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Base cation biogeochemistry and weathering under oak and pine: a controlled long-term experiment

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Abstract. Large earthen-walled lysimeters at the San Dimas Experimental Forest in southern California present a unique opportunity to assess vegetation effects on biogeochemical processes and cation release by weathering in controlled soil-vegetation systems where archived samples of soil parent material are available for comparison. The lysimeters were filled in 1937 with homogenized fine sandy loam derived on site from the weathering of diorite, and planted in 1946 with scrub oak (*Quercus dumosa*) and Coulter pine (*Pinus coulteri*). Changes in base cation contents were measured in above-ground biomass, and total and exchangeable soil pools to a depth of 1 meter. All cations in the non-exchangeable soil pool decreased relative to the initial fill material, indicating release by weathering. Sodium and K were depleted from both exchangeable and non-exchangeable pools of the soils. Plant uptake of Na was minimal, whereas K storage in vegetation exceeded the loss from the exchangeable soil pool. In both soil-vegetation systems, but especially for oak, there was an increase in exchangeable Ca and Mg. For all base cations, storage in above-ground biomass was greater for oak, whereas losses by weathering from the non-exchangeable soil pool were greater under pine. Strong evidence supports biocycling as a controlling mechanism resulting in greater Ca and Mg release by weathering under pine. In addition, decreases in non-exchangeable Ca and Mg were strongly correlated to decrease in Si under oak, whereas no correlation was observed under pine. We conclude that weathering reactions or stoichiometry differed between vegetation types.

Introduction

There are many reasons to quantify base cation biogeochemistry in terrestrial systems. Because base cations are important plant nutrients, early research focused on the effects of intensive harvesting on cation balances and site productivity (Likens et al. 1970; Alban et al. 1978). Base cations act to neutralize natural and anthropogenic acidification, and recent environmental research focused on the buffering capacity of exchangeable and primary mineral base cations (Van Breemen et al. 1983; Drever & Hurcomb 1986; Johnson & Lindberg 1992; Laudelout & Robert 1994). Base cations, especially Ca, also play an integral role in the long-term carbonate-silicate geochemical cycle, which in turn affects Earth's atmospheric CO_2 level and climate (Berner 1990;

Chadwick et al. 1994). The increase in rates of mineral weathering associated with the advent of vascular land plants in the Silurian is hypothesized to have caused a decrease in atmospheric CO_2 and, hence, global cooling (Knoll & James 1987; Schwartzman & Volk 1989).

As interest in weathering and base cation fluxes becomes more oriented toward earth-system modeling, scientists rely on measurements reported previously in the literature. These data are not always appropriate for use in the modeling exercise. Weathering rates in the field are estimated most often using watershed mass-balances (Clayton 1979), based on the difference between streamwater outputs and atmospheric inputs. No significant change in ecosystem cation pools is sometimes assumed (Johnson et al. 1968; Marchand 1971; Giovanoli et al. 1988), but most researchers recognize the need to account for biological uptake or release of cations (Cleaves et al. 1970; Likens et al. 1977; Taylor & Velbel 1991). However, changes in the soil exchangeable pool are rarely documented (Clayton 1988). Furthermore, specific effects of vegetation on weathering rates have been difficult to assess because soil properties and vegetation commonly covary in response to other environmental factors; i.e., climate, topography, parent material, and time (Jenny 1941; Yaalon 1975). Lack of a full understanding of landscape and biotic history limits the way in which many watershed datasets (e.g. Likens et al. 1977) can be used for extracting information about the weathering effects of different plant communities. Some of the questions being asked by earth-system modelers, such as whether the rise of angiosperms enhanced weathering relative to that under the existing gymnosperms (Knoll & James 1987; Volk 1989), require a better understanding of these effects.

A 47-year-old biosequence of native woody species at the San Dimas Experimental Forest in southern California provided a unique opportunity to assess vegetation effects on base cation biogeochemistry and release by weathering. Five large (5.3 by 5.3 m horizontally 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*), chamise (*Adenostoma fasciculatum*), ceanothus (*Ceanothus crassifolius*), scrub oak (*Quercus dumosa*), and Coulter pine (*Pinus coulteri*). The biosequence minimizes variation of all environmental factors except vegetation (Patric 1961a), in a setting that is less artificial than in greenhouse or laboratory experiments. In addition, every 7.5 cm fill layer was sampled and archived during the lysimeter construction. Therefore, changes in the soil exchangeable and non-exchangeable pools could be accurately measured as deviations from true parent materials.

Previous studies of the San Dimas lysimeter soils have addressed soil morphology and clay distribution (Graham & Wood 1991), soil aggregate stability (Graham et al. 1995), and 2:1 phyllosilicate mineralogy (Tice et al. 1996). Changes in soil C, N, and exchangeable cations have been determined using a mass-balance approach (Ulery et al. 1995). Our objective in this study was to quantify and contrast the influence of the oak and pine vegetation on biogeochemical processes and cation release by weathering, by incorporating above-ground biomass, changes in the non-exchangeable soil pool, and atmospheric inputs to the mass-balance analysis.

Experimental area

The study site is located at an elevation of 830 m in the San Gabriel Mountains of southern California. Native vegetation of the surrounding area is composed of chamise chaparral dominated by *Adenostoma fasciculatum*, and of mixed chaparral, including *Ceanothus* spp., *Arctostaphylos* spp., *Quercus dumosa*, and *Cercocarpus betuloides* (Mooney & Parsons 1973). The Mediterranean climate has warm, dry summers and mild, wet winters. The mean annual temperature is 14.3 °C, with August and January means of 22.2 and 8.0 °C, respectively. The mean annual precipitation is 670 mm (Dunn et al. 1988).

The lysimeters were filled in 1937 with homogenized fine sandy loam derived on site from the weathering of diorite. The excavated material from the lysimeter site was mixed and passed through a 19-mm-mesh screen to minimize textural variation. Analysis at the time showed no statistical textural difference in 100 randomly collected samples (Colman & Hamilton 1947). During the filling, each successive 7.5 cm layer was chopped thoroughly with a flat-bladed spade to minimize boundary effects with the underlying layer. The lysimeters were originally overfilled by 30 cm to allow for soil settling (Patric 1961a). The soil surfaces were maintained free of vegetation but covered with aspenwood excelsior to prevent soil erosion. In 1940, all overfill above the design surface level was removed, a 5% slope to the south was imposed on the surface, and an annual grass (*Bromus mollis*) was planted. The grass and litter cover was burned in 1945 in preparation for the final planting to woody species.

