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THE NUTRIENT BUDGETS OF ROCK OUTCROP ECOSYSTEMS AND THEIR RESPONSE TO SELECTED PERTURBATIONS

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ABSTRACT

Producer and arthropod components were eliminated from lichen-annual herb ecosystems on rock outcrops. The objective was to test the hypothesis that destruction of a biotic compartment of an ecosystem will increase system nutrient loss. Four ecosystems were described and their input-output budgets monitored. The vegetation of one ecosystem was killed with an herbicide (ROUNDUP^R). In another, an insecticide (VYDATE^R) eliminated arthropods. The remaining two were controls.

Precipitation was about 1363 mm during 1976, and input from rock inflow averaged 25369 mm. System discharge was 26422 mm. Evapotranspiration losses were calculated at 312 mm.

Concentration of H^+, Na^+, K^+, Mg^{2+}, and Ca^{2+} in precipitation, rock inflow, and system discharge were all inversely correlated to water volume. Weighted (monthly) concentrations of Na^+ in precipitation were inversely correlated with those of H^+. Average annual (1976) concentrations (mg/l) were: H 0.115, Na 0.177, K 0.142, Mg 0.032, and Ca 0.147. About half the variability in concentrations of rock inflow was attributed to precipitation concentrations. Average annual (1976) weighted concentrations (mg/l) in rock inflow were: H 0.094, Na 0.205, K 0.151, Mg 0.036, and Ca 0.183. There was a significant correlation between weighted (monthly) concentrations of H and those of K, Mg and Ca. Weighted concentrations in discharge were positively correlated with concentrations in rock inflow. Average annual (1976) weighted concentrations (mg/l) in discharge were: H 0.098, Na 0.207, K 0.174, Mg 0.044, and Ca 0.220.

Largest monthly losses of suspended particulates resulted from physical disturbance of the system edge. Bed load sediments were being accumulated, but at a slow rate.

Monthly cation inputs and outputs were dependent on water volume. During 1976, average input in dg/m^2 were H 25.6, Na 54.0, K 43.0, Mg 10.1, and Ca 49.6, while output averaged H 25.9, Na 54.8, K 45.5, Mg 11.7, Ca 58.8. Nutrient budgets were balanced.

Dissolved solids averaged 95% or more of total budgets. Ratios of nutrient standing crop in vegetation to throughput were Na <0.05, K 0.9, Mg 0.7, Ca 0.1.

Above-ground biomass of nonvascular plants, below-ground biomass, litter and soil parameters remained relatively constant over the study.

Soil water pH, exchangeable hydrogen and base saturation reflected changes in inputs.

Insecticide treatment reduced arthropod populations 91%, but densities in other systems were reduced 75% by moisture stress.

Soil microflora biomass was low and decreased with low soil moisture.

Average annual litter decay rates (k) were low: Polytrichum -0.29, Cladonia -0.38, and cellulose -0.10.

Insecticide treatment produced no significant change in any discharge variable.

Herbicide treatment increased cation concentration in discharge, however, only sodium and calcium were significant at $P = 0.06$. Drought produced a greater effect than treatment. Vegetation destruction significantly ($P<0.05$) increased budgetary losses of Na, K, Mg and Ca, but did not greatly accelerate

them. Losses were due to leaching of vegetation.

These ecosystems demonstrated high resistance to the chemical treatments, and lower resistance to drought and physical disturbance.

KEY WORDS: Arthropods, Devegetation, Ecosystem, Hydrology, Litter decomposition, Microflora, Nutrient cycling, Perturbation, Plant community, Rock outcrop, Stability, Weathering.

INTRODUCTION

Over the last several decades, watershed studies have contributed to our understanding of the function of whole ecosystems and their response to perturbation. Small watersheds have permitted study of complex ecosystems on an experimental basis (Bormann et al. 1974, Monk et al. 1977).

Ecosystem behavior, represented by watershed nutrient and water budgets, can be understood by studying the dynamics of internal processes and functional components (Monk et al. 1977). At the most general level of analysis, ecosystems can be conceptualized as being composed of several processes: primary production, consumption, decomposition, and geologic processes. Each level can be further subdivided until the functional roles of individual species populations is identified. We would assume that disruption or destruction of a lower level process would have a severe impact on ecosystem function. Indeed, Bormann et al. (1974) argued that a common ecosystem response to vegetation destruction is an immediate increased loss of nutrients. Very high rates of nutrient loss immediately after ecosystem disturbance have been incorporated into Vitousek and Reiners' (1975) hypothesis for the relationship between ecosystem maturity and its nutrient retention properties. Likens et al. (1970) suggested that destruction of a biotic compartment will lead to accelerated nutrient export and changes, often unexpected, in other compartments of the same ecosystem, assuming that the ecosystem consists of a collection of linearly linked subsystems.

Certain ecosystem responses to short-term perturbation and long-term land management goals can be estimated through budgetary analysis. Investigation of nutrient dynamics of lower level ecosystem components helps explain changes in input-output budgets. Comparison of disturbed or managed ecosystems to similar undisturbed systems, can reveal changes that have occurred in ecosystem structure and function and their magnitude. Clearly, ecosystem response to perturbation can provide understanding of the nature of man's impact on the environment.

Small montane watersheds have several disadvantages which limit their usefulness as experimental ecosystems. Because of their large size, they are very expensive to operate and replicate (Slivitzsky and Hendler 1964, Ackermann 1966, and Reynolds and Leyton 1967, cited by Hewlett et al. 1969; Bormann and Likens 1967; Mitchell et al. 1976) and some valuable experiments cannot be performed because of linkages with other ecosystems (Woodwell 1967, Likens and Bormann 1974). For example, elimination of decomposer microflora or arthropods with pesticide, or release of toxins such as heavy metals or radioisotopes to determine how these perturbations may change structure or modify energy or nutrient flow within ecosystems, would present difficulties in watershed-sized ecosystems. As a result, interest in microcosms for ecosystem study and ecological assessment of released materials has increased considerably (Anon. 1976b, Kerr 1977, Giesy 1976, Ausmus et al. 1977). But microcosms also have limitations since they may oversimplify ecosystem processes to an unrealistic extent.

Research reported here was performed on rock outcrop ecosystems. Weathering of the rock surface results in depressions which accumulate disintegrated rock and organic debris. Plants invade and form distinct aggregrations surrounded by naturally exposed rock which Burbanck and Platt (1964) called island communities, and Shure and Ragsdale (1977) called soil-island communities. These island ecosystems are intermediate in size and complexity between large, complex watersheds and small, simple laboratory microcosms. These intermediate ecosystems might be termed mesocosms (Odum et al. 1978).

These ecosystems are generally irregularly circular, only several meters in width, and the soil is usually deepest in the center or upslope edge. They are isolated except during rain, at which time they may be interconnected by runoff.

The rock outcrop communities are natural ecosystems resulting from evolutionary adaption. The microenvironment of outcrops in the southeastern U. S. is desert-like (Duke and Crossley 1975). They are characterized by intense solar radiation, extreme temperatures, and drought due to rapid runoff of precipitation and low water-holding capacity. Characteristic outcrop species have evolved in this severe microclimate (Murdy 1968).

Island ecosystems are stable over long periods of time (Burbanck and Platt 1964) and are of sufficient size to allow serial sampling, yet not so complex as to present sampling problems.

Island ecosystems are distinctly delineated, but notgeographically limited. System boundaries are well defined, and drainage inputs and outputs can be readily identified for many systems. Numerous granite outcroppings occur throughout the Piedmont region of the southeastern U. S. However, they are not restricted to this area: e.g., similar outcrops have been described elsewhere in this country, such as Texas (Whitehouse 1933) and Illinois (Winterringer and Vestal 1956), and other areas of the world, such as Nigeria (Hambler 1964), Australia (Ashton and Webb 1977), and Bulgaria (Sobka 1973). Thus, similar ecosystems are available for corroborative studies. While most ecosystem studies are based on samples of one (Regier and Cowell 1972), outcrop ecosystem studies can be replicated at a fraction of the time and cost necessary to experiment with forested watershed ecosystems. Total manipulations of various system components may also be easily performed (Platt and McCormick 1964).

Previous research has dealt with numerous aspects of granite outcrop ecosystems, but most of this research has been of a botanical nature (Sharitz and McCormick 1973). Little work has been done on the faunal component of outcrop ecosystems.

Recently McCormick et al. (1974) discussed advantages of using island ecosystems as models for experimental analysis of larger ecosystems. Lugo (1969) determined energy, water, and carbon budgets for outcrop systems, and material cycling has been examined by Garrett (1963), Braun (1969), Hay (1973), and Meyer et al. (1975). Bostick (1968) reported on the distribution of soil fungi, and Snyder and Wullstein (1973) measured nitrogen fixation by several outcrop cryptogams. In addition, litterfall and detritus runoff amounts have been assessed by Bostick (1972, 1973).

