

possible under these conditions, despite the greatly enhanced infrared opacity of the atmosphere. Rather, the surface temperature tends asymptotically toward the effective temperature at which the planet radiates to space.

The extensive extinctions that occurred near the end of the Cretaceous appear to be a combination of gradual extinctions over millions of years due to slowly changing environmental conditions and abrupt extinctions near the K-T boundary (21). Our calculations (Fig. 1) are consistent with the suggestion that the marine extinctions at the K-T boundary resulted principally from sunlight being blocked by a dust cloud, which caused a temporary cessation of photosynthesis and the collapse of food chains (1). Numerical experiments for such a situation in current marine ecosystems suggest that widespread, but not total, extinction would occur if photosynthesis were interrupted for several months (22). The high metabolic rates and lack of adaptations to seasonable variability of tropical marine organisms (22) may explain the observed preferential extinctions in tropical waters (21).

Cessation of photosynthesis may have affected terrestrial plants and animals less than marine ones because the biological carbon cycle on land has a turnover time scale of years, not months, as in the ocean (23). For terrestrial extinctions at the K-T boundary, we suggest that two other factors played dominant roles. First, the persistence of very low light for a few months might have reduced vision to such a degree that most animals, especially large ones, had difficulty locating adequate food. Second, the occurrence of substantially reduced temperatures for several months would have killed organisms that were not adapted to the cold or were not able to burrow underground. Small animals may have been better able to cope with both reduced light and temperature (6).

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25. The standard value for the injected mass is based on the typical thickness of the clay layer at the K-T boundary (1).
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The Use of Strontium-87/Strontium-86 Ratios to Measure Atmospheric Transport into Forested Watersheds

Abstract. *Strontium-87/strontium-86 ratios indicate the sources of strontium in samples of natural waters, vegetation, and soil material taken from watersheds in the Sangre de Cristo Mountains of New Mexico. More than 75 percent of the strontium in the vegetation is ultimately derived from atmospheric transport and less than 25 percent from the weathering of the underlying rock. Much of the airborne strontium enters the watersheds by impacting on coniferous foliage, but deciduous foliage apparently traps little, if any, strontium-bearing aerosol. The strontium and presumably other nutrients are continuously recycled in a nearly closed system consisting of upper soil horizons, forest litter, and the standing crop of vegetation.*

The presence of vegetation on land surfaces complicates measurements of aerosol deposition from the atmosphere. The efficiency of foliage in trapping aerosols may differ from that of artificial collectors used to measure deposition (1). In addition to aerosol-derived material, any sample of natural foliage or throughfall (precipitation that has contacted foliage) contains an unknown proportion of material that has been carried from the roots to the foliage via the transpiration stream of the plant (2). Under favorable geographic and geologic circumstances, the isotopic composition of natural Sr may be used to distinguish aerosol and transpiration components and to allow direct measurement of pres-

ent-day and long-term mean aerosol inputs to a forested watershed.

Radiogenic ^{87}Sr is continuously being added to ambient ^{87}Sr by the β decay of ^{87}Rb (half-life, 4.9×10^{10} years); ^{86}Sr is nonradiogenic, both Sr isotopes are stable, and the $^{87}\text{Sr}/^{86}\text{Sr}$ ratio can be measured with very high precision (3, 4). The $^{87}\text{Sr}/^{86}\text{Sr}$ ratio of soils and most near-surface continental rocks typically lies between 0.709, the ratio in modern ocean water, and about 0.720, the ratio in streams draining ancient Rb-enriched regions, such as the Canadian Shield (5). In old rocks that are enriched in Rb, such as Precambrian granite, the $^{87}\text{Sr}/^{86}\text{Sr}$ ratio may be much higher than the crustal average; young volcanic rocks may be

depleted in ^{87}Sr . Terranes may differ in their $^{87}\text{Sr}/^{86}\text{Sr}$ ratio, depending on age and the Rb/Sr ratio, and these differences are reflected in the $^{87}\text{Sr}/^{86}\text{Sr}$ ratios of sediments or stream water derived from them (5, 6). With these observations in mind, we have used the $^{87}\text{Sr}/^{86}\text{Sr}$ ratio to trace the source of Sr in samples of water, soil, and plant material from two forested watersheds.