A single planting of each species was done on a 17 by 24 m area including an unconfined lysimeter and surrounding buffer strips to eliminate edge effects (Colman & Hamilton 1947). Coulter pine was established with 1-year-old bare root stock (Patric 1961b). Based on incomplete records, it is uncertain whether seeds or 1-year-old seedlings were used in the case of scrub oak. The two species were originally planted with one foot spacings, then drastically thinned in 1947 and 1948. The monocultures were maintained by periodic weeding and by 1955, the two lysimeters supported pure stands and had complete litter covers (Patric 1961a,b). Except for some grass cover and a few shrubs under the pine, these stands have remained as virtual monocultures since then. In 1994, the oak stand had a stocking of 30,000 shrubs ha^{-1}, a mean height of 6.7 m, and a mean basal area (measured at 10 cm aboveground) of 27 cm^2 $shrub^{-1}$. Stocking of the pine stand was 2000 trees ha^{-1}. Mean tree height was 15.1 m and diameter at breast height was 24.1 cm (Milone 1994).

Methods

Above-ground biomass

Above-ground biomass was determined in summer 1993 as reported by Milone (1994). In order to keep destructive sampling within the lysimeters to a minimum, harvesting was restricted to two oak shrubs and two pine trees growing in the buffer strips surrounding the lysimeters. Each individual stem of the two harvested oak shrubs was weighed green in the field to calculate the total weight of each shrub. The stems of the two felled pine trees were sectioned into 2 m bolts. All limbs on each bolt were removed and weighed green. The green weight of each bolt was calculated from its volume and the specific density of a sampled disc. Total weight of each tree was then estimated by summing the green weight of branches and stem bolts. Randomly selected oak stems, pine branches and discs were transported to the laboratory for separation and drying.

Total biomass of each oak shrub located within the lysimeter perimeter was estimated using an equation developed by Riggan et al. (1988) for a 21-year-old *Q. dumosa* stand located within the San Dimas Experimental Forest. A similar relationship was developed for the lysimeter pines based on the two harvested trees (Milone 1994). Biomass of all individual plants within a lysimeter was summed and data were extrapolated to a hectare basis. Litter biomass was determined in December 1994 from cores of known volume taken in triplicate at each of the two lysimeters, i.e., the entire O horizon to the top of the mineral soil was sampled. All litter samples were brought back to the laboratory for drying and weighing.

In the laboratory, oak stems were separated into deadwood, live stems, live branches, and foliage. For the pine, samples were separated into bole wood, dead branches, live branches, and foliage. Each fraction was weighed and dried to constant weight at 70 °C to determine moisture content. Wood, foliage, and litter subsamples were then ground in a Wiley mill, and analyzed for base cations by perchloric acid digestion and atomic absorption spectroscopy.

Soils

The soils were initially sampled in 1937 by taking composite samples of each 7.5 cm incremental layer upon filling of the pits. Bulk density of the homogeneous fill material was calculated from the mass of soil added to the pits (Patric 1961a). In May 1987, three pedons on each vegetation plot were described and sampled by morphologic horizon as reported by Graham & Wood (1991). The lysimeter soils occupy small areas and are irreplaceable research resources. To keep destructive sampling to a minimum, a single pedon in each lysimeter was sampled to a depth of 1 m, while the other two were sampled to the 35 cm depth. Bulk density of the 1987 soil samples was determined on saran-coated clods, or using cores in the case of fragile surface horizons. All 1987 soil samples and corresponding original fill materials (<2 mm fraction) were analyzed for total elemental composition by fusing 0.2 g of soil with 1.2 g of $LiBO_2$, followed by dissolution in 100 ml of 5% HNO_3. Concentrations of cations in the solutions were measured by ICP. Twenty percent of all samples were analyzed in duplicate to assess the reproducibility of the analytical method. Mean variability (as % of average concentration) was 1.9 for Ca, 2.5 for Mg, 2.1 for K, 1.2 for Na, and 0.5 for Si. Exchangeable base cations of the 1987 and original fill materials were extracted using 1*M* NH_4OAc at pH 7 (Ulery et al. 1995).

Cation balance calculations

Changes in cation storage. Total changes in cation storage within each soil-vegetation system can be expressed as the sum of changes within four basic cation compartments: (1) above-ground biomass, (2) below-ground biomass, i.e., roots in the mineral soil, (3) soil exchangeable, and (4) soil non-exchangeable (Figure 1):

$$[1] \quad \Delta_{\text{system}} = \Delta_{\text{above-ground biomass}} + \Delta_{\text{below-ground biomass}} + \Delta_{\text{soil exchangeable}} + \Delta_{\text{soil non-exchangeable}}$$

where $\Delta_{\text{above-ground biomass}}$ was further defined as:

$$[2] \quad \Delta_{\text{above-ground biomass}} = \Delta_{\text{wood+foliage}} + \Delta_{\text{litter}}$$

$\Delta_{\text{below-ground biomass}}$ was not measured in this study. Cation contents in vegetation at planting were assumed negligible relative to the cation contents in the 47-year-old plants, and $\Delta_{\text{wood+foliage}}$ was calculated as the sum of the wood and foliage cation pools as determined in 1993. Δ_{litter} was similarly determined from the cation litter pools measured in 1994. $\Delta_{\text{soil exchangeable}}$ has been calculated by Ulery et al. (1995). $\Delta_{\text{soil non-exchangeable}}$ was assumed equal to cation release by weathering (Figure 1) and was obtained by subtracting