The objectives of the present study were to test the hypothesis that destruction of one or more biotic compartments of an outcrop ecosystem will increase nutrient loss, and to increase understanding of the patterns of material flow in outcrop ecosystems. Nutrient budgets for hydrogen, sodium, potassium, magnesium, and calcium were used to measure the system-level response of the ecosystems. Nutrient dynamics of various ecosystem components and processes will help explain changes in input-output budgets. Thus, the study was divided into three phases: (1) a calibration phase, (2) a perturbation period, and (3) a response period. During the calibration phase, four ecosystems were described and monitored for phenology; vegetation density and biomass, and input-output budgets were measured. Two systems were designated experimental and two became controls. Immediately following the initial phase, the two experimental ecosystems were perturbed. In one case, all vegetation was killed with a herbicide and allowed to stand in place. In a second example, an insecticide was applied monthly to eliminate arthropod biophages and saprophages, both above and below ground. Response to perturbation was followed, simultaneously with input-output budgets, by monitoring several internal components and processes: vegetation biomass and elemental concentration, soil properties, arthropods, soil microflora, and litter decomposition.

MATERIALS AND METHODS

Study Area

This study was conducted on a flat rock outcrop located in northern Rockdale County, Georgia, southeast of the junction of Big Haynes Creek and Harrison Mill Road (Nabholz et al. 1977) and is ca. 235 m above sea level. The outcrop is ca. 75 ha in size and is surrounded and partially divided by forest stands.

The geologic substrate is a contorted biotite granite gneiss, Lithonia type (Watson 1902, Crickmay 1952). Layers of quartz and feldspar alternate with layers of biotite. Rock samples also contained magnetite, hornblende, and pegmatite (personal communication, L. Jones).

The climinate is characterized by frontal storms most frequent during cooler months and thunderstorms during warmer months. Mean weekly ambient air temperature (30.5 cm above rock surface) varies from 2.5°C in January to 29.7°C in August (Hay 1973).

The Study Ecosystems

Four island ecosystems of the lichen-annual herb type (Burbanck and Platt 1964) were selected for study. These ecosystems occurred on a rock face where inflow came only from the surrounding rock upslopes (Fig. 1). In order to sample water inflow, it was necessary to divide the rock watershed area into two parts separated by a weir. The upper slope was termed the upslope watershed area (IWS) and the rock immediately surrounding the ecosystem was termed the community watershed area (CWS).

Ecosystems 1 and 2 (E1 and E2), the pair chosen for insecticide experiment, were six meters apart and about 100m from ecosystems 3 and 4 (E3 and E4), the pair chosen for the herbicide experiment, which were also six meters apart. A narrow forest stand separated the two groups. Ecosystem 1 was closest to the outcrop edge. System E3 was smallest in size and E4 had the largest watershed area (Table 1). Yet, total watershed area/system area ratios for E3 and E4 were both about 25. Ratios for E1 and E2 were also similar, 14 and 16, respectively. Watershed slopes consisted entirely of lichen-covered rock, with one exception. Ecosystem 2 had a lichen-annual herb community imbedded with its watershed boundaries. It comprised 15% of the watershed area. System E3 had the shallowest soil (Table 1). Deeper soils were distributed more toward the upslope edge in E1, E3 and E3; and near the center in E4.

Dominant vegetation in all study ecosystems was nonvascular plants: Cladonia spp., Grimmia spp., and Polytrichum commune. Annual plant species which occurred in all systems included Bulbostylis capillaris, Crotonopis elliptica, Diamorpha cymosa (syn. Sedum smallii, see Sharitz and McCormick 1973), Hypericum gentianoides, and Viguiera porteri. Arenaria uniflora (syn. Minuartia uniflora, McCormick et al. 1971) was found only in E4, Talinum teretifolium only in E1, and a perennial, Andropogon virginicus, was present in E1 and E2. Lichens, Parmelia spp., were abundant on all rock upslopes. Bare soil occurred most frequently at system edges.

Environmental Parameters

Ambient air temperature was measured near the ecosystems (Fig. 1) with two Taylor maximum-minimum thermometers mounted 59 cm above the rock surface under wooden shelters. Bulk precipitation was measured with two USDA standard rain gauges. Samples for elemental analysis were collected by water trap-type gauges (Likens et al. 1967) which were 100 cm above the rock surface. One collector was placed near each ecosystem. One ml of preservative solution, phenylmercuric acetate (435 mg/l) was added to each funnel. Samples obviously contaminated were discarded. Collectors were rinsed with distilled water after sample collection, and acid washed or replaced as needed.

Ecosystem Parameters

Input - Output Variables

Input from rock upslopes and output were samples with a weir collection system (Fig. 1). Each weir collection system consisted of a dam, a modified V-notch weir (Fig. 2), a proportional sampler (Fig. 3), and collection bottles. The input dam (Fig. 1) divided the rock watershed area into an upslope watershed area (IWS) and a community watershed area (CWS). Watershed boundaries were located by pouring water on the outcrop. Watershed areawas then determined graphically.

Dams were made from polyurethane foam (ISOFOAM^R, Witco Chemical, New Castle, Delaware) poured on the rock surface which had been brushed to remove lichens and loose rock. ISOFOAM^R adheres to the rock surface to make a watertight seal. The modified weir (Fig. 2) was of V-notch (100^o)

design containing a flow splitter (25^{o}) which diverts a fraction (about 25%) through an opening at its base into tubing. Weirs were made from stainless steel and 15 cm wide (front to back). Nylon netting (≈1.2 cm) stretched over a stainless steel rod frame (Fig. 2) was placed in the flow splitter to collect suspended coarse particulate organic matter (CPOM). Suspended fine particulate organic matter (<1.2 cm) was allowed to enter the collection system. The diverted fraction from the weir was further split into 23 portions by a proportional samples (Fig. 3), one portion going to the collection bottles. The sampler consisted of a slice of polyvinylchloride (PVC) pipe molded to PVC sheet on its lower surface, and a circular PVC sheet bolted to its upper side. Twenty-three holes were drilled through the pipe. A stainless steel strip containing 23 holes (6.35 mm) each with a knife-edge was placed next to the inside surface of the pipe and sealed with silicone adhesive. The proportional sample was mounted on three bolts embedded in the rock and leveled. The diverted fraction from the weir entered the sampler through the center of the cover. If collected samples were too small, one or more holes in the proportional samples were plugged from the outside to increase sample quantity. Samples were rinsed with distilled water after each sample collection. Collection bottles consisted of two 22.3 liter polyethlene G. I. jugs. A stainless steel tube was used to prevent back-pressure as collection jugs filled. One ml of preservative solution, phenylmercuricacetate (435 mg/1), was placed in each bottle. Nylon plastic pipe fittings were used throughout the collection system and silicone adhesive or stainless steel hose clamps were used to make the system watertight.

Accumulated sample from each weir was filtered, mixed and measured in a 20 liter graduated cylinder. Particulates retained by plankton netting were considered to be fine particulate organic matter (FPOM). Throughout the entire study, inputs and outputs of dissolved and suspended solids were sampled as soon as possible after every precipitation event; i.e., every frontal system or thunderstorm if separated by 8 to 12 hours. Sediments in front of each weir were collected periodically.

The highest water level attained at the weir during a precipitation event was measured with plexiglas tubing and powdered cork (Fig. 2). At the input weir, this variable would indicate storm intensity, and at the output weir, the effect of the ecosystem on reducing intensity of water flow could be estimated. A more detailed description of the weir collection system and the peak head recorder is provided in Nabholz et al. (1979).

Water budgets for each ecosystem were calculated for each storm event by mass balance since the modified weirs were not accurate enough to measure watershed inflow and discharge. The water balance equation was

$$Q = P + WSI - E_t - S$$

where Q = system discharge, P = precipitation received directly by the system, WSI = inflow from rock upslopes, E_t = evapotranspiration, and S = basin storage. Precipitation (l) equaled precipitation (mm) times ecosystem area (m^2). Inflow (l) from IWS and CWS was calculated as the product of precipitation (mm) and the area (m^2) minus storage (l) by the rock surface, pools, imbedded island community and/or the weir collection system. The only system with significant pool storage was E3. Storage by pools and imbedded communities equaled their basin storage less losses due to evapotranspiration (E_t), not to exceed their basin storage. Basin storage was determined by flooding each system or pool with distilled water during a drought. Basin storage was 250 liters for pools in the IWS of E3 and 173 liters for the imbedded system associated with E2. Storage by each island ecosystem was 68, 60, 44 and 76 liters for E1 through E4, respectively. Basin storage (S) was full when data collections began and when they were ended. Losses from storage were entirely from E_t.

Water loss by evapotranspiration was estimated by multiplying average seasonal E_t rate (1/da) by number of days since the last precipitation event. If E_t exceeded the basin storage of the system, E_t was set equal to storage. Seasonal evaportranspiration rates were determined from literature (Table 2). McCormick et al. (1974) enclosed island ecosystems in plastic chambers and reported data for a favorable June day. Rate of soil moisture loss was determined by Ragsdale (1969) from 19-25 October during a period of seasonably warm, clear weather. Fall E_t rate was also used for spring because of similarity between mean temperatures. Winter evaportranspiration rate was estimated about half the spring-fall rate based on changes in seasonal E_t rates and mean temperature. Evaporation from pools associated with E3 were estimated from observed drying times: 2, 4, and 6 days for summer, spring-fall, and winter, respectively.