The Santa Fe Range of the Sangre de Cristo Mountains in New Mexico is an exposure (50 by 15 km) of Embudo granite. A 1.6-billion-year-age has been determined for the Embudo (7). The $^{87}\text{Sr}/^{86}\text{Sr}$ ratio in these rocks is higher than in the surrounding, topographically lower terrane, which is composed of phanerozoic (younger than 0.6 billion years) sedimentary and volcanic rocks. We studied two small (3 ha) watersheds lying at elevations above 3100 m in the Tesuque watersheds (8) in the summer of 1975. One was covered with a stand of aspen (*Populus tremuloides*) and the other with Engelmann spruce and subalpine fir (*Picea engelmannii* and *Abies lasiocarpa*).

Four polyethylene funnels were deployed to collect bulk precipitation above an elevation of 3200 m, and one was located at the Santa Fe Airport, 20 km west of the Embudo outcrop, at an elevation of 1935 m. Eighteen similar collectors were set out under the spruce-fir stand and 12 under aspen to sample throughfall. Samples were collected and stored every 2 weeks. Two composite samples were then made from the collec-

tions at each site, one spanning the interval 12 June through 16 July and the other 17 July through 20 September. We obtained samples of water from the unsaturated zone by applying a partial vacuum to porous ceramic cups buried in the soil. We added a few drops of HClO_4 to each sample before subboiling evaporative concentration. The Sr in the concentrate solution therefore represents the sum of that originally in solution and that in acid-soluble solid phases.

The parent material for the soils of the study area consists of rock fragments and mineral grains derived from the underlying Embudo granite. Because the mineralogical and chemical composition of the Embudo is variable (7), we created composite regolith samples by sampling rock fragments from the surface of each watershed according to a predetermined grid.

Samples of rock, ashed vegetation, and soil horizons were completely dissolved in HF prior to Sr separation. Details of sampling and analysis are given in (9); the results are presented in Table 1. Complete major element analyses of the samples of rock, vegetation, precipitation, throughfall, soil solution, and runoff are reported in (9).

The $^{87}\text{Sr}/^{86}\text{Sr}$ ratio of precipitation collected at Santa Fe Airport (0.7088) implies a source that is predominantly marine limestone or young volcanic rocks mixed with older, more radiogenic material. As all of the samples collected from the study area contain Sr more radiogen-

ic than this, we will use 0.7088 as a local reference value and define $\Delta^{87}\text{Sr}$ as follows:

$$\Delta^{87}\text{Sr} = \left(\frac{R}{R + 1} - \frac{0.7088}{1.7088} \right) \times 10,000 \quad (1)$$

where $R = ^{87}\text{Sr}/^{86}\text{Sr}$ of the sample. The quantity $\Delta^{87}\text{Sr}$ is therefore a measure of the amount of radiogenic Sr in a sample relative to the reference material. The $\Delta^{87}\text{Sr}_M$ of a mixture of two components is a linear function of the $\Delta^{87}\text{Sr}$ of each component weighted by its mass contribution to the mixture (3):

$$\Delta^{87}\text{Sr}_M = x\Delta^{87}\text{Sr}_A + (1 - x)\Delta^{87}\text{Sr}_B \quad (2)$$

where the subscripts A and B denote components A and B; x is the fraction of the Sr in the mixture derived from component A.

The Sr collected in throughfall has three immediate sources: (i) precipitation, (ii) soluble aerosols captured by foliage, and (iii) leachates or exudates from the foliage. The contribution of precipitation was measured independently and may be subtracted from the total throughfall to yield net throughfall (Table 2). The $\Delta^{87}\text{Sr}$ of foliar leachates is taken to be that of the sapwood of the tree bole (10). The $\Delta^{87}\text{Sr}$ of the aerosol component is taken as 0, that is, the value of precipitation at the Santa Fe Airport. This assumption results in a measurement of the input of aerosols originating beyond the boundaries of the Precambrian terrane, at least 5 km distant from and 1 km below the study area.

Table 3 shows that 66 percent of the Sr in spruce-fir throughfall is derived from atmospherically transported material that was deposited on the foliage. The total input of Sr to the spruce-fir watershed via the atmosphere exceeds that measured by continuously open precipitation collectors by a factor of 4.6. The sources of Sr in throughfall are shown graphically in Fig. 1.

The variation in $^{87}\text{Sr}/^{86}\text{Sr}$ of various portions of a spruce tree from the study area also indicates the trapping of aerosols (Table 1). The bark and sapwood have $\Delta^{87}\text{Sr}$ values that are indistinguishable, but the Sr of the foliage, the part of the tree with the highest surface-to-volume ratio, is distinctly less radiogenic. *Usnea*, a genus of epiphytic lichen that derives all of its nutrients from the atmosphere and throughfall, has the lowest measured $\Delta^{87}\text{Sr}$; this species has a higher proportion of atmospherically derived Sr than any other botanical sample tested. These isotope ratios suggest that the

Table 1. The $^{87}\text{Sr}/^{86}\text{Sr}$ ratio and Sr concentrations for samples from the Tesuque watersheds; ppm, parts per million.