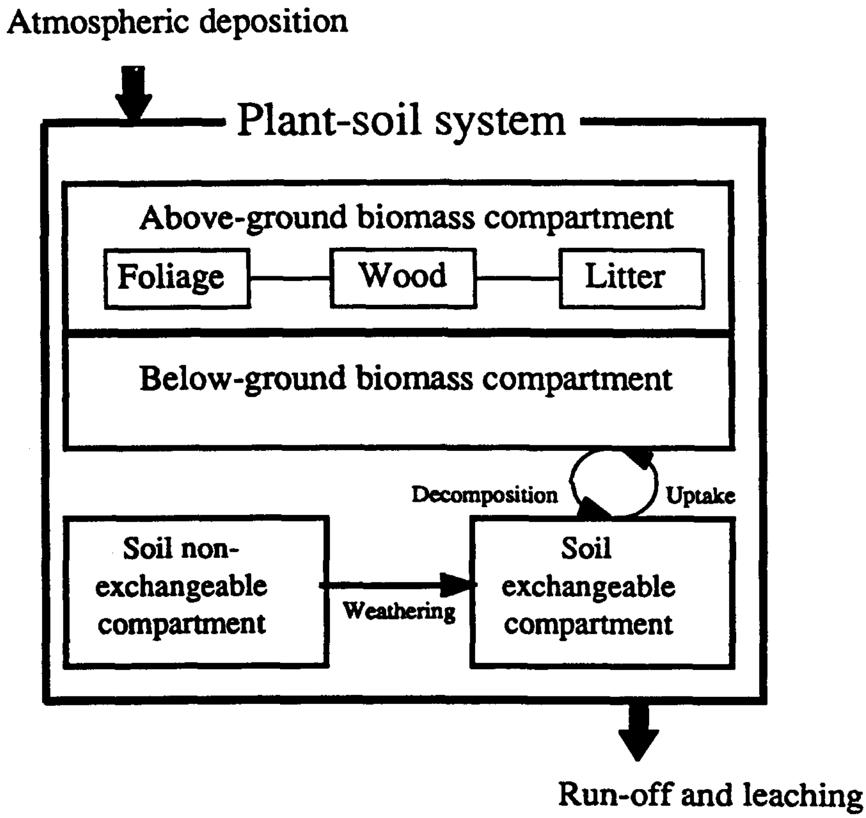

Figure 1. Schematic representation of cation fluxes at the oak and pine lysimeters.

changes in the exchangeable pool from total soil changes. Total soil changes were calculated using the following equation (Brimhall et al. 1992):

$$[3] \qquad \delta_{j,w} = C_{j,w}\,\rho_w\,(\varepsilon_{i,w} + 1) - C_{j,p}\,\rho_p$$

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 (Table 1). Bulk density of the homogeneous fill material (ρ_p) was 1.57 Mg m^{-3} for the two lysimeters. The strain, $\varepsilon_{i,w}$, allows for compensation of soil volumetric change with time and is defined as:

$$[4] \qquad \varepsilon_{i,w} = (\rho_p\,C_{i,p} / \rho_w\,C_{i,w}) - 1$$

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 to 1.0 mm) was used as the immobile component, i, to calculate strain for each 1987 soil horizon, as reported by Ulery et al. (1995). The calculated $\delta_{j,w}$ values were summed to a depth of 1 m.

To determine annual rates of cation change, we divided total changes in biomass and soil pools by appropriate time intervals: for biomass, the time between planting and harvesting (47 years for $\Delta_{\text{wood+foliage}}$ and 48 years for Δ_{litter}); for soil, the time between initial and final samplings (50 years).

Input and output fluxes. While cation outputs by leaching and run-off were not measured in this study, they can be related to total changes in cation contents within the systems (Δ_{system} as defined in equations [1] and [2]) and cation inputs by atmospheric deposition as follows:

$$[5] \qquad \text{Leaching} + \text{Run-off} = \text{Atmospheric deposition} - \Delta_{\text{system}}$$

Atmospheric deposition at the lysimeters was calculated as the sum of wet-only and dry deposition. A weather monitoring station has been in operation since 1933 at Tanbark Flats, located about 200 m south of the experimental area. This provided us with annual rainfall data from the time of the lysimeter construction until present. In 1982, Tanbark Flats became one of the long-term atmospheric monitoring stations operated by the National Atmospheric Deposition Program/ National Trends Network (NADP/ NTN). Wet-only deposition has been collected on a weekly basis since that time, and analyzed for base cation concentrations (National Atmospheric Deposition Program 1995). Thus, wet-only deposition was estimated from the rainfall record for the 1936–1994 period and mean cation concentrations of the rain for the 1982–1994 period.

Between 1986 and 1989, total atmospheric deposition was collected annually from a dust trap located at an elevation of 933 m near Glendora Ridge road, about 2 km west of the lysimeter installation, and samples were analyzed for total elemental content (Reheis & Kihl 1995). The trap consisted of an angel-food cake pan mounted on a steel fence post 2 m above-ground. Glass marbles filled the upper part of the pan above a galvanized hardware cloth fitted 3–4 cm below the rim, and prevented dust that had washed down into the bottom of the pan from being blown away. Dry deposition to the lysimeters was estimated by subtracting cation inputs by rain from this record of total deposition.

Table 1. Bulk densities (ρ_w), strain ($\varepsilon_{i,w}$), and total cation concentrations in 1987 soil horizons (w) and corresponding fill materials (p); standard deviations are in parentheses.