Cation budgets for each study ecosystem were calculated as the difference between inputs associated with bulk precipitation and rock inflow and outputs related with system discharge. Inputs and outputs due to animal movements were assumed to be random and balanced. Inputs from wind-blown allocthonous and rock weathering were not included in the cation budgets. Addition of wind-blown allocthonous material to the systems was probably a small proportion of the amount of wind-blown allocthonous carried by inflow from rock upslopes. No accumulation of wind-blown material was observed in the weir or in front of it between precipitation events.

Rock weathering was investigated with a leaching experiment. Exfoliated rock from under a nearby lichen-annual herb system was collected and air dried. Ten rock samples were rinsed with distilled water and each placed in a one liter TRI-POUR^R beaker and covered with 100 ml of distilled water. A beaker without a rock was used as a control. PARAFILM^R held down by a watch glass covered each beaker. Leachate was replaced after 1, 3, 6, 12, 24 hours; 2, 4, 8, 16, 33, and 73 days. Rock samples were oven dried (100^{o}C for 24 hours). weighed and measured for volume and surface are estimates.

Total amount of each element leached was 52.8 ± 4.9 μg of Na, 106.8 ± 8.7 μg of K, 5.8 ± 0.4 μg of Mg, and 42.3 ± 4.8 μg of Ca. Surface area of the leached granite was determined to be 99 ± 5 cm^2; this includes top, bottom and sides. Leaching rates decreased rapidly the first day and declined to a value of 0.192 ± 0.019 μg/da for Na, 0.236 ± 0.020 μg/da for K, 0.0004 ± 0.0002 μ g for Mg, and 0.100 ± 0.010 μg/da for Ca during the last 73 day leaching period.

These data suggest a serial order of K>Na>Ca>Mg for relative rates at which these cations are weathered. Annual input (dg/m^2·yr) was estimated using mean leaching rate for each element: 0.14 Na, 0.29 K, 0.02 Mg, and 0.11 Ca. These inputs were small (<1%) when compared to annual budgets.

Systems received nutrients directly from precipitation. In addition, they received dissolved and suspended solids in water inflow from community watershed areas (CWS) and from upslope watershed area (IWS) (Fig. 1). Systems received about 75% of the solids from IWS, and none of the bed load from IWS because of the input weir collection system. Community watershed area inputs were estimated from IWS data. Amount of dissolved cations was determined as the product between cation concentration and volume of water. If any concentration value was missing, its last known value was used.

Input of particulate matter suspended in rock inflow to each study ecosystem was the sum of the particulates washed from the community watershed area (CWS) and 75% of the particulates from the input watershed area (IWS). The amount of particulates from the CWS was estimated by converting the total amount of particulates from the IWS to a meter^2 basis and multiplying by the CWS area. The total amount of coarse particulates from the IWS was obtained by multiplying the amount of coarse particulates retained by the weir flow splitter by four, since the weir was designed to retain only 25% of the total amount passing through it. Fine particulates filtered from the collection jugs were first multiplied by a proportionality constant before being multiplied by four, since the proportional sampler was designed to split the sample removed by the weir flow splitter into 23 portions. The constant for E3 and E4 was 23, but the constant for E1 and E2 was 13, since 10 holes in the proportional sampler were plugged to increase sample quantity. Amount of cations in suspended coarse and fine particulate matter was determined as the product between cation concentration and amount of material. If a concentration for fine particulates was missing, the concentration for coarse particulates was used. If both values were missing, the last known value was used. Data from each ecosystem were used for that ecosystem only.

Output of coarse particulates suspended in discharge was estimated by multiplying the amount of coarse particulates retained by the weir by four, since the weir was designed to retain only 25% of the total output. Calculation of the total amount of fine particulates in discharge was identical to fine particulate input from the IWS, with one exception. The proportionality constant for E1 was 14, since nine holes in the proportional sampler were plugged.

Experimental systems received inputs of bed load sediment only from the community watershed (CWS) during the study. This input was calculated by converting accumulated sediment from the input watershed (IWS) to a meter^2 basis and multiplying by CWS area.

The contribution of cations by bed load sediments was limited to those considered biologically available: the organic fraction and exchangeable cations. Additions and losses of cations by organic sediments were calculated as the product of cation concentration of the coarse material (>2.0mm), and total amount of organic matter.

Exchangeable cations were calculated as the product of the amount of exchangeable cations per unit of sediment and the amount of sediments.

Total output of each nutrient will be subtracted from total input to calculate net difference. Input-output variables were evaluated for each storm event and summed for monthly and annual budgets. Nutrient budget amounts were expressed in dg/m^2 of ecosystem which is equivalent to kg/ha making this study comparable to other studies.

Internal System Components

Each island ecosystem was mapped during the calibration period by subdividing it into 20 x 20 cm quadrats. Soil depth, percent cover of non-vascular plants, *Andropogon virginicus*, bare soil, rock, and wood. Numbers of vascular plants were also determined for each quadrat.

Core sampling, composite sampling of vegetation and soil, and a litter decomposition study were begun just prior to system perturbations. Internal processes and functional components were monitored through these studies during the perturbation and response phases in both undisturbed and disturbed ecosystems.

Two circular cores (5.2 cm diam.) were removed from each system each sample date. Location of core samples were stratified according to vegetation and soil depth. Species of vascular plants usually exhibit concentric zonation (Burbanck and Platt 1964) and nonvascular plants form patches of their own. Deeper soil occurs near the system center. I also observed that animal disruption of system edges; e.g., a bird scratching, caused a washout of plant and soil material. Each sample had to contain a much information as possible, yet had to avoid any sampling-induced effects. For these reasons, sample cores were limited to two: one from near the edge and another from near the center. Sample locations were selected to be representative of the entire ecosystem and to include as many groups of plants as possible, but the edge was not sampled to maintain system integrity. Each core was analyzed for water content, arthropod density, plant biomass, litter, root biomass, soil pH, cation exchange capacity (CEC), and organic matter.

Cores were placed on cheesecloth inside plastic bags and kept on ice immediately after removal. They were weighed upon return to the lab and placed in Berlese-Tullgren funnels for 15 days under 25-watt bulbs (Gist and Crossley 1975) for arthropod extraction. Extractions were carried out in a cold room (5°C) to reduce alcohol evaporation and increase the temperature and humidity gradient. Animals were collected in vials containing 70% ethanol. After removal, cores were again weighed for water content determination and analyzed.

Samples of Grimmia, Polytrichum, and Cladonia were removed from each system for elemental analysis. Nine samples were combined to form one composite sample of each plant type each sample date for representativeness.

Vascular plant density and phenology was sampled periodically throughout the study by use of quadrats (5, 7, 10 or 20 cm square), photographic methods, and/or total system counts depending on size and number of plants. Biomass of large vascular plants was estimated by sampling average sized individuals from each community or adjacent lichen-annual herb communities.

Soil microflora biomass was estimated with the adenosine triphosphate (ATP) assay (Holm-Hansen and Booth 1966). In addition, the state of growth of the soil microflora was ascertained through the adenylate energy charge (EC) ratio (Wiebe and Bancroft 1975). Chapman et al. (1971) and Wiebe and Bancroft (1975) demonstrated that actively growing and dividing cells have an EC ratio of 0.8 - 0.95. Cells in stationary growth mantain a ratio of about 0.6, and scenescent or dying cells have a ratio of <0.5.

A composite soil sample consisting of nine subsamples (core, 8 mm diam.) was removed from each system each sample date. Collected soil was thoroughly mixed and kept on ice until returned to the laboratory. Amounts of adenosine triphosphate (ATP), diphosphate (ADP), and monophosphate (AMP) were extracted by the boiling $NcHCO_3$ method of Bancroft et al. (1976). Methods of adenylate analysis were those described by Chapman et al. (1971). Remaining soil was weighed, dried at 50°C for 24 hours, reweighed for water content determination, and analyzed.

Litter decomposition rates for moss (*Polytrichum*), lichen (*Cladonia*) and cellulose strips were determined using the litter bag method (Crossley and Hoglund 1962). Moss and lichen were removed from each system, air dried one week and irradiated with 4 million R of gamma radiation to kill them. This dose is used locally to sterilize soil samples (personal communication,

R. L. Todd). Four sets of seven bags (12 x 4 cm with ca. 1 mm^2 openings) of each type were prepared and weighed. Each bag contained ca. 1 g of material. Bagged material was returned to the system from which it had been removed. One bag of each type was removed each sample date. Recovered bags were placed in Berlese/Tullgren funnels for 5 days to extract arthropods, air dried one week, weighed, and analyzed.

Percentage weight loss was determined from original litter bag weights, and percentage nutrient loss from original samples. Litter weight and nutrient losses were quantified for litter bags using a linear decay model and the exponential decay model of Olson (1963).

