathering under ceanothus than under chamise. Second, the ceanothus aboveground biomass exhibited a higher Ca/Mg ratio than the chamise. Third, differences between vegetation types widened with time since construction of the lysimeter installation in both the aboveground biomass and exchangeable soil pools. Differences in cation storage measured for the lysimeter chamise and ceanothus stands appear representative of natural chaparral communities throughout California, and may result in distinct Ca and Mg biogeochemical processes in associated ecosystems.

VEGETATION MAY PLAY A CENTRAL ROLE in controlling cation levels on the exchangeable pool of soils. For example, the decrease in exchangeable Ca measured in temperate forest soils of England and the eastern USA has been related to the sequestering of this cation in woody biomass (Ovington, 1958; Alban, 1982; Federer et al., 1989). In desert areas of Australia and the southwestern USA, root uptake from a large volume of soil and concentration at the soil surface by litterfall has been observed to increase salinity beneath plant canopies (Sharma and Tongway, 1973; Tiedemann and Klemmenson, 1973); trees in tropical ecosystems also have been hypothesized to enrich the soil around them in exchangeable cations by efficiently capturing precipitation inputs (Kellman, 1979). In contrast, the understanding of soil-plant cation relationships in Mediterranean ecosystems remains sketchy. The majority of studies in the Mediterranean climatic zone of southern California has focused on N and P (e.g., Zinke, 1969; Marion and Black, 1988; Fenn et al., 1993).

Chaparral, dominated by sclerophyllous shrubs such as chamise and ceanothus, is widespread on dry slopes and ridges over much of California, making up >7% of the native cover of the state (Hanes, 1976). Results from study sites throughout California document differences in ceanothus and chamise base cation requirement, as reflected by significantly higher Ca concentrations in ceanothus biomass than chamise (Table 1). These differences in plant uptake may be particularly significant to soils of the mixed chaparral, a heterogeneous landscape in which individual plant species are interspersed as small patches (Hanes, 1976). However, understanding the specific influence of chaparral vegetation on soil properties so far has been limited by a lack of appropriate study sites. Vegetation and soils commonly covary in response to other environmental factors (Birkeland, 1984), and it often is unclear whether differences in soil properties are a result of different vegetation types, or have preceded and influenced the spatial distribution of plant species.

The lysimeter installation at the San Dimas Experimental Forest in southern California is a unique long-term experiment allowing quantification of pedological and nutrient-cycling processes in a setting where all environmental factors except vegetation are kept constant. Five large (5.3 × 5.3 m horizontal and 2.1-m-deep) earthen-walled pits, referred to as *unconfined lysimeters*, were filled in 1937 with homogenized soil material and planted in 1946 with monocultures of buckwheat (*Eriogonum fasciculatum* Benth.), chamise, ceanothus, scrub oak (*Quercus dumosa* Nutt.), and Coulter pine (*Pinus coulteri* B. Don.). In 1960, a wildfire burned the chamise and ceanothus plants to the ground, introducing an unplanned but ideal fire-induced chronosequence experiment.

Past research at the San Dimas lysimeter installation has addressed vegetation effects on soil morphology (Graham and Wood, 1991), exchangeable cations (Ulery et al., 1995), aggregate stability (Graham et al., 1995), and organic C sequestration (Quideau et al., 1998). Differences in 2:1 phyllosilicate mineralogy and base cation release by weathering have been reported for the oak and pine lysimeters (Tice et al., 1996; Quideau et al., 1996), but no studies have been published concerning the influence of the chamise and ceanothus vegetation on weathering fluxes. Here we quantified changes in Ca and Mg storage in the chamise and ceanothus plant-soil systems as a function of time, including atmospheric deposition, aboveground biomass, and changes in the exchangeable and nonexchangeable soil pools, to determine vegetation effects on cation biogeochemistry.

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Abbreviations: ICP-MS, inductively coupled plasma mass spectrometry.

MATERIALS AND METHODS

Experimental Area

The lysimeter installation is located at an elevation of 830 m in the San Dimas Experimental Forest within the San Gabriel Mountains of southern California. Vegetation at the Forest is mainly composed of chamise chaparral (dominated by *Adenostoma fasciculatum*) and of mixed chaparral, including *Ceanothus* spp., manzanita (*Arctostaphylos* spp.), *Quercus dumosa*, and mountain-mahogany (*Cercocarpus betuloides* Nutt.) (Mooney and Parsons, 1973). The climate is Mediterranean with hot, dry summers and mild, moist winters. The mean annual precipitation is 670 mm and mostly falls as rain between December and March. The mean annual air temperature is 14.3°C, with August and January means of 22.2 and 8.8°C, respectively (Dunn et al., 1988).

The lysimeters were filled in 1937 with a fine sandy loam (58% sand, 31% silt, 11% clay) derived on site from the weathering of diorite. To ensure homogeneity, the fill material was sieved (<19-mm diam.) and thoroughly mixed before filling. Analysis at the time showed no statistical textural difference in 100 randomly collected samples (Colman and Hamilton, 1947). In addition, each incremental 7.5-cm-thick fill layer was thoroughly chopped with a spade to minimize boundary effects with the underlying layer.

In 1946, planting of each species was done from 1-yr-old seedlings on a 17- by 24-m area, including an unconfined lysimeter and surrounding buffer strips to eliminate edge effects (Colman and Hamilton, 1947). Although design of the installation did not allow for lysimeter replication, homogeneity of the original fill material warranties that differences between lysimeters solely reflect differences in vegetation. The monocultures were periodically weeded during the first few years following planting, and by the mid-1950s, the lysimeters supported pure stands and had complete litter covers (Patric, 1961). In 1960, a wildfire swept the lysimeter installation and burned the chamise and ceanothus stands to the ground, leaving only charred stems and a 1-cm thick layer of ash (Zinke, 1977). However, by 1972, vegetation was again vigorous and in virtually pure stands as originally planted (J.H. Patric, unpublished report, 1974). These conditions have prevailed to the present without further disturbance.