Horizon	Depth	ρ_w	$\varepsilon_{i,w}$	Ca_p	Ca_w	Mg_p	Mg_w	K_p	K_w	Na_p	Na_w	Si_p	Si_w
	cm	Mg m^{-3}		%									
Oak													
A	0–7	0.92	0.52	1.99	2.01 (0.03)	1.25	1.18 (0.04)	1.86	1.73 (0.04)	1.81	1.72 (0.03)	27.89	26.34 (0.17)
AC	7–20	1.71	–0.11	1.99	1.88 (0.04)	1.22	1.13 (0.03)	1.81	1.80 (0.13)	1.84	1.85 (0.03)	28.09	28.48 (0.07)
C1	20–35	1.70	–0.04	1.94	1.95 (0.06)	1.21	1.18 (0.01)	1.88	1.76 (0.02)	1.81	1.84 (0.08)	28.26	28.47 (0.09)
C2	35–50	1.70	–0.08	1.99	1.97	1.22	1.22	1.80	1.74	1.90	1.84	28.13	27.99
C3	50–65	1.70	–0.12	2.01	1.94	1.25	1.20	1.68	1.74	1.84	1.80	27.92	28.17
C4	65–80	1.71	–0.14	1.97	1.92	1.21	1.16	1.78	1.74	1.84	1.85	28.02	28.56
C5	80–100	1.71	–0.16	2.05	2.02	1.28	1.23	1.69	1.71	1.85	1.87	27.85	27.99
Pine													
A	0–1	1.08	0.35	2.07	2.00 (0.05)	1.24	1.08 (0.06)	1.77	1.86 (0.02)	1.84	1.91 (0.04)	28.27	28.32 (0.42)
BAt	1–10	1.75	–0.11	1.99	1.96 (0.01)	1.25	1.19 (0.01)	1.78	1.74 (0.04)	1.79	1.83 (0.03)	28.16	28.12 (0.20)
Bt	10–20	1.76	–0.16	2.03	1.99 (0.02)	1.22	1.22 (0.04)	1.77	1.72 (0.15)	1.80	1.82 (0.01)	28.30	28.07 (0.37)
BCt	20–35	1.72	–0.11	1.99	1.93 (0.07)	1.28	1.18 (0.03)	1.83	1.75 (0.10)	1.81	1.80 (0.05)	27.92	28.31 (0.25)
C2	35–50	1.73	–0.12	2.01	1.73	1.25	1.07	1.80	1.86	1.82	1.75	28.04	29.04
C3	50–65	1.74	–0.13	2.02	1.91	1.24	1.19	1.79	1.78	1.79	1.80	27.91	28.23
C4	65–80	1.78	–0.16	1.97	2.02	1.24	1.24	1.82	1.64	1.83	1.86	27.85	27.93
C5	80–100	1.80	–0.19	1.99	1.90	1.23	1.21	1.79	1.83	1.83	1.77	28.14	28.34

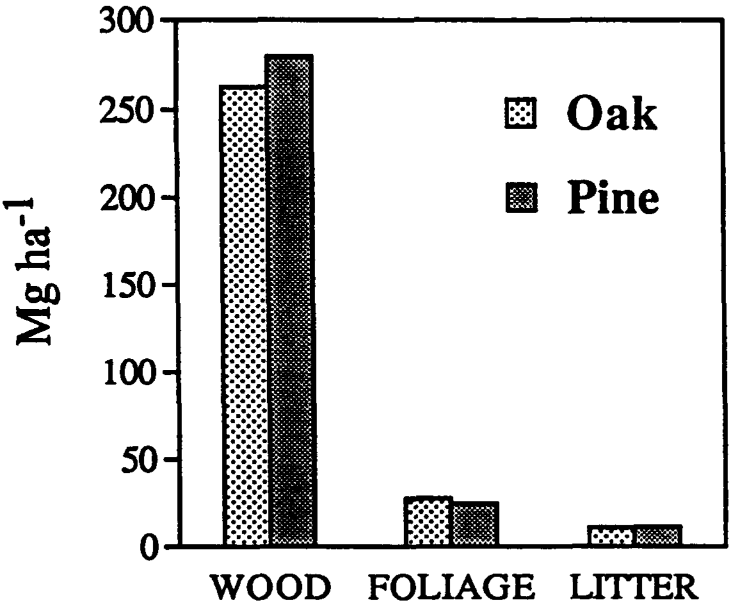

Figure 2. Dry matter accumulation in above-ground biomass at the oak and pine lysimeters.

Results and discussion

Cation accumulation in above-ground biomass

$\Delta_{wood+foliage}$. Stand biomass (including wood and foliage) was 304 Mg ha^{-1} for pine (Figure 2). This placed the lysimeter-grown pine at the high end of biomass values for pine stands, although the average lifetime annual woody increment (5.9 Mg ha^{-1} yr^{-1}) was within the range (4.3–8.7 Mg ha^{-1} yr^{-1}) reported for pine plantations from Tennessee and North Carolina (Edwards et al. 1989). Furthermore, biomass of an individual lysimeter-grown pine (152 kg) was comparable to that of *P. ponderosa* trees (135–189 kg tree^{-1}) from arid and montane areas of Nevada (Callaway et al. 1994).

In contrast, biomass of the oak stand (301 Mg ha^{-1}) far exceeded typical values (14–75 Mg ha^{-1}) quoted for chaparral ecosystems (Gray & Schlesinger 1981), and was two to three times that of the most productive chaparral measured previously, 21-year-old Ceanothus stands growing within the San Dimas Experimental Forest (Riggan et al. 1988). In addition to high stand stocking (30,000 shrubs ha^{-1}), this high biomass was due to the large individual scrub oaks, which, at an average height of 6.7 m, were taller than the 1–5 m height characteristic of this species (Specht 1988). Also, individual shrub biomass (9.7 kg) exceeded that of 35-year-old *Q. dumosa* (4.9 kg shrub^{-1}) from San

Table 2. Base action concentrations in above-ground biomass at the oak and pine lysimeters; standard deviations are in parentheses.

	Ca	Mg	K	Na
			%	
Oak				
Wood	0.54	0.07	0.22	0.007
Foliage	0.78	0.23	0.59	0.009
Litter	1.40 (0.16)	0.22 (0.06)	0.20 (0.05)	0.009 (0.001)
Pine				
Wood	0.11	0.04	0.12	0.001
Foliage	0.20	0.12	0.33	0.006
Litter (total)	0.77 (0.09)	0.24 (0.02)	0.13 (0.02)	0.010 (0.001)
Oi1	0.56 (0.03)	0.14 (0.02)	0.08 (0.01)	0.008 (0.002)
Oi2	0.75 (0.07)	0.18 (0.05)	0.10 (0.01)	0.011 (0.001)
Oe	0.85 (0.11)	0.27 (0.02)	0.15 (0.02)	0.011 (0.001)

Diego county (Riggan et al. 1988). Thus, it appears that growth conditions at the lysimeter installation were optimum for *Q. dumosa*, possibly resulting from the fact that the soil had been sieved (<19 mm diameter) to remove rock fragments, and was at least 2 m deep. In comparison, the soils prevalent at the San Dimas Experimental Forest (Crawford 1962) and common throughout mountainous areas of southern California are shallow (<0.6 m) and gravelly.