Sample	Dates of collection (1975)	$^{87}\text{Sr}/^{86}\text{Sr}^*$	$\Delta^{87}\text{Sr}$	Concentration	
				ppm	$\mu\text{g/liter}$
Airport rain	6/12 to 9/20	0.7088 ± 0.0001	0		8.4
Mountain rain	6/12 to 7/16	0.7104 ± 0.0004	5.5		1.55
Mountain rain	7/17 to 9/20	0.7100 ± 0.0007	4.1		1.16
Mountain rain	6/12 to 9/20	0.7102 ± 0.0006	4.8		1.31
Spruce-fir					
Throughfall	6/12 to 7/16	0.7106 ± 0.0001	6.2		36.2
Throughfall	7/17 to 9/20	0.7103 ± 0.0002	5.1		3.3
Throughfall	6/12 to 9/20	0.7105 ± 0.0002	5.8		12.1
Needles (ash)		0.7122 ± 0.0003	12		
Bark (ash)		0.7138 ± 0.0004	17	994	
Bole (ash)		0.7141 ± 0.0004	18	1001	
Lichen (<i>Usnea</i>) (ash)		0.7115 ± 0.0002	9	281	
Litter layer (ash)		0.7142 ± 0.0002	18	315	
Regolith		0.7348 ± 0.0004	88	252	
Soil solution, 30 cm		0.7131 ± 0.0003	15		
Soil solution, 150 cm		0.7138 ± 0.0005	17		30.3
Aspen					
Throughfall	6/12 to 9/20	0.7169 ± 0.0007	28		4.7
Bole (ash)		0.7197 ± 0.0002	37	2497	
Regolith		0.7529 ± 0.0003	147	143	

*All measurements are corrected for fractionation on the assumption that $^{86}\text{Sr}/^{88}\text{Sr} = 0.1194$ and adjusted so that the Eimer and Amend standard gives $^{87}\text{Sr}/^{86}\text{Sr} = 0.70800$ and the National Bureau of Standards standard gives $^{87}\text{Sr}/^{86}\text{Sr} = 0.71022$. The within-run analytical precisions are given.

total atmospheric input of Sr to the ground is even greater than that measured in throughfall since some of the atmospherically transported Sr remains on the foliage until it falls as litter.

The $\Delta^{87}\text{Sr}$ of the Sr added to precipitation by contact with aspen foliage is indistinguishable from that of the tree (Table 1); the addition of atmospheric dust is thus immeasurably small. Since the topography of the two watersheds is similar, we attribute the difference in atmospheric input to differences either in the duration of foliation or in the aerosol-capturing efficiency of the foliage.

The Sr in the forests is ultimately derived from two sources: (i) weathering, which is the chemical alteration and partial dissolution of the parent material of the soil, and (ii) dust from remote areas transported through the atmosphere. We presume that the immediate source of the Sr in the wood of trees is the soil solution. The $\Delta^{87}\text{Sr}$ of the wood is therefore a measure of the proportion in which these two sources have supplied dissolved Sr to the solution of the rooting zone. The contribution of atmospherically transported soluble Sr exceeds that of weathering by a factor of 4 in the spruce-fir watershed and by a factor of 3 at the aspen site (Table 3; Fig. 1). The Sr in the vegetation is therefore derived principally from eolian dust rather than from the underlying rock. These proportions of Sr addition apply only to the soil solution in the rooting zone. The depth of the rooting zone is undetermined, but the $^{87}\text{Sr}/^{86}\text{Sr}$ ratio of runoff indicates that weathering adds Sr to solution below the rooting zone (9).

The similarity in isotopic composition of the Sr in the sapwood, bark, soil litter, and soil solution of the spruce-fir stand (Table 1) indicates that botanical nutrient-cycling processes rapidly homogenize the Sr added by the weathering of bedrock and the dissolution of aerosols. We anticipate that any Sr transferred to the atmosphere as aerosols from the watershed would have a $\Delta^{87}\text{Sr}$ of approximately 15 to 18.