Soil Sampling and Analysis

Composite samples of each 7.5-cm soil layer were taken in 1937 upon filling of the lysimeters, and the bulk density of the homogeneous fill material was calculated from the mass of soil added to the pits, adjusted for settling (Patric, 1961). Five replicate samples of the surface 2.5-cm soil layers were taken at the chamise and ceanothus lysimeters in 1958, immediately after the fire in 1960, and in 1975 (Zinke, 1977; P. Zinke, personal communication, 1996). The ash layers (1 cm thick) were sampled 1 wk after the fire in five replicates at the two lysimeters. In 1987, soils on each vegetation plot were described and sampled by morphological horizon, as reported by Graham and Wood (1991). The soils under chamise and ceanothus were classified as coarse-loamy, mixed, mesic Typic Xerorthents. Bulk density of the 1987 samples was determined on saran-coated clods, or using cores in the case of fragile surface horizons.

Extractable Ca and Mg of all soil and samples (<2-mm fraction) were determined using 1 M NH₄OAc at pH 7 and analyzed by atomic absorption spectroscopy (Zinke, 1977; Ulery et al., 1995). Extractable base cations are equivalent to exchangeable base cations, since CaCO₃ and soluble salts are absent (Ulery et al., 1995). The 1987 soil samples and corre-

Table 1. Calcium and Mg concentrations in chamise and ceanothus stands from California. Calcium concentrations in chamise and ceanothus stands were statistically different at the 0.05 probability level, as determined by a paired *t*-test. No significant differences were found for Mg concentrations ($\alpha = 0.05$).

Location	Tissue	Vegetation	Ca	Mg
			- g kg ⁻¹ -	
Los Padres National Forest, Santa Barbara Co.†	twigs‡	<i>A. fasciculatum</i>	9.4	0.95
		<i>C. cuneatus</i>	11.7	0.85
	stems§	<i>A. fasciculatum</i>	7.2	0.39
		<i>C. cuneatus</i>	8.2	0.36
Sequoia National Park, Sierra Nevada¶	stems	<i>A. fasciculatum</i>	3.3	0.6
		<i>C. leucodermis</i>	8.0	0.9
	foliage	<i>A. fasciculatum</i>	8.4	1.5
		<i>C. leucodermis</i>	12.0	1.8
Echo Valley, San Diego Co.#	stems	<i>A. fasciculatum</i>	3.2	0.9
		<i>C. gregii</i>	6.8	1.0
	foliage	<i>A. fasciculatum</i>	7.3	1.6
		<i>C. gregii</i>	11.3	2.3
Descanso, San Diego Co.††	stems	<i>A. fasciculatum</i>	4.6	0.3
		<i>C. crassifolius</i>	7.3	0.3
	foliage	<i>A. fasciculatum</i>	10.0	0.8
		<i>C. crassifolius</i>	9.8	1.0
	roots	<i>A. fasciculatum</i>	16.7	1.1
		<i>C. crassifolius</i>	14.0	1.1
	litter	<i>A. fasciculatum</i>	14.1	1.8
		<i>C. crassifolius</i>	16.4	1.8
Bear Valley, Mariposa Co.††	roots	<i>A. fasciculatum</i>	4.5	0.5
		<i>C. cuneatus</i>	12.3	1.1
Kiethly Ranch, Lake Co.††	stems	<i>A. fasciculatum</i>	5.5	0.5
		<i>C. cuneatus</i>	8.5	0.3
	foliage	<i>A. fasciculatum</i>	8.4	1.2
		<i>C. cuneatus</i>	13.1	1.3
	roots	<i>A. fasciculatum</i>	3.2	0.4
		<i>C. cuneatus</i>	11.8	0.5
	litter	<i>A. fasciculatum</i>	11.2	2.2
		<i>C. cuneatus</i>	13.3	1.9
Pattymocus, Tehama Co.††	stems	<i>A. fasciculatum</i>	5.0	0.7
		<i>C. cuneatus</i>	7.9	0.5
	foliage	<i>A. fasciculatum</i>	12.8	2.0
<i>C. cuneatus</i>		13.7	2.1	
Sunrise, San Diego Co.††	roots	<i>A. fasciculatum</i>	14.9	1.2
		<i>C. crassifolius</i>	28.0	1.6

† From Debano and Conrad, 1978.

‡ <0.64-cm diam.

§ >0.64-cm diam.

¶ From Rundel and Parsons, 1980; reported data are the mean values of four study sites.

From Shaver, 1983.

†† From Zinke, unpubl. data.

sponding original fill materials were analyzed for total elemental composition by fusing 0.2 g of soil with 1.2 g of LiBO₂, followed by dissolution in 100 mL of 5% HNO₃. Concentrations of Ca and Mg in the solutions were measured by inductively coupled plasma mass spectrometry (ICP-MS). Twenty percent of all samples were analyzed in duplicate to assess the reproducibility of the analytical method. Mean variability (as a percentage of average concentration) was 1.9 for Ca and 2.5 for Mg. Total Ca and Mg analyses were run on the ash samples by perchloric digestion and atomic absorption spectroscopy (Zinke, 1977; P. Zinke, personal communication, 1996).

Aboveground Biomass

Aboveground biomass was estimated in 1958, 1969, and 1975 by cutting a uniform area of the chamise and ceanothus stands (Zinke, 1969 and 1977). Vegetation was sampled in 30- to 100-cm height increments and separated into deadwood, livewood, and foliage. In 1993, aboveground biomass was determined as reported by Milone (1994). To keep destructive sampling to a minimum, harvesting was restricted to two cham-

ise and one ceanothus shrubs growing in the buffer strips surrounding the lysimeters. Each individual stem of the three harvested shrubs was measured and weighed green in the field, and randomly selected stems were transported to the laboratory for separation and drying. This procedure provided a range of stem diameter classes that could be used to develop the following allometric equations (Eq. [1] and [2]) (Milone, 1994):

$$Y_a = -30.283X + 3.832X^2 - 0.035X^3$$

$$(r^2 = 0.94; n = 30) \tag{1}$$

and

$$Y_c = -1.704\log_{10}X + 1.800X^2 (r^2 = 0.85; n = 11)$$

$$\tag{2}$$

where *Y* is the total predicted biomass for chamise (a) and ceanothus (c), and *X* is stem diameter at a 10-cm height. Total biomass of each individual stem located within the lysimeter perimeter was then estimated using these equations. Additionally, biomass components within each lysimeter were randomly sampled at ≈1-m height increments to be analyzed for elemental composition (Milone, 1994).