Calcium, Mg, K, and Na concentrations in oak were higher than those in pine for both wood and foliage (Table 2). Cation accumulation in above-ground vegetation, calculated from the weights of the different biomass compartments, and corresponding concentrations, followed the same trend as concentrations; i.e., was higher in oak than in pine for all cations (Figure 3). In addition, ranking of cation concentrations differed for the two plant species. In wood and foliage of pine, concentrations decreased in the order: K> Ca> Mg> Na (Table 2), which followed the distribution observed in a current year's foliage of *P. resinosa* (Bockheim et al. 1986) and *P. taeda* (Johnson et al. 1991). Ranking of cations in wood and foliage of oak was: Ca> K> Mg> Na (Table 2), similar to that reported for *Q. suber* or *Q. coccifera* from southern France (Specht 1988). As a result, while Mg and K accumulation in the lysimeter-grown oak was 50 to 80% greater than in the pine, Ca accumulation showed the greatest difference between plant species, and was more than four-fold higher for oak (Figure 3).

Δ_{litter}. Litter biomass at the pine and oak lysimeters was small (11.0–11.2 Mg ha^{-1}), and contributed less than 4% of total above-ground biomass (Figure

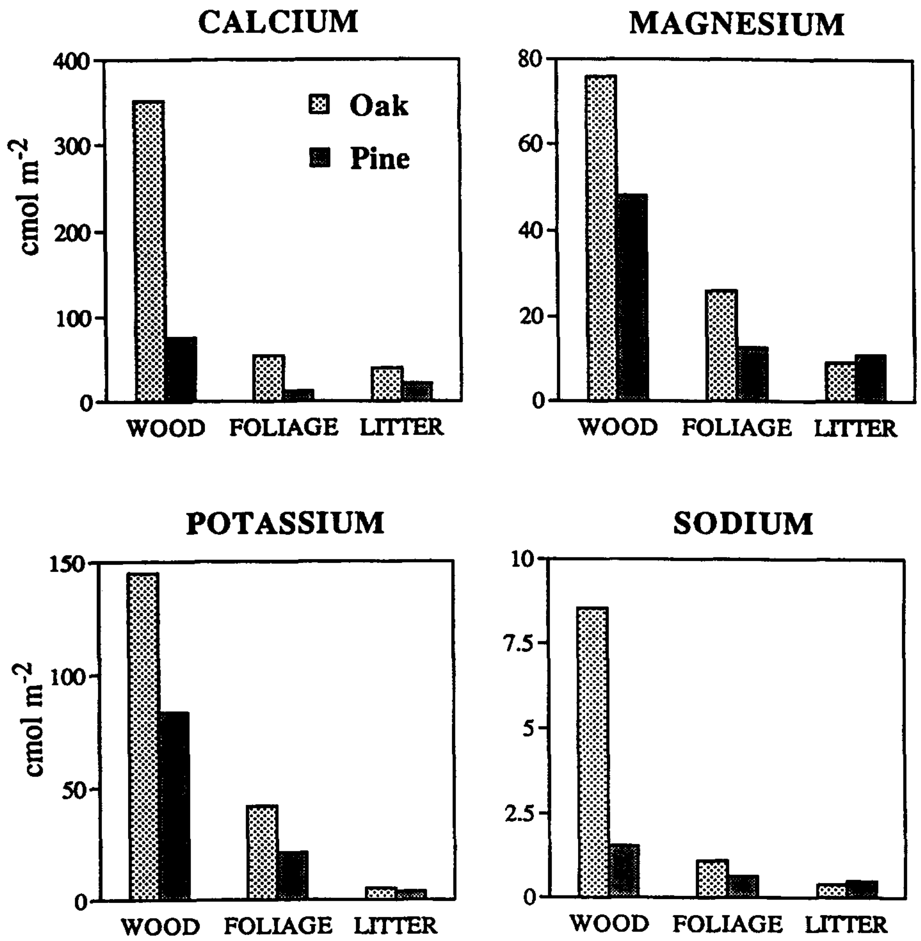

Figure 3. Cation contents in above-ground biomass at the oak and pine lysimeters. Note different scales for each element.

2). This was less than the 43.7 Mg ha^{-1} recorded for *Q. dumosa* in a 31-year-old stand (Kittredge 1955), or the 54.3 Mg ha^{-1} measured in a 35-year-old stand (Riggan et al. 1988). Foliage biomass for these two *Q. dumosa* stands was lower than that measured in our study, suggesting that decomposition was especially rapid at the lysimeter installation. While *Q. dumosa* sheds its leaves annually (Specht 1988), longevity of needle fascicles for *P. coulteri* is 3 to 4 years (Ewers & Schmid 1981). Considering that foliage biomass was slightly higher for oak than for pine (Figure 2), these results indicate that litterfall for oak was roughly 3 to 4 times greater than that for pine. Furthermore, since litter biomass was comparable for the two plant species, decomposition rate of the oak litter was likely 3 to 4 times that of the pine.

Differences in cation concentrations between the litter of the oak and pine were smaller than in wood or foliage, which may result from changes in composition of the two litter layers through decomposition processes (Table 2). Ranking of cation concentrations was similar for the litter of the two plant species (Ca> Mg> K> Na), with Mg and K reversing their rankings relative to those in wood and foliage. This is consistent with chemical element change observed in decomposing litter, with K being released through leaching or mineralization at a more rapid rate than Mg, and especially Ca (Lousier & Parkinson 1978). While smaller differences in cation contents between the litter of oak and pine were noted compared to wood and foliage (Figure 3), a greater fraction of the total above-ground cation pool was contained in the pine litter compared to that of oak. In turn, this suggests that the percentage of total above-ground cation pool returned annually to the mineral soil from the decomposing litter was higher for the oak.