Dust input from remote areas to the aspen watershed provides 75 percent of the Sr in the vegetation, and yet the throughfall data show little aerosol component for the periods sampled. There are two plausible explanations for this apparent contradiction. First, the aspen location was covered by a stand of spruce and fir prior to a forest fire in 1886. The aspen trees may be absorbing aerosol-derived Sr that was captured by the foliage of coniferous stands present before 1886 and has been retained within

the rooting zone. Second, there may be a present-day input of dust to the aspen watershed that was not sampled. March and April in northern New Mexico are marked by low precipitation, high surface winds, and convective overturn of the atmosphere, conditions that favor the entrainment of dust from the soil surface. During this time, the aspen stand is not in leaf. If sparingly soluble aerosols are deposited by sedimentation on the mountain watersheds at this time of year, they would fall directly to the surface of the aspen watershed soil but might be retained by the foliage of the spruce-fir stand and be leached by rainfall during the sampling period. This ex-

planation is consistent with the observation that three times more atmospherically transported Sr was collected in spruce-fir throughfall during the first month of sampling than during the last two. These explanations are not mutually exclusive.

We have found that the Sr isotopic composition is a useful tracer in distinguishing far-traveled aerosols from bedrock inputs to the nutrient reservoir of a forest. This same technique is applicable wherever the $^{87}\text{Sr}/^{86}\text{Sr}$ ratio of the bedrock is different from that of the material delivered to the site from remote sources. A large part of the forest nutrient reservoir in the cases studied is

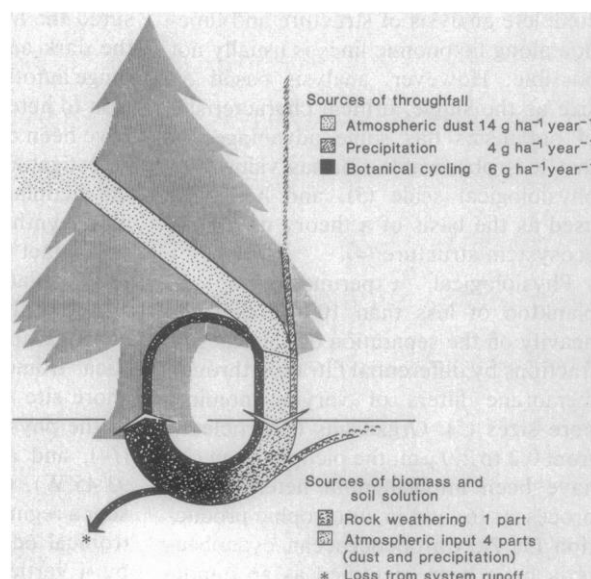
Table 2. Calculation of net throughfall.

Sample	Total throughfall		Precipitation		Net throughfall	
	Deposition (g/ha)	$\Delta^{87}\text{Sr}$	Deposition (g/ha)	$\Delta^{87}\text{Sr}$	Deposition (g/ha)	$\Delta^{87}\text{Sr}$
Spruce-fir						
6/12 to 7/16	21.7	6.2	1.7	5.5	20.0	6.3
7/16 to 9/20	5.4	5.1	2.0	4.1	3.4	5.7
6/12 to 9/20	27.1	6.0	3.7	4.8	23.4	6.2
Aspen						
6/12 to 9/20	12.9	27.6	3.7	4.8	9.2	36.9

Table 3. Calculation of mixing proportions. Mixing percentages were calculated from Eq. 2.

Mixture	$\Delta^{87}\text{Sr}$	Mixing component	$\Delta^{87}\text{Sr}$	Contribution (%)	Atmospherically transported Sr, $\Delta^{87}\text{Sr} = 0$ (%)
Net throughfall					
6/12 to 7/16	6.3	Spruce wood	18	35	65
7/16 to 9/20	5.7	Spruce wood	18	32	68
6/12 to 9/20	6.2	Spruce wood	18	34	66
6/12 to 9/20	36.9	Aspen wood	37	100	0
Aspen tree	37	Aspen regolith	147	25	75
Spruce tree	18	Spruce-fir regolith	88	20	80

Fig. 1. The Sr cycle of a spruce-fir stand. The widths of the arrows above the ground are proportional to the magnitude of the flux in 1975. The widths of the arrows below the ground represent the time-averaged ratio of the weathering and atmospheric supplies; the present-day fluxes and changes in the amount of Sr stored in the biomass were not measured. The loss from the system represents leakage of Sr from the rooting zone to the deeper soil and aquifer; its magnitude is not known.



trapped aerosol from distant sources. Where aerosols of local origin are derived in part from the vegetation, they will also contain a significant proportion of material that was not ultimately derived from the local bedrock. These observations have implications for prospecting techniques based on vegetation or aerosol samples (11). The local nutrient reservoir is recycled from the forest floor to the standing crop of vegetation much more rapidly than nutrients are added to or lost from the reservoir. If that nutrient reservoir is lost, it is reestablished by both bedrock weathering and aerosol trapping, time-dependent processes with different rate controls. The time-integrated input of aerosols to forest nutrient reservoirs cannot be measured reliably without the use of an isotopic tracer.