Leaf litter was sampled in 1958, 1969, and 1975 in five replicates at the two lysimeters (P. Zinke, personal communication, 1996), and litter biomass was determined in 1994 from triplicate cores of a known cross-sectional area (227 cm²). Wood, foliage, and litter samples were dried to a constant weight at 70°C, ground, and analyzed for Ca and Mg by atomic absorption spectroscopy following a perchloric acid digestion.

Cation Balance Calculations

To estimate changes in Ca and Mg storage since construction of the lysimeter installation, each plant-soil system was divided into three compartments: (i) biomass, and (ii) exchangeable and (iii) nonexchangeable soil pools (Fig. 1). Root biomass was not measured in this study, so changes in the biomass compartment correspond with changes in above-

ground vegetation, including wood, foliage, and litter. For aboveground vegetation, biomass at planting was assumed to be negligible and changes in storage were assumed equal to cation contents measured in 1993 to 1994. Changes in Ca and Mg contents of the total and exchangeable soil pools were calculated using Eq. [3] (Brimhall et al., 1992):

$$\delta_{j,w} = C_{j,w} \rho_w (\epsilon_{i,w} + 1) - C_{j,p} \rho_p \tag{3}$$

where $\delta_{j,w}$ is the absolute gain or loss of an element *j* per unit volume of the original fill material; $C_{j,w}$ and $C_{j,p}$ represent the concentration of *j* in a 1987 soil horizon and corresponding fill material layer; and ρ_w is the 1987 bulk density. Bulk density of the fill material (ρ_p) was 1.55 Mg m⁻³ for the two lysimeters. The strain, $\epsilon_{i,w}$, is further defined in Eq. [4] as

$$\epsilon_{i,w} = (C_{i,p} \rho_p / C_{i,w} \rho_w) - 1 \tag{4}$$

where $C_{i,w}$ and $C_{i,p}$ are concentrations of an immobile component *i* in the 1987 soil and original fill material. The medium plus coarse sand fraction (0.25–1.0 mm) was used as the immobile element (Ulery et al., 1995). Changes in Ca and Mg contents in the nonexchangeable soil pool were obtained by subtracting changes in the exchangeable pool from total soil changes.

A weather monitoring station has been in operation since 1933 at Tanbark Flats, about 200 m south of the lysimeter installation. Wet-only deposition to the lysimeters was calculated from this long-term record of annual rainfall and from cation concentrations in rain, measured by the National Atmospheric Deposition Program since 1982 (NADP, 1995). Between 1986 and 1989, total deposition was collected from a dust trap located ≈2 km west of the experimental site and consisting of a cake pan mounted 2 m aboveground and filled with glass marbles (Reheis and Kihl, 1995). Total elemental content of collected samples was used to estimate total atmospheric deposition to the lysimeters.

RESULTS AND DISCUSSION

Changes in Aboveground Biomass

Both chamise and ceanothus recovered rapidly following the 1960 fire. The rate of biomass accretion in aboveground vegetation (including wood and foliage) during the 1960 to 1969 period was 249 g m⁻² yr⁻¹ for chamise and 679 g m⁻² yr⁻¹ for ceanothus (Table 2), which was 1.7 to 3 times greater than the pre-fire accretion rates (i.e., the 1946–1958 period). As a result, wood and foliage biomass were greater in 1969 than in 1958 at the two lysimeters, despite the 1960 fire. Following 1969, the chamise biomass (including wood and foliage) continued to increase and reached a maximum of 7 × 10³ g m⁻² in 1993. Ceanothus biomass reached a maximum of 13.9 × 10³ g m⁻² in 1975.

Calcium and Mg storage in the woody tissues of the ceanothus stand exceeded that of chamise for all collection dates (Table 2). Except for the Mg content in the 1993-sampled vegetation, cation content in foliage was also greater for ceanothus. The litter pool did not show clear differences between the two vegetation types, but cation accumulation in total aboveground biomass (including wood, foliage, and litter) was typically higher for the ceanothus than for the chamise lysimeter (Table 2).

Differences in cation storage at the two lysimeters were partly due to differences in total biomass accumu-

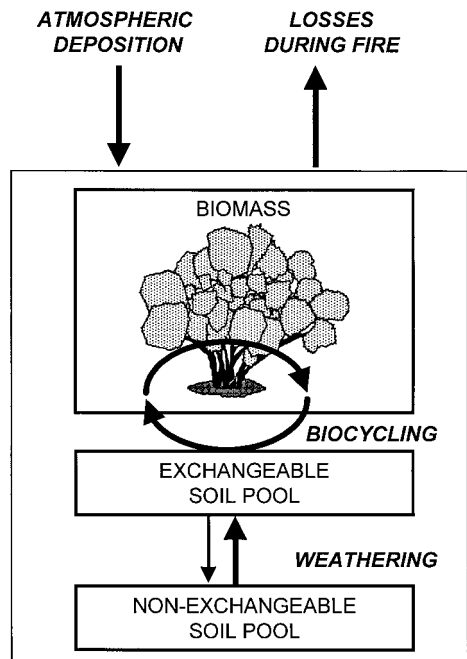


Fig. 1. Schematic representation of the Ca and Mg pools and fluxes estimated at the chamise and ceanothus lysimeters.

Table 2. Biomass, Ca, and Mg storage in chamise and ceanothus wood, foliage, and litter.