Decomposition rates have been related to various litter characteristics, including nutrient and polyphenolic (tannins and lignin) content (Schlesinger & Hasey 1981; Horner et al. 1988). At the lysimeter installation, it appears that mesofaunal activity was also playing a major role in regulating decomposition rates. The litter under pine was composed of three distinct horizons, including an Oi1 of fresh pine needles (10–6 cm), an Oi2 with partially decomposed needles (6–4 cm), and an Oe of mostly decomposed needles (4–0 cm) (Graham & Wood 1991). In contrast, the oak litter consisted of a loose layer (6 cm) of oak leaves, indicating rapid litter incorporation into the mineral soil. While earthworms were absent under pine, earthworms casts were found in the oak litter, and composed 95% of the underlying A horizon (Graham & Wood 1991). Earthworms increase decomposition rates by ingesting large quantities of surface litter. The ingested material is macerated, mixed with ingested inorganic soil material, and excreted as casts, which contain large quantities of carbon (Lee 1985). At the lysimeter installation, carbon concentration in the A horizons was 3.5% under oak and 1.3% under pine (Ulery et al. 1995).

Changes in cation soil pools

Initial conditions and strain. Total base cation content of the initial fill material was greatest for Ca (2.00%), followed by Na (1.83%), K (1.79%), and Mg (1.24%). The exchangeable fraction contributed 8.6% of the total Ca and 5.6% of the total Mg, whereas exchangeable K and Na constituted much lower proportions of the total soil pool (0.3% each). As described by Brimhall et al. (1992), determination of strain is the first step in computing cation mass changes due to pedogenesis (Table 1). Negative strain below the A horizons of the two lysimeter soils results from increased bulk density of the 1987-sampled soils as compared to the original fill material, and reflects soil

Table 3. Cation balances for the oak and pine lysimeters. Soil balances for the upper 1 meter of soil.

	Ca	Mg	K	Na
	Kmol ha^{-1} yr^{-1}			
Wet deposition	0.02	0.02	0.01	0.09
Dry deposition	0.28	0.03	0.07	0.05
Atmospheric deposition	0.30	0.05	0.08	0.14
Oak				
$\Delta_{\text{above-ground biomass}}$	0.95	0.24	0.41	0.02
$\Delta_{\text{soil exchangeable}}$	2.57	0.55	–0.02	–0.31
$\Delta_{\text{soil non-exchangeable}}$	–10.70	–11.71	–7.23	–9.13
Pine				
$\Delta_{\text{above-ground biomass}}$	0.23	0.16	0.23	0.01
$\Delta_{\text{soil exchangeable}}$	2.12	0.14	–0.02	–0.32
$\Delta_{\text{soil non-exchangeable}}$	–15.42	–15.05	–8.57	–12.20

compaction and settling with time. In contrast, faunal activity and incorporation of low density organic matter decreased bulk density and resulted in positive strain in the A horizons (Ulery et al. 1995).

$\Delta_{soil\ exchangeable}$. Changes in the soil exchangeable pool were described thoroughly elsewhere (Ulery et al. 1995), and are summarized here. Except for the A horizon under pine, exchangeable Ca in the 1987 soil samples was greater than in the initial fill material. Similarly, an increase in exchangeable Mg was noted in the two lysimeter soils below the 10 cm depth. In contrast, exchangeable Na was lower throughout the 1987 soil profiles than in the corresponding parent material samples. Exchangeable K increased in the A horizons, but decreased with depth relative to the fill material (Ulery et al. 1995). Integrated over the 1 m depth, exchangeable Ca and Mg accumulated in the two lysimeter soils, with the soil under oak exhibiting the greater increase in both cations (Table 3). Exchangeable Na and K decreased under the two plant species, although $\Delta_{\text{soil exchangeable}}$ (i.e. absolute value) for K and Na was smaller than for Ca and Mg.

$\Delta_{soil\ non\text{-}exchangeable}$. All base cations in the soil non-exchangeable pool decreased relative to the parent material, and showed greater losses under pine than under oak (Table 3). With 44% greater decrease under pine than under oak, Ca was the cation exhibiting the greatest difference between the two plant species. The amounts of non-exchangeable Ca, Mg, and K lost under oak were greatest in the A horizon, with progressively fewer losses to the 30

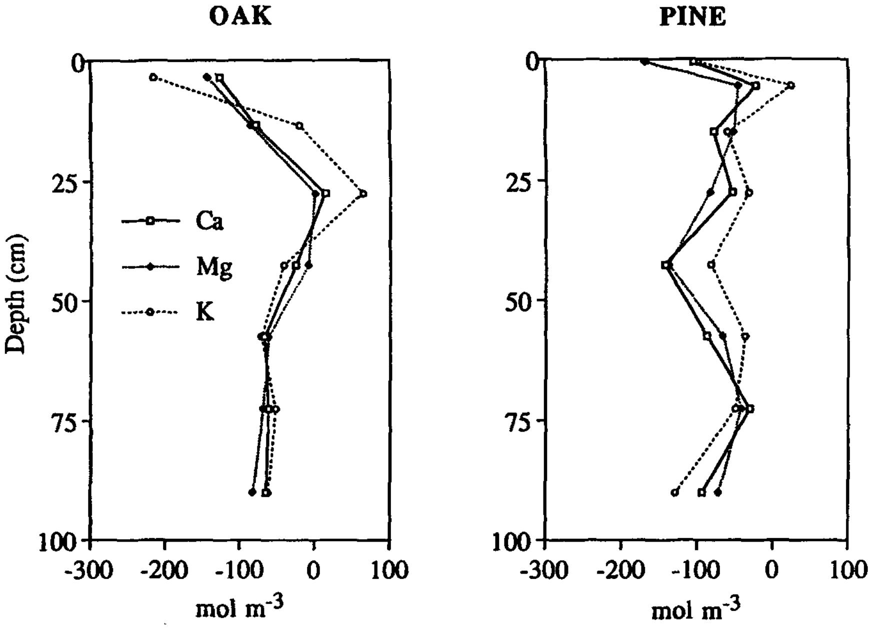

Figure 4. Changes ($\delta_{j,w}$) in non-exchangeable Ca, Mg, and K with depth at the oak and pine lysimeters, corrected for soil volume and density changes.

cm depth, below which losses again increased and then remained constant (Figure 4). Under pine, variability in cation losses with depth was higher than under oak, and did not show any consistent trend. As mentioned previously, a major difference between the oak and pine lysimeters was the presence of earthworms under oak. The A horizon under oak consisted almost entirely of earthworm casts, and worm krotovinas extended with decreasing frequency to about the 20- to 35-cm depth (Graham & Wood 1991). It may be that the soil material excreted in the earthworm casts at the surface was impoverished in non-exchangeable Ca, Mg, and K as compared to bulk soil lower in the soil profile. This, in turn, would result in a relative increase in base cations at the depth where the worms ingest the soil material. Earthworms preferentially ingest finer soil fractions (Mulongoy & Bedoret 1989), and worm casts picked from the litter layer under oak contained more silt and clay than the initial fill material (Graham & Wood 1991). The silt and clay fractions are dominated by vermiculite and kaolin, and contain fewer primary minerals than the bulk soil (Tice et al. 1996), hence they probably have lower base cation concentrations as well. Thus, this sorting mechanism by earthworms could be responsible for depleting non-exchangeable cations in surface soil material under oak.