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Autotrophic Picoplankton in the Tropical Ocean

Abstract. *In phytoplankton of the eastern tropical Pacific Ocean from 25 to 90 percent of the biomass (measured as chlorophyll *a*) and 20 to 80 percent of the inorganic carbon fixation were attributable to particles that could pass a screen with a 1-micrometer pore diameter. Evidence is presented that these are indeed autotrophic cells and not cell fragments.*

Members of the diverse ocean plankton community vary in size over seven orders of magnitude; their taxonomy and even trophic status, is often uncertain (1). Because of the complexity, a complete analysis of structure and function along taxonomic lines is usually not possible. However, analysis based on size as the single, critical characteristic of organisms has some advantages in that it is observable (2), has value as a physiological scale (3), and has been used as the basis of a theory of pelagic ecosystem structure (4).

Physiological experimentation on plankton of less than 10 μm depends heavily on the separation of various size fractions by differential filtration through membrane filters of varying nominal pore sizes (5). Organisms ("particles") from 0.2 to 2.0 μm , the picoplankton (2), have been implicated in heterotrophic processes (6) and in autotrophic production (5, 7). Chroococcacean cyanobacteria have been identified as an impor-

tant fraction of the picoplankton (8), suggesting that this fraction is photoautotrophic, but their rate of fixation of inorganic carbon in the light in the open ocean is not known. Sorokin (9) measured the fixation of inorganic carbon in the dark and considers that in this size range autotrophy is negligible in comparison to heterotrophy (10), but his results have been challenged (11). Finally, some investigators claim (12) that particles in the picoplankton size range that contain photosynthetic pigments do not represent intact viable cells but are fragments or degradation products of larger cells.

We studied two sites in contrasting oceanographic regimes (13): the Costa Rica Dome (9°25'N 89°30'W), an off-shore site where upwelling is important to the physical and ecological dynamics (14), and a site called Biostat (9°45'N 93°45'W), which was selected to represent a regime typical of large tracts of the tropical ocean. Biostat is characterized by a vertical structure that is stable in

time and highly uniform in horizontal extent. Samples were taken daily for 6 days at each station in March 1981.

Many of our results refer to measurements made on size-fractionated samples. We assume (15) that perforated polycarbonate membrane filters (Nuclepore) effect a quantitative separation of size fractions of seston. Our operational definition of picoplankton is particles that pass a 1- μm Nuclepore filter at 18-kPa vacuum but are retained on either Whatman GF/F glass fiber filters or 0.2- μm Nuclepore filters. At Biostat, 94 percent of the $^{14}\text{CO}_2$ fixation measured on 0.2- μm Nuclepore filters is retained on GF/F filters (16). The two sites were similar in that a substantial proportion of the total chlorophyll *a* (as determined fluorometrically on acetone extracts) was found in particles passing 1- μm Nuclepore filters (Fig. 1). At the Costa Rica Dome, where day-to-day variability in unfractionated chlorophyll was appreciable (Fig. 1C), most samples had between 25 and 70 percent of particulate chlorophyll *a* in the picoplankton size fraction (Fig. 1A). At Biostat, where the absolute concentration of chlorophyll was lower (Fig. 1D), 55 to 90 percent of the total chlorophyll *a* was commonly found in this fraction (Fig. 1B). Measurements of fluorescence in vivo on whole and size-fractionated samples, with and without the addition of the photosynthetic inhibitor DCMU (17), indicated the same relationship between size fractions and between sites as did measurements of extracted chlorophyll.

Samples were preserved with glutaraldehyde plus paraformaldehyde and concentrated on 0.4- μm Nuclepore filters. The filters were examined by epifluorescence microscopy (excitation, 365 nm; emission, > 450 nm) which revealed red and orange autofluorescing particles similar to the coccoid cyanobacteria (8). The particles were concentrated more in the euphotic zone (0 to 50 m) than below it, and they were much more abundant at the Costa Rica Dome (Fig. 1E) than at Biostat (Fig. 1F).

The high counts from the euphotic zone at the Costa Rica Dome (0.5×10^6 to 1.5×10^6 cells per milliliter) are about three times the maximum reported by Waterbury *et al.* (8) and 15 times the maximum reported by Johnson and Sieburth (8). The concentrations of cyanobacteria at Biostat were two orders of magnitude lower than at the Costa Rica Dome and were at the low end of the range reported by Waterbury *et al.* but similar to the direct counts reported by Johnson and Sieburth for the open