A lab experiment was performed to determine the effect of radiation treatment on leachability of cations from plant material. Cladonia and Polytrichum were removed from a lichen-annual herb community near the experimental system and air dried. After half of the material had been irradiated, litter bags were prepared from irradiated and non-irradiated material of each plant type identical to the field study. Two sets of bags were made, except for non-irradiated lichen material which had three. An empty bag was used as a control. Subsamples were retained for chemical analysis. Each bag was placed in a one liter TRI-POUR^R beaker and covered with 100 ml of distilled water. Bags were kept from floating by the use of glass rods and beakers were covered with PARAFILM^R held down by a watch glass. Leachate was poured off and replaced after 1, 3, 6, 12, 24 hours; 2, 4, 8, 17, 32, and 55 days. Bags were air dried, weighed and material chemically analyzed.

Radiation treatment affected both total amount and rate at which cations were lost from moss and lichen material. Greater total amounts of cations were leached from non-irradiated material than from irradiated material in all cases except potassium from Cladonia. Generally, cation losses from irradiated material were greater only during the first 10 hours of the experiment, see Fig. 4 for an example using Polytrichum. Thus annual nutrient loss rates in the litter decomposition study were probably not affected by using material killed by radiation if estimated over a year.

Analytical Techniques

Polyethylene and plypropylene bottles (60 or 120 ml) were used to contain water samples. All plastic ware was rinsed five times with 2N HCl and five times with distilled water. Bottles were rinsed with sample and filled to the brim, if sample quantity permitted. All were kept on ice until returned to the laboratory. Samples for elemental determination were kept at 5°C until analyzed. Samples for pH determination were warmed to 25°C and analyzed upon return to the laboratory. Preservative solution increased sample acidity slightly, but corrections were made through regression analysis. Solid samples were collected and stored in WHIRL-PAK^R bags. Suspended coarse particulate organic matter (CPOM) and FPOM were frozen at -15°C until analysis. Organic matter was dried at 50°C for 24 hours, weighed, dry ashed at 500°C for four hours, diluted (1:20, w:v) with 20% HNO_3 containing 50 μg/l molybdenum (Mo), and stored in 30 ml polypropylene bottles at 5°C until analyzed.

Soil and sediment samples were air dried and hand screened through a 2.00 mm sieve. Soil water pH was determined according to the method of Peech (1965) and exchangeable hydrogen was determined by the method of Adams and Evans (1962). The double acid (0.05N HCl in 0.025N H_2SO_4) extraction method of the Univ. of Georgia Soil Testing and Plant Analysis Laboratory (Nelson and Jones 1972) was used to determine total exchangeable cations. Cation exchange capacity (CEC) was estimated by summing exchangeable hydrogen and extractable cations (Brady 1974). Organic matter (1%) was determined by two methods: Walkley-Black method (Jackson 1958) and dry combustion (500°C for four hours). Dry combustion samples were corrected to oven dry weights by heating disintegrated rock containing essentially no organic matter. Oven dry weights were determined by drying subsamples at 100°C for 24 hours.

Hydrogen ion activity (pH) was measured with a Beckman Expandomatic S-22^{R} pH meter coupled to a Corning glass combination electrode (#476050). Hydrogen ion concentrations were calculated from pH values after Fisher et al. (1968). Elemental determinations were done with a Jarrell-Ash Inductively Coupled Argon Plasma-Emission Spectrograph and with Perkin-Elmer Models 305 and 306 Atomic Absorption Spectrophotometers, following standard procedures. Lanthanum was added to samples prior to Mg and Ca determinations.

Data analysis using the Statistical Analysis System (Barr et al. 1976, Helwig 1977) were performed with a computer. Statistical significance is indicated by asterisks (* = $P<0.05$, ** = $P<0.01$ and *** = $P<0.001$) throughout the study. When regression analysis was used a_0 indicated the Y intercept, and a_1 the slope. Means were reported with one standard error ($\overline{X}\pm SE$).

Weighted cation concentrations for a time period were calculated by dividing the total amount of element for the period by the total water volume for the period.

Ecosystem Perturbations

A herbicide formulation of isopropylamine salt of glyphosate, ROUND-UP^{R} (Monsanto) was used to kill the producer component in a study ecosystem. This is a broad spectrum herbicide and is easily absorbed and translocated throughout contacted plants (Hilton 1974, Anon. 1976a). Glyphosate is relatively nonpersistant in soils, being decomposed by microflora and metabolized by plants. Toxicity to many insect and wildlife species appears to be extremely low. One liter of herbicide solution made up with distilled water was applied with a hand-held polyethylene compression sprayer in a fine spray at highest recommended dosage (365 mg/1).

The insecticide, VYDATE^R L (oxamyl insecticide/nematicide) (DUPONT^R Co.), was used in another system to eliminate consumer and decomposer arthropods above and below ground. The intention was to reduce arthropod populations as previous litter decomposition studies have done with naphthalene (Edwards et al. 1973), but without its phytotoxic effects (Williams and Wiegert 1971, and personal communication, K. Cromack, Jr.). The amount applied (312 mg/1) was sufficient to kill all tested arthropods, but below the maximum rate tested without crop injury. VYDATE^R L has the advantages of being a broad spectrum insecticide translocated throughout plants, yet having minimal phytotoxic effects; and rapid and complete degradation in the field (50% in less than 7 days) at application rates used here (E. I. duPont 1975). Five liters of insecticide solution made up with distilled water were applied monthly with a hand-held compression sprayer in a coarse spray. Insecticide penetrated vegetation and soaked the soil. Distilled water was applied to control system just prior to treatment of experimental ecosystems.

Chemical perturbations were initiated in late November, 1976 after an 11 month calibration period. It was throught that the herbicide would have its greatest effect on the mosses and lichens, the dominant plants in the study systems, at this time. Optimum effect is achieved when ROUNDUP^R is applied while plants are actively growing (Hilton 1974). Desiccation becomes less frequent during November (Hay 1973, Shure and Ragsdale 1977), and growth occurs only under moist conditions in lichens (Hale 1973) and mosses (Anderson and Bourdeau 1955, Keever 1957). In addition, the summer annuals have died and the life cycle of winter annuals has just begun with the establishment of seedlings (Sharitz and McCormick 1973).

RESULTS

Temperature

Ambient air temperature was sinsuoidal over the year (Fig. 5). Mean yearly air temperature was 16.1°C. Highest temperatures occurred in July and the coldest month was January. Large diel fluctuations were measured throughout the year. Ambient air temperatures varied an average of 23°C over 24 hours throughout the year, with largest fluctuations (31°C) in February.

Hydrology

Water flow in all systems can be characterized as ephemeral. Flow began after the rock surface had absorbed ca. 0.9 mm precipitation and ended quickly following a storm event. Total discharge was comprised almost entirely of direct runoff (stormflow). Water flow channels were present in E1, E2 and E4 along one edge of the system. In E3, water flow was restricted to overland flow or subsurface stormflow. The island ecosystems significantly ($P<0.05$) reduced the peak flow rate 15±1%, as measured by the tube gauges at the input and output weirs.

The average monthly water budget (Table 3) indicated that island ecosystems were subjected to large amounts of water flow. Inputs (P + WSI) were highly correlated ($r = 1.00$) with discharge (Q). Losses due to evapotranspiration (E_t) were small. They ranged from 6.2% (June 1977) to 0.3% (December 1976). Inflow from rock upslopes greatly exceeded inputs due to precipitation (ca. 5%), although precipitation alone could have satisfied water requirements most months.

Although precipitation appeared relatively evenly distributed during the study (Table 4), a more important variable for island ecosystems was days without rain. Basin storage is small and lichen-annual herb ecosystems lose water exponentially (Ragsdale 1969). Drought occurs when potential evapotranspiration exceeds available soil moisture. I estimated that drought occurred in the study ecosystems when water lost by evapotranspiration exceeded basin storage, therefore, drought occurred in the study ecosystems after about 9 days without rain in summer, 17 days in spring-fall, and 32 days in winter. Drought events were observed six times in 1976: once each in April and June, and twice each in July and August; and five times in 1977: once each in April through July, and October. Severest droughts were in 1977.

Precipitation amount is not as important as duration between events. A 5.0 mm storm event, assuming only 40% infiltration, could easily replenish the basin storage of a study ecosystem. Seventy-eight percent of storm events during the study period were greater than 5.0 mm.

Mean amounts of precipitation received by the pairs of ecosystems were not significantly ($P<0.05$) different during the study. Storm intensity, measured at the input weir, was variable throughout the study, showing no significant ($P<0.05$) seasonal differences.

Input Variables

Precipitation

No significant differences between mean weighted monthly concentrations due to location during the study were found. Cation concentrations were inversely related to storm size. Higher concentrations were generally associated with storms less than 20 mm.

Concentration of hydrogen was 36% less variable than concentrations of Na^+, K^+, Mg^{2+}, and Ca^{2+} (Fig. 6) which all had similar coefficients of variation (90 to 92%). Minimum values of all cations were observed during late fall and winter. Maximum H^+ concentrations occurred in July both years (Fig. 6) and most peak values of K^+, Mg^{2+}, and Ca^{2+} were associated with months of low rainfall, i.e., February, April, and September 1976; and February and June 1977 (Table 3). Sodium was the only cation whose weighted monthly concentrations were inversely correlated ($r = -0.49^*$, $N = 19$) with those of hydrogen.