Comparing release rates of different cations may also provide insight to the weathering processes at the lysimeters. Decreases in non-exchangeable

Table 4. Coefficient of determination (r^2) for cation changes in the soil non-exchangeable pool at the oak and pine lysimeters.

	Ca	Mg	K	Na
Oak				
Ca	–	0.89**	0.66*	0.04
Si	0.66*	0.63*	0.88**	0.60
Pine				
Ca	–	0.85**	0.62*	0.03
Si	0.06	0.00	0.50*	0.38

*: significant at the 5% level; **: significant at the 1% level.

Ca and Mg were strikingly similar in the soil profiles (Figure 4), and showed highly significant coefficients of determination (Table 4). While the decrease in non-exchangeable K was also correlated to Ca, the decrease in non-exchangeable Na was not. Silicon under oak exhibited a similar loss pattern as non-exchangeable Ca, Mg, and K (Figures 4 and 5), and was most strongly correlated to K (Table 4). For losses under pine, K was also weakly correlated to Si, but Ca and Mg were not (Table 4). Taken together, these results suggest: (1) that the mechanisms controlling release of Na by weathering were different from those controlling Ca, Mg, and K release, and (2) the greater depletions of non-exchangeable Ca and Mg under pine were not solely due to greater rates of weathering. Weathering reactions or stoichiometry were different between lysimeters, at least for reactions involving Ca and Mg.

Cation balances

Δ_{system}. Cation release by weathering ($\Delta_{\text{soil non-exchangeable}}$) was by far the largest measured flux within the two soil-vegetation systems, and exceeded changes in the above-ground biomass and exchangeable soil pools (Table 3). While accumulation of Na in above-ground vegetation was minimal, K storage in vegetation exceeded the loss from the exchangeable soil pool. For Ca in the two soil-vegetation systems, and Mg in the oak system, accumulation in the exchangeable soil pool was greater than that in above-ground biomass. In contrast, for pine, Mg accretion in biomass slightly exceeded increase in the exchangeable soil pool.

Changes in the fourth compartment of the soil-vegetation systems ($\Delta_{\text{below-ground biomass}}$) were not measured in this study but can be inferred from root:shoot (R:S) biomass ratios reported in the literature. Chaparral vegetation typically possesses a large underground woody structure (Canadell & Zedler 1994), with *Q. dumosa* being one of the most deeply rooted species

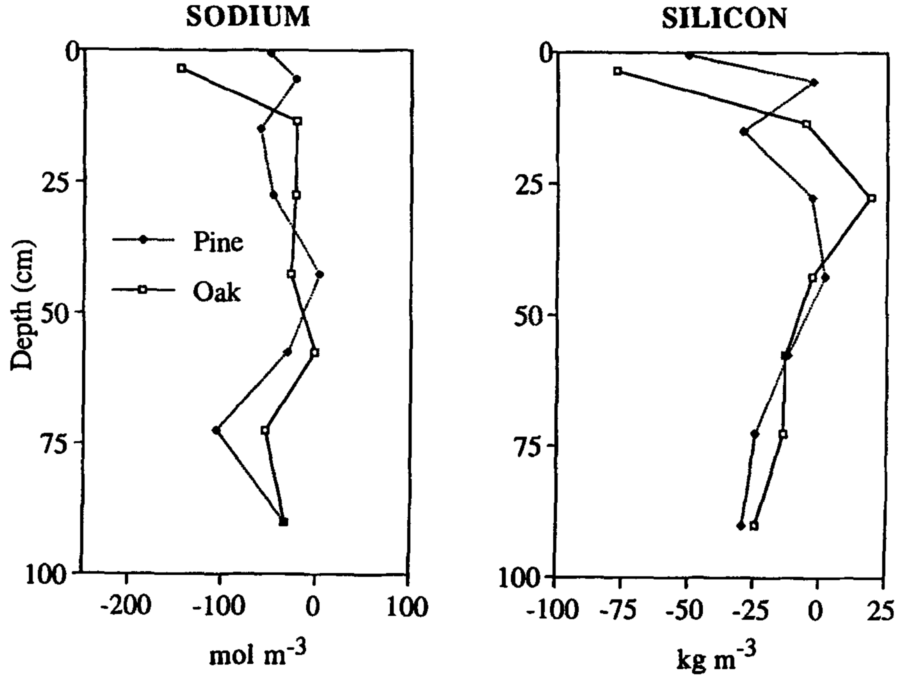

Figure 5. Changes ($\delta_{j,w}$) in Si and non-exchangeable Na with depth at the oak and pine lysimeters, corrected for soil volume and density changes.

(Hellmers et al. 1955). R:S biomass ratios of 14 individual shrubs from southern California and Chile ranged from 0.25 for the shallow rooted *C. gregii* to 0.93 (Miller & Ng 1977). A R:S ratio of 1.9 was measured in 9-year-old *Q. dumosa* from Cleveland National Forest in southern California (Kummerow & Mangan 1981). In contrast, trees are expected to show lower R:S ratios than chaparral shrubs. From data compiled by Bray (1963) and Santantonio et al. (1977), R:S ratios for pine trees (>20-year-old) ranged from 0.16 to 0.31. Considering that above-ground biomass at the lysimeter installation was only slightly higher for pine than for oak, and assuming that cation concentrations in pine roots were not higher than in oak, we conclude that cation storage in below-ground biomass paralleled what we observed in above-ground and was greater for the oak.