Year	Biomass				Ca				Mg			
	Wood	Foliage	Litter	Total	Wood	Foliage	Litter	Total	Wood	Foliage	Litter	Total
g m^{-2}												
Chamise												
1958	773	239	374 (45)†	1 386	6.5	4.6	8.1 (1.4)	19.2	0.4	0.7	1.0 (0.1)	2.1
1969	1 957	280	4279 (511)	6 516	7.6	3.5	58.2 (8.1)	69.3	1.1	0.7	16.5 (2.9)	18.3
1975	2 207	284	2269 (385)	4 760	8.2	2.8	35.3 (6.8)	46.3	1.1	0.5	8.6 (1.6)	10.2
1993–4	5 795	1204	1074 (121)	8 073	20.7	11.9	17.0 (2.6)	49.6	3.6	2.7	3.8 (0.8)	10.1
Ceanothus												
1958	3 882	870	3085 (384)	7 837	46.8	11.5	68.7 (11.6)	127.0	2.6	1.2	9.6 (1.5)	13.4
1969	4 477	1630	2819 (491)	8 926	25.6	20.1	41.3 (9.1)	87.0	3.5	4.1	9.3 (1.6)	16.9
1975	12 922	980	3012 (360)	16 914	46.6	11.6	51.2 (5.2)	109.4	4.0	1.7	11.6 (1.9)	17.3
1993–4	10 231	1200	1373 (352)	12 804	55.0	12.3	19.8 (4.8)	87.1	5.9	2.0	3.2 (0.7)	11.1

† Standard sampling errors for litter are indicated in parentheses ($n = 3-5$).

lation, which was 1.4 to 5.6 times greater for ceanothus than chamise, depending on the sampling date (Table 2). This was particularly true for Mg, which did not exhibit distinct differences in biomass concentration between the two lysimeters. In contrast, except for the 1958-sampled foliage, Ca concentrations in all sampled tissues and for all collection dates were higher for ceanothus than chamise. Differences in aboveground biomass composition measured at the lysimeter installation thus appear representative of chaparral ecosystems throughout California, with significantly higher Ca concentrations in ceanothus than chamise vegetation (Table 1). While belowground biomass was not analyzed at the lysimeter installation, it is also worth noting from Table 1 that Ca concentrations in root tissues paralleled those in stem and foliage in that they were typically higher for ceanothus than for chamise.

Changes in Soil Pools

The fill material of the lysimeters contained $1.67 \pm 0.08 \text{ g kg}^{-1}$ exchangeable Ca and $0.77 \pm 0.01 \text{ g kg}^{-1}$ exchangeable Mg (Table 3). The concentration of exchangeable Ca increased with time at the two lysimeters, except for a decrease from 1958 to 1960, indicating some convectonal losses as ash particles during the fire. Comparing the chamise and ceanothus lysimeters illustrates another effect of the 1960 fire. While levels of exchangeable Ca and Mg were higher for ceanothus than chamise in 1958, lower Ca and Mg levels were measured in this soil, compared with chamise following the fire. It is not until 1987 that Ca and Mg concentrations of the ceanothus soil again exceeded those of chamise (Table 3).

As discussed by Brimhall et al. (1992), determination of strain allows for compensation of soil volumetric changes during pedogenesis. Faunal activity and incorporation of low-density organic matter at the soil surface decreased the bulk density of the original fill material and resulted in positive strain values in the A1 horizons

sampled in 1987 (Table 4). In contrast, soil compacting and settling with time yielded negative strain values below the surface horizons of the chamise and ceanothus soils.

Mean total concentrations in the original fill material were $19.8 \pm 0.4 \text{ g kg}^{-1}$ Ca and $12.2 \pm 0.2 \text{ g kg}^{-1}$ Mg (Table 4). Nonexchangeable Ca and Mg constituted 91.6 and 93.7% of the total soil pools. Integrated over the 65-cm depth profile, the $\delta_{j,w}$ values for nonexchangeable Ca and Mg were negative under both chamise and ceanothus, indicating cation release by weathering. Mineralogy of the lysimeter soils consists of a biotite-vermiculite-kaolinite clay fraction among coarser quartz, feldspar (mostly plagioclase), and mica grains (Tice et al., 1996). Calcium may be released by weathering of the plagioclase, and weathering of biotite is the probable source of Mg. Calcium release by weathering was slightly greater under ceanothus than under chamise, but the opposite was true for Mg (Table 4).

The concentration of exchangeable Ca under chamise and ceanothus increased by $\geq 1 \text{ g kg}^{-1}$ in the 1987-sampled A horizons relative to the fill material. Under ceanothus, exchangeable Ca was higher than in the corresponding parent material samples in most of the soil profile, and increased by 263.4 g m^{-2} over the 65-cm depth profile (Table 4). In contrast, the soil under chamise exhibited a decrease in exchangeable Ca below the 35-cm depth, resulting in a smaller gain of Ca (15.1 g

Table 3. Exchangeable Ca and Mg concentrations in chamise and ceanothus soils (0–2.5 cm).

Date	Chamise		Ceanothus	
	Ca	Mg	Ca	Mg
g kg^{-1}				
1937	1.67 (0.08)†	0.77 (0.01)	1.67 (0.08)	0.77 (0.01)
1958	1.72 (0.04)	0.73 (0.01)	1.78 (0.03)	0.74 (0.02)
1960	1.70 (0.34)	0.62 (0.12)	1.39 (0.29)	0.48 (0.10)
1975	1.82 (0.07)	0.79 (0.04)	1.71 (0.05)	0.61 (0.04)
1987	2.47 (0.18)	0.63 (0.03)	3.20 (0.39)	0.70 (0.09)

† Standard sampling errors are indicated in parentheses ($n = 3-5$).

Table 4. Bulk densities (ρ_w), strain ($\epsilon_{i,w}$), total Ca and Mg concentrations (g kg^{-1}) in 1987 soil horizons (w) and corresponding fill materials (p), and changes in non-exchangeable (δ_{nex}) and exchangeable (δ_{ex}) Ca and Mg, corrected for soil volume and density changes.