Average annual (1976) weighted concentrations were 0.115, 0.177, 0.142, 0.032, and 0.147 mg/l for H^+, Na^+, K^+, Mg^{2+}, and Ca^{2+}, respectively. Relative contribution of cation input on a weight basis was Na>Ca>K>H>Mg. On an equivalent basis H ions dominate: H>Na>Ca>K>Mg. Hydrogen constituted 84% of cationic strength measured. Comparison of average weighted concentrations for the first nine months of 1976 with those of 1977 showed a 19% decrease in H^+, 39% increase in Na^+, 21% increase in K^+, and a 60% increase in Mg^{2+} and Ca^{2+}. These changes were a result of a 16% decrease in mean storm size (24.5±4.9 to 19.4±2.8 mm). The number of storms in each nine month period were similar: 40 in 1976 and 41 in 1977.

Rock Inflow

Inflow from upslope watersheds of the four study ecosystems had similar concentrations of each cation. Analysis of variance indicated no significant differences between the four study ecosystems over the study period.

Cation concentrations were affected by amount of inflow from all IWS areas. All concentrations had significant inverse correlations to inflow volume. About half of the variability in the concentrations of inflow can be attributed to concentrations in precipitation. Regression analysis indicated coefficients of determination (r^2) of 0.39**, 0.64**, 0.52**, 0.54**, and 0.61** for H^+, Na^+, K^+, Mg^{2+}, and Ca^{2+}, respectively. The dependence of cation concentration in watershed inflow on precipitation can be seen by comparing Fig. 6 and Fig. 7. Interaction with the outcrop surface increased dependence of concentration on volume for every cation except calcium, decreased concentration of hydrogen, and increased concentrations of the other cations.

Annual (1976) weighted mean concentrations of H^+, Na^+, K^+, Mg^{2+}, and Ca^{2+} in rock inflow were 0.094, 0.205, 0.151, 0.036, and 0.183 mg/1, respectively. Relative contribution of each cation was the same as observed for precipitation, but on an equivalent basis calcium replaced sodium (H>Ca>Na>K>Mg) signifying weathering of the rock surface.

Minimum concentrations of all ions occurred in November or December (Fig. 7). Maximum concentrations of Na^+ were observed in April of both years, and maximum for other cations generally occurred in months with lower inflow amounts, especially late spring and summer of 1977 (Table 3). There was a significant correlation (19 df) between weighted monthly concentrations of H^+ and those of K^+ (r = 0.47*), Mg^{2+} (r= 0.48*), and Ca^{2+} (r = 0.52). These relationships in watershed inflow were a reverse of those observed in precipitation.

Suspended particulate matter

Suspended particulates consisted largely of foliose (Parmelia) and crustose lichens. Leaves, pine needles (Pinus taeda), twigs, matted pollen, and insect remains were occasionally present. Monthly inputs of suspended particulates were variable for all systems and showed no seasonal patterns. Minimum amounts generally occurred during months with little rainfall; i.e., April and September 1976. Monthly inputs were significantly ($P<0.05$) correlated with rainfall amount in only two systems: E2 (r = 0.74**) and E3 (r - 0.50*).

Ecosystem 3 generally received greater inputs than E4, and those of E1 were larger than E2. Inputs to E1 and E4 were underestimated. It was discovered that inflow water approached both weirs at an oblique angle and created an eddy which tended to float suspended material out of the flow splitter. This is probably the reason why inputs were not more dependent on rainfall. Fine particulates (<1.2 mm) made up the bulk of inputs most months. System E1 had the greatest input of coarse material because of its close proximity to a forest stand. The fraction of coarse material increased during fall and periods of drought when leaf abscission and needle loss was intensified.

Elemental concentrations of suspended particulates were variable and showed no seasonal trends. Concentrations showed similarity between systems, size fractions, and years.

Bed Load Sediment

Sediments were composed of disintegrated granite mixed with a small amount of coarse and fine organic material, consisting largely of <u>Parmelia</u> lichen fragments. Sediment texture is sandy; percentage of sediment with particles less than 2.0 mm is 77.8±2.7% (N = 16). Organic matter content averaged 9.1±0.5%. Bed load sediment was largely deposited at the upslope edge of the study systems.

Sediment inputs to E1, E3 and E4 were correlated with total amount of precipitation over the accumulation interval; however, the correlation was significant (r = 0.98*) only in E4. Inputs to E2 decreased slightly with greater amounts of precipitation.

The amount of bed load sediment actually received by the experimental tems during the study was only a fraction of the amount received prior to the study. Installation of the weir collection system (I), to sample inputs from rock upslopes (Fig. 1), deprived the study ecosystems of bed load sediments from the IWS. The input of bed load sediment to these lichen-annual herb ecosystems in a natural state, i.e., unmonitored state, are available from the authors. The natural input of bed load sediment was artificially reduced to the island systems by the input dam 74, 68, 84 and 93%, respectively.

Herbicide and Insecticide Application

Cation inputs from herbicide and insecticide were estimated based on cation analysis and assuming complete decomposition of the chemicals. Ecosystem 3 was treated with 7 liters of ROUNDUP^R solution from 21 Nov. 1976 to 25 Apr. 1977 (one liter per application). Total cations added during the perturbation period were 0.001 dg/m^2 of Na, <0.037 dg/m^2 of K, 0.0001 dg/m^2 of Mg, and <0.004 dg/m^2 of Ca. Ecosystem 1 was sprayed with 40 liters of VYDATE^R L from 24 Nov. 1976 through 26 May 1977 (5 liters per application). Total cations added were 0.042 dg/m^2 of Na, <0.09 dg/m^2 of K, <0.001 dg/m^2 of Mg, and <0.009 dg/m^2 of Ca. Inputs from herbicide and insecticide solutions were relatively minor additions.

Output Variables

Discharge

Concentration of all measured cations in discharge from the four study ecosystems was inversely related to discharge volume (Table 4). Higher concentrations resulted from smaller discharge volumes. For each cation, all systems had similar intercepts (a_0) and slopes (a_1). Similar relationships were present in precipitation and rock inflow and were maintained in system discharge.

Weighted (monthly) cation concentrations (mg/l) in ecosystem discharge are presented in Fig. 8 for E3 and E4. Low concentrations of Na, K, Mg, and Ca in discharge from E3 during April 1976 (Fig. 8) are anomalies, and should probably be 2 to 4 times greater. No samples of discharge could be collected during the first significant precipitation event for the month due to equipment failure. During data processing, the last known concentration was substituted for a missing concentration rather than relying on an estimation technique. Concentrations used were too low. This is the only case in which the above algorithm gave erroneous results.

Higher concentrations of all cations generally occurred during months with lower rainfall. Fall and winter months had lowest concentrations. Weighted (monthly) concentrations of K, Mg, and Ca were positively correlated with those of hydrogen in control ecosystems E2 and E4 (r's ranged from 0.48* to 0.71***). Relationships of E4 were all stronger than those of E2. Relative contribution of cations in discharge, both on a weight (mg/l) and equivalent (μeq/l) basis, was similar to that observed in rock inflow.

Weighted (monthly) cation concentrations of discharge from the undisturbed ecosystems (Fig. 8) were highly correlated with concentrations in rock inflow (Fig. 6). Correlation coefficients (r) ranged from 0.63*** for Na in E4 to 0.94*** for H in E2 (N = 21). The greatest differences between output and input concentrations occurred during months in which drought was recorded.

Weighted annual (1976) concentrations of Na, K, Mg and Ca in discharge from E2 and E4 (Table 5) were 1% to 49% greater than concentrations in rock inflow. Hydrogen concentrations were balanced: in E2 hydrogen concentration was higher by 5%, and in E4, lower by 5%.

Drought stress during spring and summer 1977 had a greater effect on cation concentrations in discharge than either treatment. Precipitation amount from April through June 1977 was 54% below the same period of 1976. Weighted cation concentrations for the three-month period, April through June 1977, of discharge from E3 and E4 were compared to concentrations for E4 for the same period in 1976. Concentrations of Na, K, Mg, and Ca in the control system, E4, increased 64, 74, 99, and 38%, respectively, over 1976 concentrations, and can be attributed to drought conditions. Concentrations in the disturbed system, E3, also under drought stress, increased 72, 128, 138, and 75%, respectively. These data suggest that 8% of the increase in Na concentrations, 54% of K, 39% of Mg, and 37% of Ca, were due to herbicide treatment alone or an interaction between herbicide treatment and drought.

There were no large increases in discharge concentrations of E3 over E4 during the ten months subsequent to initiation of herbicide treatment (Fig. 8). The largest increases in discharge concentrations from E3 over E4 were observed in May 1977 (78% for Na, 154% for K, 98% for Mg, and 70% for Ca).

The pattern of sodium and calcium concentrations also appeared to change in response to the devegetation experiment. During the first half of 1976, concentrations were consistently higher in E4 (Fig. 8). In 1977, concentrations were similar or higher in the disturbed system, E3.