Thus, it seems clear that more cations are being conserved in the oak system than in the pine system. The four cation compartments contributed in the same direction to these overall differences between pine and oak; i.e., by having either larger increases ($\Delta_{\text{above-ground biomass}}$, $\Delta_{\text{below-ground biomass}}$, and, for Ca and Mg, $\Delta_{\text{soil exchangeable}}$) or smaller decreases ($\Delta_{\text{soil non-exchangeable}}$) for oak than for pine.

Atmospheric deposition. With the exception of Na, measured dry deposition exceeded wet (Table 3). Sodium accounted for over 50% of base cation flux in precipitation, which is likely related to the site proximity to the ocean (35 km to the west). Calcium was the dominant cation in dry and total deposition. The ratio of dry to wet deposition (D:W) was highest for Ca (14 D:W), followed by K (7 D:W), Mg (2 D:W), and Na (0.6 D:W). Contribution of dry deposition to total atmospheric inputs for Ca, Mg, and K was 3 to 12 times greater than observed in wetter areas of the U.S. (e.g. Johnson & Lindberg, 1992), and almost twice as high as that observed in the Santa Ynez mountains of Santa Barbara County (Schlesinger et al. 1982). Increased dry deposition at the San Dimas Experimental Forest is probably due to the Santa Ana winds that carry considerable dust from sources to the northeast, primarily the Mojave Desert (Reheis & Kihl 1995).

Due to potential dust interception by the plant canopies, dry deposition measured by Reheis & Kihl (1995) should be considered an underestimate of the actual inputs to the two lysimeters. In a study by Schlesinger & Hasey (1980), interception of dry aerosols by chaparral foliage was measured using plastic foliage (LA = 3.5) mounted above precipitation collectors. Deposition of cations in these collectors was 2 to 3 times that in bulk precipitation. At the lysimeter installation, the pine canopy, with its potentially greater surface area, likely intercepted more dust than the broad-leaved oak shrubs. Reid (1988) recorded higher cation levels in canopy throughfall under *P. coulteri* than under *C. leucodermis*. Thus, underestimation of dry deposition inputs in our study (Table 3) was likely greater for pine than for oak.

Leaching and run-off. Cation losses by leaching and runoff may be related to atmospheric deposition inputs and Δ_{system} as expressed in equation [5]. For all cations, absolute values of atmospheric deposition and Δ_{system} were greater for pine than for oak, implying that run-off and leaching losses were greater under pine. The minimal slopes at the lysimeter installation suggest that most of the losses were due to leaching rather than run-off.

Implications for weathering rates

Plants and soil organisms have long been recognized as vital factors enhancing weathering rates of minerals (Robert & Berthelin 1986). One mechanism involves plant regulation of cation concentrations in the soil solution. For instance, biotite transformation to vermiculite upon plant-induced removal of K has been observed in greenhouse experiments (Mortland et al. 1956; Boyle & Voigt 1973; Hinsinger et al. 1992). A second mechanism responsible for weathering enhancement by plant communities is the release of organic acids and chelates into the soil solution, through foliar and litter leaching, root excretion, and microbial production. Numerous laboratory studies have shown that mineral dissolution was increased in the presence of low-molecular weight chelating agents, such as oxalate and citrate (Amrhein & Suarez 1988; Lundström & Öhan 1990), as well as higher molecular-weight humic materials, such as water-soluble fulvic acids (Kodama et al. 1983; Tan 1986). These studies provide important insight on the mechanisms of weathering by plants, but are typically designed to investigate a specific process, and results cannot be applied readily to rates of weathering in a natural soil environment.

Results from the closely controlled biosequence experiment at the San Dimas Experimental Forest illustrate the importance of biotic effects on weathering in an environment that is less artificial than in greenhouse or laboratory studies. The greater weathering rates in the soil under pine have developed in response to two controlling factors. First, higher weathering under pine resulted from lower cation concentrations in the soil solution, as evidenced for Ca and Mg by lower values in the soil exchangeable pool (Table 3). Based on cation storage in above-ground biomass, biological uptake was greater for oak than for pine (Figure 3), and the difference between species was probably underestimated since below-ground biomass was not included in the calculations. In addition, decomposition of the oak litter was more rapid than that of pine, and likely returned to the mineral soil a higher proportion of the biomass cation pool. Thus, it appears that this efficient biocycling by the oak system was an important factor controlling cation concentrations in the soil solution and release by weathering. In contrast, the pine system was characterized by a slower biological cycle and larger output fluxes by leaching and run-off.

Second, weathering rates were regulated by the presence of organic and inorganic acids in solution. Concentrations of organic acids in litter leachates and soil solutions are typically higher under conifers than under broad-leaved vegetation (Pohlman & McColl 1988; Ugolini et al. 1988), resulting in lower soil pH, as observed for the A horizon under pine (Ulery et al. 1995). While these acids may increase rates of mineral weathering, they can also affect the stoichiometry of weathering (Kodama et al. 1983). This may explain why the correlation between decreases in Si and non-exchangeable Ca and Mg in our study was different under pine and oak (Table 4). It is also highly probable that the more acidic conditions under pine were responsible for the greater losses in non-exchangeable Na, since biocycling processes are unlikely to significantly affect solution concentrations of this cation.

Finally, it should be noted that the soil-vegetation systems present at the lysimeter installation may not be a realistic analog for many forested ecosystems that have been allowed to develop for long periods of time on stable landscapes. Mixing of the soil material during construction of the lysimeters probably exposed fresh mineral surfaces to the action of weathering agents. Estimates of weathering rates in our study were two to 300 times greater than those from field studies reported in the literature (Likens et al. 1977; Clayton 1979; Clayton & Megahan 1986), and should be expected to decrease in the future as mineral surfaces become progressively coated with secondary minerals and organic substances. On the other hand, the lysimeter system provides an understanding of the initial effects of vegetation on soils, and clearly demonstrates, under these conditions, greater weathering under pine than under oak. It is clear that the scenario adopted by earth-system modelers (e.g. Knoll & James 1987; Volk 1989), linking the rise of angiosperm ecosystems to an increase in weathering relative to that under the existing gymnosperms, needs to be critically re-examined in view of these conclusions.

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