Horizon	Depth	ρ_w	$\epsilon_{i,w}$	Ca_p	Ca_w	Mg_p	Mg_w	$\delta\text{Ca}_{\text{nex}}$	$\delta\text{Mg}_{\text{nex}}$	$\delta\text{Ca}_{\text{ex}}$	$\delta\text{Mg}_{\text{ex}}$
	cm	Mg m^{-3}		g kg^{-1}				g m^{-2}			
Chamise											
A1	0–1	1.38	0.01	19.7	20.1 (0.3) [†]	12.0	10.7 (0.2)	–38.9	–38.9	10.5	–0.2
A2	1–7	1.65	–0.06	20.2	19.6 (0.1)	12.2	11.5 (0.2)	–101.4	–82.7	23.9	5.3
AC	7–20	1.79	–0.08	19.7	19.6 (0.2)	12.0	11.6 (0.1)	131.6	–1.3	67.5	39.3
C1	20–35	1.69	–0.12	20.0	19.2 (0.3)	12.4	12.0 (0.2)	–394.8	–227.0	–27.0	1.3
C2	35–50	1.71	–0.11	19.8	19.0	12.1	11.2	–294.0	–295.2	–29.0	–1.3
C3	50–65	1.73	–0.10	19.9	19.8	12.2	11.9	–21.6	–93.3	–30.8	–4.1
Total	0–65							–719.1	–738.4	15.1	40.3
Ceanothus											
A1	0–2	0.92	0.57	20.4	20.3 (0.6)	12.4	10.2 (0.2)	–97.9	–96.6	38.1	–2.3
A2	2–10	1.67	–0.05	20.0	19.8 (0.2)	12.4	12.0 (0.1)	–65.1	–57.8	56.3	6.5
AC	10–20	1.67	–0.22	19.9	19.4 (0.2)	12.4	12.0 (0.2)	–571.2	–374.5	–13.2	–6.4
C1	20–35	1.72	–0.07	20.0	18.5 (0.5)	11.8	11.4 (0.2)	–355.0	–67.5	35.9	12.3
C2	35–50	1.66	–0.01	18.7	19.6	12.1	11.9	316.0	51.0	60.7	2.1
C3	50–65	1.61	0.04	19.9	18.9	12.2	11.8	–82.8	50.8	85.6	–9.0
Total	0–65							–856.0	–494.6	263.4	3.2

[†] Standard sampling errors for Ca_w and Mg_w are in parentheses ($n = 3$).

m^{-2}) over the 65-cm depth profile (Table 4). The increase in exchangeable Mg was greater under chamise than under ceanothus.

Atmospheric Deposition

Wet deposition to the lysimeter existence was calculated to be 3.9 g m^{-2} for Ca and 1.7 g m^{-2} for Mg over the course of the lysimeter installation (Quideau et al., 1996). Estimated dry deposition was 63.3 g m^{-2} for Ca and 5.5 g m^{-2} for Mg, and composed the major part of total deposition for the two cations (Fig. 2). The prevalence of dry deposition at the San Dimas Experimental Forest is due to the Santa Ana winds that carry considerable amounts of dust from sources to the north and east, namely the Mojave Desert (Reheis and Kihl, 1995). It is worth noting, however, that inputs to the lysimeters by atmospheric deposition were 10 to 100 times smaller than the amount of cations released by weathering (Fig. 2).

The 1960 Fire

Changes in Ca and Mg storage (g m^{-2}) at the chamise and ceanothus lysimeters due to the 1960 fire were estimated by subtracting cation contents in the wood, foliage, litter, and soil (0–2.5 cm) exchangeable pools as determined in 1958 from cation contents in the ash and soil sampled a week after the fire (Table 5). The ceanothus stand measured in 1958 (including wood, foliage, and litter) had accumulated about 6.5 times more Ca and Mg than the chamise stand, and Ca and Mg contents in the ash layer were greater for ceanothus than chamise. However, cation recovery by ashfall at the ceanothus lysimeter was <40% of the original storage in vegetation and was lower than at the chamise lysimeter (>55%

recovery). Furthermore, Ca and Mg losses from the exchangeable soil pool (0- to 2.5-cm layer) under ceanothus represented 22 to 35% of the pre-fire storage, and exceeded that under chamise (1–14% of original storage). It is likely that the greater fuel load present at the ceanothus lysimeter resulted in increased fire intensity and greater particulate losses in heat plumes, compared with conditions at the chamise lysimeter.

Atmosphere–Plant–Soil Systems

Cation levels on the exchangeable pool of soils reflect the cumulative balance of many intra-system (e.g., weathering, plant uptake, litterfall) and inter-system (e.g., atmospheric deposition, leaching) fluxes (Fig. 2). The increase in exchangeable Ca and Mg measured in the lysimeter soils indicated that inputs through atmospheric deposition, weathering, and nutrient return from the plant to the mineral soil by throughfall leaching, litter decomposition, and root turnover exceeded outputs by leaching and root uptake. Except for Ca for the chamise lysimeter, cation inputs by atmospheric deposition were not sufficient to account for cation accumulation in aboveground biomass and the exchangeable soil pools. This is especially true since not all cations in dry deposition are in the exchangeable form, nor are they readily available for plant uptake. The water-soluble component of dry deposition was estimated from a dry-only deposition study conducted at Tanbark Flats between 1982 and 1985 (NADP, 1995). Concentrations of dissolved Ca and Mg were measured after dust samples were left to equilibrate with distilled water for 24 h; water-soluble Ca and Mg represented on average 15 and 35%, respectively, of total dry deposition, excluding samples that contained extraneous debris such as insects