The effect of the herbicide treatment was evaluated using the paired watershed method (Hewlett and Nutter 1969). The correlation between weighted (monthly) concentrations in discharge from the experimental and control ecosystems was evaluated during the calibration period by regression analysis. This regression equation was compared to a regression equation computed for the treatment period. Slopes for Na, K, Mg, and Ca steepened during the treatment period, and the slope for H decreased. The Y intercepts remained similar. No pair of slopes was significantly different at P = 0.05, however Na (t = 2.018) and Ca (t = 2.019, 16 df) were significant at P = 0.06 (df = 16). This analysis indicated that concentrations of Na and Ca in discharge were probably altered by the devegetation experiment. Concentrations from E3 rose faster than concentrations from E4 over the range of concentration values encountered during the treatment period.

A similar analysis of the insecticide experiment revealed no significant changes in the relationships between E1 and E2 during the treatment period.

Suspended Particulate Matter

Particulates suspended in discharge were similar to those sampled in rock inflow with additions of fragments of fruticose lichens, mosses, and vascular plants.

Losses from E2 and E4 were overestimated, and probably underestimated for E3. All weirs were not at right angles to water flow. This was discovered after observing the sediment accumulation pattern over many storm events. Water splitters were set in the dam in such a way that they either oversampled or undersampled suspended particulates.

Herbicide and insecticide treatments produced no observable changes in quantity of composition of suspended particulates. Although masses of dead Collembola were observed in the fine particulate fraction occasionally during insecticide treatment, they were a minor component of the total sample.

Outputs of all systems were variable. Losses were generally smaller during fall and winter seasons. Minimum losses from E1, E4 and E4 occurred during April 1976, the month with the least precipitation (Table 3). Largest monthly losses from E3 and E4 resulted from washouts caused by a bird or small mammal disturbing the system edge. Loss of suspended material from E2 during February 1976 was more than two times greater than the next largest monthly loss, and comprised 31% of total annual losses. Losses during June 1977 from E4 were 22% of total annual loss. A significant relationship between monthly loss of suspended particulates and monthly rainfall amount (r = 0.59*, 15 df) for E4 was demonstrated if the June 1977 value is ignored.

Losses consisted primarily (<50%) of coarse particulate (>1.2 mm) in E1, E2 and E4 (Table 12). Amounts of fine and coarse materials were variable and followed no seasonal trends.

Annual (1976) losses of suspended particulates exceeded inputs in E2 and E4, and were less than inputs in E1 and E3. These data indicated net losses of suspended particulates of -274 and -291 dg/m^2 for E2 and E4, respectively; and net gains of 13 dg/m^2 for E1 and 769 dg/m^2 for E3. Considering known biases of the input and output weirs in sampling suspended particulates, losses from E2 and E4 were too large, the gain for E1 was too small, and the gain for E3 was too large. All the study ecosystems were probably balanced or slowly accumulating suspended particulates during the study period. Indeed, data for the four systems were averaged, and a net gain of 54.3 dg/m^2 was calculated. This annual gain of suspended particulates was only 9% of mean output.

Elemental concentrations of suspended material in discharge were variable and no seasonal patterns were observed. Concentrations were similar over locations, size fractions, and year. There was general agreement between cation concentrations of material in discharge and rock inflow.

Bed Load Sediment

Output sediments were similar in composition and texture to input sediments. Sediment texture was sandy; proportion of sediments with particle sizes<2 mm were 69.2±3.6% (N = 16). Organic matter averaged 18.1±1.6% during the study. This was a significant ($P<0.001$) increase of organic matter relative to input sediment. The amount of sediment lost during each sample interval from E1, E3 and E4 was correlated with amount of precipitation during the interval, but only losses from E3 had a significant relationship ($r = 0.97^*$, N = 4). Losses from E2 were inversely related to rainfall ($r = -0.96^*$).

Rates of sediment loss from E1 and E3 were not affected by experimental perturbations; therefore, annual losses were estimated for the period 13 May 1976 to 12 May 1977. Annual losses and gains of sediment during the study were balanced in E2, E3 and E4. Ecosystem 3 showed a net loss of 14.6 dg/m^2, and E2 and E4 gained 29.1 and 14.3 dg/m^2 of sediment, respectively. Net gains and losses for E2, E3 and E4 were less than 13% of inputs or outputs. Ecosystem 1 had large net losses of 808.4 dg/m^2 and losses were observed every sample interval throughout the study period.

As discussed earlier, the input dam deprived the study ecosystems of sediment from the IWS. Sediment budgets for these systems in an unmonitored state can be obtained by subtracting losses from total inputs. These lichen-annual herb ecosystems in a natural state would have shown large net annual gains of sediment: 77.4 dg/m^2 for E1, 568.0 dg/m^2 for E2, 2003.7 dg/m^2 for E3, and 3800.6 dg/m^2 for E4. Mean (N = 16) inputs for the unmonitored systems were significantly greater than outputs (t = 3.746***, 30 df).

Nutrient Budgets

Average annual nutrient budgets for the four lichen-annual herb ecosystems undisturbed by the chemical perturbations are given in Table 6. Annual budgets of dissolved and suspended particulates included data from 1976, and bed load sediments from the period 13 May 1976 to 12 May 1977, in spite of the fact that the calibration period ended 24 Nov. 1976. Dissolved cation inputs from the chemical treatments were relatively insignificant and outputs were not affected until 1977. Losses of suspended and bed load sediment were never affected by the experimental perturbations during the study.

Dissolved solids dominated all the budgets comprising 95% or more of the cation flow. Cation input and output by suspended particulates was generally 10 times greater than amounts in bed load sediment. Total cation budgets were balanced. Systems were losing small amounts of cations in the form of dissolved solids and bed load sediments, and gaining small amounts in suspended particulates; however, inputs were not significantly ($P<0.05$) different from outputs.

Budgets for these systems in a natural state, i. e., no input dam, would have been larger than those presented (Table 6). Inputs of dissolved and suspended solids were reduced about 19±1% by the input weir collection system. Assuming the study ecosystems also received bed load sediment from their IWS areas, average cation inputs from bed load sediment would be 0.032 ±0.011, 0.580±0.279, 0.154±0.035, and 0.489±0.103 dg/m^2 of Na, K, Mg, and Ca, respectively. Under this condition, input of sediment sodium, magnesium and calcium would be increased significantly ($P<0.05$). Potassium was significant at $P = 0.14$. Also, inputs would exceed outputs: Mg at $P<0.05$, but Ca, Na, and K significant only at $P = 0.08$, $P = 0.13$, and $P = 0.16$, respectively. However, the contribution of cations to the total budget would increase only about 1%.

Monthly input and output of cations for the study ecosystem E3 is presented in Fig. 9. Input included precipitation and dissolved and suspended load in watershed inflow. Output was comprised of dissolved and suspended load in discharge. Bed load sediments were excluded because they were sampled every 130 da, while dissolved and suspended materials were monitored after every rainfall event.

Outputs of cations were strongly dependent on inputs. Hydrogen showed the greatest dependence, and magnesium and calcium displayed least.

Both inputs and outputs of most cations were related to amount of precipitation. Hydrogen and sodium were generally more dependent than K, Mg, and Ca. Low flows occurred when rainfall was small; e.g., April 1976, and increased with greater precipitation.

Elemental flow in E2, E3 and E4 was larger than flow in E1. Mean monthly cation input (H+Na+K+Mg+Ca) to E1 was significantly ($P<0.05$) less than input to the other study systems, which were similar to one another.

Net gains and losses of cations were difficult to visualize because of the correlation between input and output, and monthly variability. Therefore, net amounts are presented in Figs. 10 and 11. Net gains and losses of cations averaged 66±3% smaller than the amounts flowing through the study ecosystem. Mean monthly throughput of cations ($N = 21$) was greater than average absolute net amount, and highly significant ($P<0.001$) for all study ecosystems. Net amounts were generally not correlated to monthly precipitation:

only net amounts of hydrogen in E3 and calcium in E4 were inversely related to precipitation, having coefficients of determinations (r^2) of 0.50** and 0.24*, respectively. In E3, potassium showed a direct correlation (r^2 = 0.24*).

Cation budgets showed that E2 was slowly accumulating Na, K, Mg and Ca throughout the study, while E1 was losing nutrients. During the months in which E2 showed the greatest gains in potassium, E1 showed its greatest losses. Losses and gains of calcium and magnesium were more closely related in the two systems. Greatest net losses of cations generally occurred during or following periods of drought stress; e.g., April and July 1976, and July 1977.

Insecticide treatment did not significantly affect any nutrient budget. Although losses of K and Ca in late summer 1977 from the disturbed ecosystem, E1 (Fig. 10), exceeded losses during the same period in 1976, severity of drought stress was greater in 1977, and losses quickly diminished with increased precipitation during August and September. The correlation between cation output from E1 and E2 during the calibration phase was not significantly ($P>0.05$) altered for any cation during the treatment period.

Ecosystems 3 and 4 displayed different patterns of net gains and losses of cations than those observed in E1 and E2 (Fig. 11). Both systems suffered their greatest losses in the calibration period, during spring and summer 1976. Losses of Na, K, Mg and Ca from E4 were generally greatest in May 1976. During the same month net losses of K and Mg also peaked in E3. A two-month time lag in losses in Na and Ca was observed in E3. The only disturbance observed during this period was drought stress in April 1976. Only potassium showed losses during the summer 1977 similar to those observed in E1 and E2.

Herbicide treatment increased nutrient loss from the lichen-annual herb ecosystem, but did not greatly accelerate cation loss. Prior to the perturbation, E3 generally had larger net gains or smaller net losses of Na, K, Mg and Ca than

E4 (Fig. 11). Two to four months after initiation of herbicide sprayings, losses from E3 usually exceeded those of the undisturbed system, E4. Total 1977 budgets showed losses of Na, Mg and Ca from the devegetated ecosystem, compared to gains of Na and Ca in the undisturbed system, E4, and a balanced Mg budget. Losses of K were similar, however, net loss from E3 in 1977 increased 9.3 dg/m^2 over 1976, while loss from E4 rose only 1.7 dg/m^2.

Treatment effect was appraised with the paired watershed method using monthly output. Potassium showed a significant decrease in slope (t - 2.125*, 16 df). Greater discharge amounts from E3 were associated with lower discharge from E4, and smaller outputs at the upper range of values for E4 following devegetation. Although slopes for Na, Mg and Ca remained similar to pre-perturbation values, regressions were significantly ($P<0.05$) elevated. Outputs from E3 increased over those from E4, relative to the nine months prior to treatment. Discharge of hydrogen was not significantly affected by the experiment.

Ecosystem Components and Processes

Vegetation

Nonvascular plant biomass remained relatively constant over time and sample location. Only in E2 was plant biomass near the system center consistently greater (76%) than near the edge. In fact, biomass of edge cores was generally greater than those centrally located in E3. Therefore, mean nonvascular plant biomass in each system was estimated by averaging the samples during 1976 and 1977 (Table 7). Ecosystem 1 had the least amount of Grimmia, and E3 had the least amount of Polytrichum. Although no death of nonvascular plants was observed during 1977, there was evidence of death in April 1978.

In E1, E2 qnd E4 large patches (about 25 to 30%) of Polytrichum were dead. Evidently, the series of drought events from April through October 1977 caused this mortality, but could not be detected until sufficient decay had occurred.

Numbers and biomass of live vascular plants changed greatly over time. Plant density was high in spring and decreased during the growing season largely from moisture stress. Biomass in the herbicide-free systems increased through June, but decreased in E2 and E4 by October due to death and stunting from drought. Indeed, flowering of summer annuals was delayed about a month in 1977 compared to 1976 flowering dates. Late summer annuals that survived periods of moisture stress during summer increased their potential to gain biomass greatly in fall; e.g., only one V. porteri survived to flower in E1, yet it comprised 96% of the vascular plant biomass during October 1977, and outweighed all other vascular plants in the other study systems combined. Maximum vascular plant biomass during the study was generally less than 1% (0.9, 0.8, 1.4 and 0.4%, respectively) of total above-ground biomass in any system.

Below-ground biomass consisted largely of moss rhizoids (Table 7). Polytrichum moss had deep rhizoids that penetrated a centimeter or more into the soil; in contrast, Grimmia was very shallowly rooted. Total root biomass was generally greater near the center rather than the edge, and constant over time in all systems. Root biomass sampled in each system was 17, 8,2 and 10%, respectively, of total above-ground plant biomass. Vascular plant root biomass was probably underestimated. Significant amounts of roots were probably under rock exfoliations which occur under the systems. During the study, four adjacent lichen-annual ecosystems had to be excavated; beneath three of these systems rock exfoliations were discovered with a dense of roots between them and the outcrop surface. These areas represent an unknown variable that cannot be sampled without destroying the system.

Herbicide treatment of E3 had completely eliminated annual herbs by January 1977; *Polytrichum* was dying, and *Grimmia* showed numerous brown patches. Treatment was stopped on 25 April 1977; *Polytrichum* had died, and *Grimmia* was dying throughout the system. This system was remapped 24 October 1977; *Grimmia* (>90% killed), and *Polytrichum*, although dead, were identifiable and their gametophytes still standing upright. *Caldonia* lichen seemed unaffected by the herbicide treatment. The entire community was still intact; percent cover estimates were very close to July 1976 values (Table 1) for all categories. The number of dead *Hypericum* stems had not changed greatly. One hundred and twenty stems were counted in July 1976, 111 stems were still present 15 months later (4 stems were removed for analysis). Only 5 stems had been lost between sampling dates.

The initial states of vegetation recovery were observed at this time. *Diamorpha* seedlings were present throughout the community, especially on bare soil areas between *Grimmia* patches and those created by core sampling. During the July 1976 mapping, *Diamorpha* was restricted to the outer edges (40 cm or less), and was present in 62% of sampling quadrats. *Diamorpha* seedlings were present in 96% of quadrats in October 1977. In addition, bright green patches composed of a very fine layer of plant growth, either moss protonema with bud-like gametophytes, or algae (or both) was observed on soil and dead moss.

On 9 April 1978, ecosystem 3 was still intact, and adult *Diamorpha* plants were present throughout the system, but still largely restricted to the edge. It appeared that *Cladonia* was playing an important role in limiting *Diamorpha* density, either through physical or chemical interference during

Diamorpha's seedling or rosette stages. Diamorpha was the only spring annual present, and seedlings of summer annuals were not observed. Polytrichum gametophytes were upright and still identifiable. Grimmia patches were intact but gametophtes were no longer identifiable.

The summer annual, H. gentianoides, did not reinvade E3 the year following devegetation. Only four small clumps of B. capillaris grass were observed on 31 July 1978.

Elemental concentrations of nonvascular plants prior to disturbances and vascular plants were similar in all systems. Fluctuations of cation concentrations in Cladonia from November 1976 to June 1977 were variable, but similar in control and experimental systems. Most concentrations either fluctuated around initial values, such as potassium and magnesium in ecosystems 1 and 2, or increased 22 to 84%. Concentrations which increased were sodium in systems E1 and E2, magnesium in E3 and E4, and calcium in all. Sodium and potassium concentrations in E3 and E4 decreased; losses ranged to 66% of November concentrations.

Cations concentrations in Polytrichum had increased by May 1977 in all systems; increased ranged to 168%, relative to November values. Many concentrations decreased in June, and were similar in E1, E2 and E3; decreased in the herbicided system, E3, were relatively larger (Fig. 12). Sodium and potassium showed the greatest change; magnesium was less dramatic. Calcium concentrations continued to increase through June in both the disturbed and undisturbed system.

Concentrations of all cations in Grimmia increased through June (ranged to 85%) in E1, E2 and E4. In the disturbed system, E3, cation concentrations of Grimmia increased from 31 to 161% by May, and then sharply decreased during June 32 to 43%.

Changes in elemental standing crops of nonvascular plants were strongly associated with fluctuations in their elemental concentrations. Elemental standing crops of vascular plants were correlated to changes in their biomass. The maximum amount of nutrients in vascular plants during 1977 was a small percentage of nutrients contained in nonvascular biomass during November 1976 (Na, 1%; K, 5%; Mg, 3%; and Ca, 9%; percentages were averaged over systems).

Soil Properties

Amounts of litter, soil bulk density, organic matter content and cation exchange capacity were variable and showed no consistent pattern during the study (Table 8). Biomass to litter standing crop ratios were 24 and 29 in E1 and E2, respectively, and larger than E3 and E4, 15. Cation concentrations of litter were similar in all systems and averaged 55±7 μg/g of Na, 828±72 μg/g of K, 621±53 μg/g of Mg, and 2060±302 μg/g of Ca (N = 26). Organic matter content and cation exchange capacity were positively correlated: r = 0.64** (N = 83).

Soil water pH generally increased 0.48 and 0.42 units by May 1977 in E1 and E2, respectively, and 0.13 and 0.15 units by April in E3 and E4. All values returned to November 1976 levels during June. Amounts of exchangeable hydrogen in the study ecosystems generally decreased through May and were associated with increases in base saturation of 81, 6, 114, and 82% respectively, by June. Changes in these soil parameters were concurrent with decreases in hydrogen concentrations and increases in amounts of cations dissolved in precipitation (Fig. 6) and rock inflow (Fig. 7). Soil water content (Fig. 13) significantly decreased during the study period, and was correlated (f = 0.57**, N = 28) with monthly rainfall amounts (Table 3).

Chemical perturbations produced no observable changes in any soil parameter. Fluctuations in soil components were similar in disturbed and control systems and were generally associated with changes in water and cation inputs.

Arthropods

Arthropod densities prior to chemical perturbations were similar in all study systems. There were no significant differences in density due to location: edge versus center samples. Mite (Acarina) populations were comprised largely of immatures, while most Collembola were adults. Mites made up 84% of the total population, and Cryptostigmata were the most abundant mite (53%). Collembola were next most abundant group (15%), and spiders (Araneida) and insects (Insecta) were also present (about 1%).