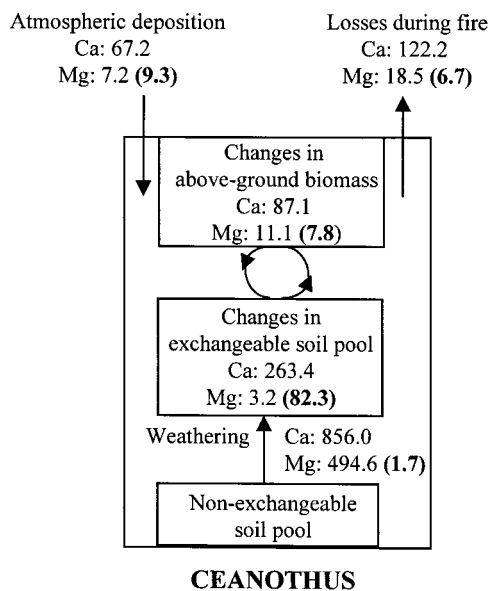
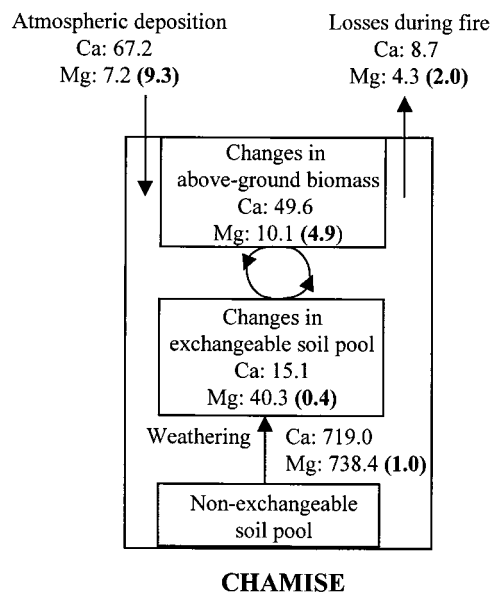


Fig. 2. Calcium and Mg fluxes (g m^{-2}) for the chamise and ceanothus since construction of the lysimeter installation. Calcium/Mg ratios of fluxes are indicated in parentheses. Values for soil pools are for the 0- to 65-cm depth intervals.

or plant parts. While an estimate of exchangeable Ca and Mg in dry deposition was not available, it is reasonable to assume that part of the deposited dust remained in the nonexchangeable form. This fraction would have been incorporated in calculations of changes in the non-exchangeable soil pools (Table 4 and Fig. 2), resulting in underestimations of the weathering fluxes and of the differences between weathering and atmospheric deposition.

Release by weathering was by far the largest of the cation fluxes at the chamise and ceanothus lysimeters, and the magnitude of the weathering fluxes designates the nonexchangeable soil pool as a likely source for the increase in the exchangeable soil pool (Fig. 2). It should

Table 5. Calcium and Mg storage at the chamise and ceanothus lysimeters before and after the 1960 fire.

	Chamise		Ceanothus	
	Ca	Mg	Ca	Mg
	g m^{-2}			
Pre-fire biomass	19.2	2.1	127.0	13.4
Pre-fire soil (0–2.5 cm)†	63.8	27.3	67.4	28.0
Total pre-fire	83.0	29.4	194.4	41.4
Post-fire soil (0–2.5 cm)†	63.3	23.1	52.5	18.1
Ash	11.0	2.0	19.8	4.8
Total post-fire	74.3	25.1	72.3	22.9
Changes in cation storage‡	-8.7	-4.3	-122.1	-18.5

† Exchangeable Ca and Mg as extracted by 1 M NH_4OAc .

‡ Calculated by subtracting cation storage at the lysimeters prior to the fire (total pre-fire) from cation storage after the fire (total post-fire).

be pointed out that the lysimeter installation depicts the initial stages of soil formation following the establishment of a vegetative cover. It may not be a realistic analog for ecosystems that have been allowed to develop for long periods of time on stable landscapes. Weathering rates under chamise and ceanothus were similar to those at the oak and pine lysimeters (Quideau et al., 1996), but 2 to 300 times greater than those reported from other field studies (Clayton, 1979; Clayton and Megahan, 1986; Likens and Bormann, 1995). Mixing the fill material during construction of the lysimeters probably exposed fresh mineral surfaces to the action of weathering agents; and weathering rates are expected to decrease in the future as these mineral surfaces become progressively coated with organic substances and secondary minerals.

Vegetation Influence on Cation Fluxes

Calcium storage was greater for ceanothus than chamise in both the aboveground biomass and the exchangeable soil pool (Fig. 2). These data suggest that Ca biocycling (i.e., root uptake at depth with subsequent return to or near the mineral soil surface by litterfall, fine root turnover, and throughfall leaching) may be greater for the ceanothus plant-soil system than for the chamise. The importance of biocycling in regulating cation release by weathering has been discussed for the oak and pine lysimeters (Quideau et al., 1996). Mineralogical differences have also been measured for the soils under oak and pine vegetation, and were related to differences in K biocycling (Tice et al., 1996). For the chamise and ceanothus lysimeters, however, analysis was complicated by a different response for Ca and Mg. Magnesium content was slightly higher in ceanothus biomass than in chamise, but the reverse was true for exchangeable Mg (Fig. 2). Furthermore, Ca release by weathering was greater under ceanothus, but Mg release was greater under chamise. Taken together, these data indicate that rather than their absolute concentrations, the relative abundance of Ca and Mg in the biomass may be the controlling factor regulating cation biogeochemistry at the chamise and ceanothus lysimeters. To further investigate this hypothesis, we used the Ca/Mg ratio as an index of vegetation influence on biogeochemical fluxes (Fig. 2).

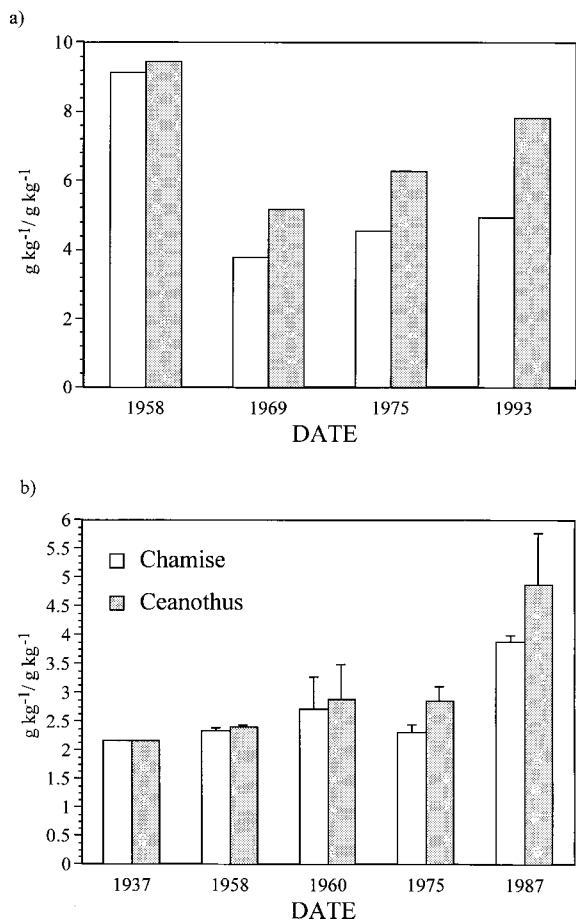


Fig. 3. Changes with time in Ca/Mg ratios ($\text{g kg}^{-1}/\text{g kg}^{-1}$) at the chamise and ceanothus lysimeters: (a) aboveground biomass (includes wood, foliage, and litter), and (b) exchangeable soil pool (0–2.5 cm). For the soil pool, error bars represent one standard error from the mean ($n = 3\text{--}5$) and are an estimate of the sampling error.

Calculating the Ca/Mg ratios (on a g kg^{-1} basis) in aboveground biomass (including the wood, foliage, and litter pools) allowed comparison of the relative abundance of these two cations in chamise and ceanothus vegetation (Fig. 3a). Ceanothus aboveground biomass (including the wood, foliage, and litter pools) showed a higher Ca/Mg ratio than chamise at all dates, and the difference between plant species increased with time. In 1993, the Ca/Mg ratio in the ceanothus aboveground pool was more than 50% higher than in the chamise. Except for foliage and root tissues collected at the Descanso site, results from other Californian sites also display higher Ca/Mg ratios in ceanothus biomass than chamise (Fig. 4).

The exchangeable pool of the homogenized fill material (1937) at the chamise and ceanothus lysimeters exhibited a Ca/Mg ratio of 2.17 (Fig. 3b). This ratio tended to increase with time under the two vegetation types (0–2.5 cm soil depth). A maximum value of 3.9 to 4.9, depending on the plant species, was reached in 1987. As early as 1958, the soil under ceanothus contained slightly more exchangeable Ca than Mg, relative to the soil under chamise, i.e., the Ca/Mg ratio was higher for ceanothus. Differences in Ca/Mg ratios between the two plant species increased with time. In the 1975 and 1987

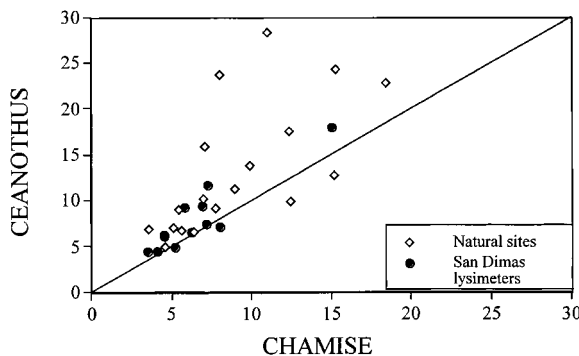


Fig. 4. Calcium/Mg ratios in ceanothus biomass plotted against Ca/Mg ratios in chamise growing at the same sites. Ratios were calculated from concentration values as presented in Tables 1 (natural soils) and 2 (San Dimas lysimeter soils). Points above the solid line (1:1) represent higher Ca/Mg ratios for ceanothus than for chamise.

soil samples, the exchangeable Ca/Mg ratio under ceanothus was roughly 20% higher than under chamise. When compared with changes in Ca and Mg storage in aboveground biomass (Fig. 3a), these data strongly suggest that biocycling is playing a controlling role in regulating Ca/Mg ratios on the exchangeable soil pools under chamise and ceanothus vegetation.

Proportionally, more nonexchangeable Ca than nonexchangeable Mg was released under ceanothus than under chamise, as illustrated by a higher Ca/Mg ratio of the weathering flux under ceanothus (Fig. 2). Numerous laboratory and greenhouse experiments have allowed identification of the mechanisms responsible for weathering regulation by plant communities: (i) enhancement of mineral dissolution by organic acids and chelates produced by the vegetation and associated microbes (e.g., Tan, 1986), and (ii) regulation of cation concentrations in the soil solution by plant uptake (e.g., Hinsinger et al., 1992). Although it is not possible at the lysimeter installation to pinpoint the mechanisms responsible for the plant-induced differences in weathering rates, it is important to recognize the importance of these differences. They may have contributed to the differences in exchangeable Ca and Mg in two ways: (i) as a direct source of cations for the exchangeable soil pool, and (ii) as a source for plant uptake, with subsequent biocycling to the mineral soil.

Input by atmospheric deposition exhibited a high Ca/Mg ratio and may be responsible for part of the Ca/Mg increase with time, observed in the exchangeable soil pool (Fig. 2). However, atmospheric deposition fluxes were too small to account for the entirety of exchangeable cation accretion. Also, estimated cation losses during the 1960 fire implied a greater loss of Ca than Mg from the ceanothus lysimeter, compared with the chamise (Table 5), which ruled out fire as a possible contributor to the differences between the ceanothus and chamise soils. Subsequent dissolution of the ash layers may provide a source of Ca and Mg for the exchangeable soil pools. The soil pH measured at the lysimeter installation immediately after the fire in 1960 was 6.6 (± 0.1) for the 0- to 2.5-cm soil depth (P. Zinke, personal communication, 1996). Elevated pH levels of ash materials and associated soils are attributable to oxides, hydroxides, and carbonates that form during, or soon after, plant

combustion; these compounds are typically very soluble and do not persist in soils after the wet season (Ulery et al., 1993). In our study, the soil pH had returned to pre-fire levels by 1969 (pH = 6.0 ± 0.1). Elemental composition of the ash layer present at the chamise lysimeter was enriched in Ca, compared with the ceanothus lysimeter (Table 5). Specifically, the Ca/Mg ratio of the ash layer was 5.5 for the chamise and 4.1 for the ceanothus lysimeter. Dissolution of the ash materials at the chamise lysimeter thus would have released proportionally more Ca than Mg as a potential source for the exchangeable soil pool, compared with the ceanothus lysimeter. Taken together, results indicate that intra-system fluxes (weathering and biocycling) were more important than inter-system fluxes (atmospheric deposition and losses due to fire) in controlling composition of the exchangeable soil pool.

CONCLUSIONS

The fire-induced chronosequence at the San Dimas lysimeter installation allowed quantification of changes in the chamise and ceanothus plant-soil systems as a function of time. Both chamise and ceanothus recovered rapidly following the fire, and exchangeable soil pools showed a net gain over the course of the lysimeter history. Results from the cation balances identified weathering as the largest flux at the chamise and ceanothus lysimeters. In contrast to cation inputs from atmospheric deposition, cation release by weathering exceeded accumulation in the aboveground biomass and exchangeable soil pools.

Comparing the chamise and ceanothus lysimeters was best achieved by using the Ca/Mg ratio of the different cation pools and fluxes as an index. The ceanothus exchangeable soil pool contained proportionally more Ca than Mg, compared with the chamise soil; that is, the Ca/Mg ratio in the ceanothus exchangeable soil pool was higher than that in chamise. Furthermore, differences between the chamise and ceanothus exchangeable soil pools increased with time. Strong evidence supported biocycling as the basis for these differences. The ceanothus aboveground biomass exhibited a higher Ca/Mg ratio than the chamise, and the difference between plant species increased with time. Also, a greater amount of Ca than Mg was released by weathering under ceanothus than chamise. In contrast, atmospheric deposition inputs and cation fluxes due to the 1960 fire could not account for the observed differences between lysimeters.

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Horizons and Humus Forms in Beech Forests of the Belgian Ardennes

Jean-François Ponge*

ABSTRACT

Forest soil organic horizons are named on the basis of visual observations made directly in the field, thus this is often subjective. To find more objective bases for their classification, humus form horizons in 13 beech stands (*Fagus sylvatica* Ehrh.) were compared. Test sites were located in the Belgian Ardennes (western Europe), which encompasses a wide range of ecological conditions. I used a semi-quantitative micromorphological method for the description of horizons, and a multivariate method for data analysis. These methods helped to discern objective discontinuities among Oi, Oe, and Oa horizons, adding new criteria for their characterization, such as the root system of trees. Within these horizons, transitions between sub-horizons are gradual and thus do not lie on clear-cut criteria. The transition between Oa and A horizons was also gradual. The composition of Oa and A horizons varies according to humus form. The vertical distribution of soil organisms and their vertical movements were considered the origin of discontinuous and continuous processes taking part in the transition from one horizon to another. The observation of horizons under a dissecting microscope may help to find more reliable bases for their nomenclature, even without the use of costly soil sections.

SINCE THE PIONEERING WORK of Müller (1889), who described two basic humus forms, mull and torf, beneath Danish beech forests, on the basis of microscopic observations, there have been many attempts to classify humus profiles in forest soils. Different horizons or sub-horizons are generally recognized within the O (Brady, 1984) or Ao (Duchaufour, 1997) horizons. Although discrepancies concerning the terminology of these strata exist, three main strata are recognized, Oi (entire leaves), Oe (fragmented leaves), and Oa (holorganic fecal pellets). Differences in the development of these horizons, together with structure and chemical properties of the underlying A horizon, allow recognition of three main humus forms, now called mull, moder, and mor (Klinka et al., 1981; Delecour, 1983; Green et al., 1993; Brêthes et al., 1995; Jabiol et al., 1994, 1995).

The mor humus form, together with dysmoder (moder with a thick H stratum), has been also called raw humus (Kubišna, 1953; Delecour, 1980). The recognition of biological processes taking place in the development of humus profiles (Hartmann, 1965; Zachariae, 1965; Bal, 1982) suggested that some features, such as compaction of the soil matrix, deposition of fecal pellets, skeletonization of leaves or tunneling of needles, are the direct result of soil faunal activity. Thus, as for most biological processes, the transition from one horizon to another should be considered discontinuous because of tolerance limits and food and habitat preferences of soil organisms.

Characterization of organic horizons and humus forms on the basis of morphological features is common; however, the existence of clear-cut changes between one horizon and another has been poorly demonstrated through quantitative or semi-quantitative morphological data. Federer (1982) pointed out that simple remeasurements of thickness of forest soil horizons may lead to false conclusions if done by two individuals. Discrepancies between field and laboratory observable features of horizons have been reported (Bernier et al., 1993). This may indicate that some morphological criteria used for the definition of organic horizons are inadequate or difficult to employ with accuracy in the field. This is particularly true for the transition from Oa to A horizons and for subdivisions which have been recognized within Oi and Oe horizons (Babel, 1971).

In the present study, my purpose was to determine whether the transition from one organic horizon to another is a continuous or, rather, a step-by-step process, with sharp delineations in horizon properties. In doing so, I addressed the question as to whether horizons exhibit true emergent properties and have not been created by soil scientists for classification purposes only.

MATERIAL AND METHODS

Nomenclature

Comparable organic horizons have several different names depending on the taxonomic system in use. The commonly

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