Insecticide treatment reduced total arthropod populations in E1 by 91% by June (Fig. 14), but densities in other systems also became reduced about 75%. These reductions probably resulted from moisture stress. Minimum densities of many groups occurred either in April or May, which were months of minimum rainfall (Table 3) and soil moisture (Fig. 13). Mites were more sensitive to the treatment than Collembola. White mite numbers were depressed 84 and 81%, respectively, in undisturbed systems (E2 and E4), collembolan numbers dropped only 29 and 64%, respectively. Rapid rises in density were observed for all arthropod groups except mites in E1 and spiders. Increases in Acarina groups, Isotomidae, and Hypogastruridae generally occurred in January or February (Fig. 14); Entomobryidae and Sminthuridae were later, either in March, May or June. Increases ranged to 2800%, but averaged 500%. Densities of mites were prevented from rising by the insecticide in E1, and spiders were never abundant.

Herbicide treatment of E3 seemed to enchance collembolan families, Entomobryidae and Sminthuridae. Although Entomobryids showed increases in E2 and E4 of 60% and 100%, respectively, over November densities numbers in E3 rose 329% and were 800% denser than E4. While numbers of total Collembola decreased 64% in E4, density rose 143% in E3. Although the collembolan population showed large gains in E3 by June, numbers were still relatively low, only 34 ind/25 cm^2.

Soil microflora

Standing crops of soil microflora, indicated by concentration of total adenylates, was about double in E1 and E3 than E2 and E4 prior to chemical perturbations. Adenylate energy change (ED) ratio ranged from 0.5 to 0.6 and indicated that microflora populations were in a stationary growth phase.

Fluctuations in adenylates were similar in all systems during the study and were therefore averaged. Microflora biomass decreased through April (Fig. 15) reaching their lowest standing crop and then increasing to predisturbance levels.

Adenylate energy charge ratios ranged from 0.42 to 0.80. Average EC ratios were highest in February (0.71) and lowest during April and May (0.58) (Fig. 15). Lowest microflora biomass and slowest growth states were associated with greatest soil moisture stress (Fig. 13) and was probably the cause of the reductions.

Litter Decomposition

Weight loss of _Polytrichum_, _Caldonia_, and cellulose from litter bags approximated a simple linear decay function over the 334 day study. Neither devegetation nor insecticide treatment had any observable effect on decay rates.

The study was continued for 120 days after cessation of insecticide application without any observable increase in decay rates. Loss rates of each type of material were similar in all study ecosystems regardless of treatment, so an average rate of decay was calculated (Table 9). Losses of Cladonia were greater than losses of Polytrichum, but loss rates were not significantly different (P>0.05). Loss rates of cellulose were considerably lower than those of moss and lichen.

In general, fluctuations in the amounts of nutrients in Polytrichum and Cladonia were very variable, and could be fitted neither to a linear decay model (Table 9), nor to an exponential decay model (Olson 1963). Losses of sodium and potassium from Polytrichum and Cladonia were characterized by large nutrient losses during the first 45 days in the field. Sodium content of Polytrichum moss decreased an averaged of 58±9% from initial values; Polytrichum potassium, 83±5%. Cladonia Na and K losses were 77±3 and 92±1%, respectively. From January to June 1978, nutrient content of Polytrichum remained stable, and Cladonia nutrient content increased: sodium accumulated at an annual rate of 16%, and potassium was accumulated significantly at a rate of 31% (r = 0.70**, N = 28).

Magnesium and calcium losses from Polytrichum significantly fit the linear loss model once each: magnesium in E2 (K = -0.43, r = 0.79*), and calcium in E3 (K = -0.77, r = 0.90**). Cladonia litter generally accumulated Mg and Ca throughout the study. Only magnesium was less in E4 (K = -0.28); annual accumulation rates ranged from 9% to 267%. Cladonia accumulation rates for magnesium in E3 (118%/yr, r = 0.72*) and calcium in E1 (267%/yr, r = 0.89**) were significant.

Number of arthropods extracted from litter bags were variable (0 to 422) but generally increased during the study. Numbers were severely depressed during April 1977 in all systems. Insecticide treatment in E1 kept numbers in litter bags low through June 1977, but by October (120 days after the last insecticide treatment), total numbers in E1 were similar to the other systems. During the study, mites outnumbered Collembola 2 to 1. Mites were 1.3 times more abundant in _Cladonia_ litter, and 1.3 times more Collembola were extracted from _Polytrichum_ litter bags. Herbicide treatment of E3 appeared to have little effect on arthropod numbers. In lichen bags, mites were generally more abundant in E4 than E3; Collembola were more abundant in E3. In _Polytrichum_ bags, numbers were similar in both systems.

DISCUSSION

Lichen-annual herb ecosystems in this study receive more water on an areal basis than do some tropical rain forests (Odum 1971, Golley et al. 1975), yet they are characterized by vegetation adapted to arid conditions. Mosses and lichens are resistant to desiccation. Succulents are present, such as Diamorpha and Talinum. Viguiera porteri can remain wilted as long as 14 days and still recover (McCormick et al. 1974). Unlike montane watersheds which receive water directly from precipitation, most water to outcrop systems comes as indirect drainage of precipitation from surrounding rock upslopes. Rapid flows of short duration pass around and through outcrop systems with only a small portion being retained by the shallow soil mass. High rates of evapotranspiration (McCormick et al. 1974) can deplete soil moisture quickly, producing moisture stress and selecting for drought resistant species.

Land sandhill ecosystems, outcrop ecosystems can be characterized as "deserts in the rain" (E. P. Odum, personal communication). Yet, soil-island ecosystems contain a unique vegetation community that appears to be maintained by a combination of frequent rains to restore soil moisture for vascular plants and frequent dews for the maintenance of the nonvascular species. Polytrichum commune must receive actual precipitation in the form of fog, dew, or rain for growth (Anderson and Bourdeau 1955). Frequent dew, especially during the summer (Court 1974, Trewartha 1968), allows a morning pulse of photosynthesis in lichens and mosses, and dew is probably also utilized by animals (Noy-Meir 1973).

Water from precipitation is the primary transporter of dissolved and suspended solids and sediments into and out of the systems. Bulk precipitation contributes a major portion of the dissolved solids (86% of Na, 94% of K, 89% of Mg, and 80% of Ca during 1976), and hydrogen which dissolves cations from the outcrop surface. The latter process may be increasing since hydrogen ion activity (pH) of precipitation has decreased in NE Georgia from 5.20 in 1965-66 (Cogbill 1976) to 3.94 in 1976 (this study), an increase in H^+ concentration of about 19 fold.

Lichens on the outcrop surface can also contribute considerable amounts of acid, which can generate additional cations through weathering of the rock surface. For example, hydrogen concentration of rock inflow was greater than its concentration in precipitation by 8% in May and 25% in June 1977 (Figs. 6 and 7) and resulted in increased calcium concentrations of 157 and 52%, respectively. Ascaso and Galvan (1976) have demonstrated the ability of organic acids found in thalli of Parmelia conspersa to release cations from granite and gneiss. Rock decomposition is accelerated during warmer months when surface temperatures are elevated (Shure and Ragsdale 1977), conditions of lichen growth are optimal, and precipitation hydrogen concentration is highest (Fig. 6). This acceleration is concurrent with growth of vascular plants in outcrop systems.

Unlike findings reported for Coweeta and Hubbard Brook watersheds (Johnston and Swank 1973, Likens et al. 1967), cation concentrations in watershed inflow and discharge showed significant inverse correlations with water amount (Table 4). Annual weighted concentrations of cations in inflow and discharge (Table 5) from outcrop island ecosystems were also considerably lower than those reported by the above studies. Inflow water does not all pass through the system soil mass, and the portion that infiltrates passes through the soil volume quickly. Sandy soils of these outcrop ecosystems (>85%, Meyer et al. 1975) lack the large buffering capacity of mountain watersheds, and thus do not enrich percolating water with cations leached from parent material.

In spite of the inverse relationship between concentration and water volume, monthly input and output of cations were still strongly dependent on volume of water flow. Changes in concentration of a cation could not be interpreted as an accurate index of input or output amounts for outcrop systems as Vitousek and Reiners (1975) and Vitousek (1977) have suggested for larger mountain watershed ecosystems.

Nutrient budgets for the undisturbed island ecosystems during 1976 (Table 6) indicated that gains and losses of nutrients were balanced. Dissolved solids comprised 95% of the cation flow, and nutrient flow due to suspended solids was 10 times greater than amounts in bed load sediment. The input weir collection system reduced input of dissolved and suspended solids about 19±1% and bed load sediment 80±6%; however, total budgets would remain balanced with its removal. Most of the added dissolved and suspended solids would probably flow through the systems, since throughput comprises 91±3% of the nutrient flows. Although significant gains of some nutrients from bed load sediment can be demonstrated, the contribution by sediment to the total budgets would increase only about 1%. Material budgets (biologically available plus unavailable) of bed load sediment indicated that these lichen-annual herb ecosystems in an unmonitored state would show significant ($P<0.001$) net gains of sediment. Taken together, the four lichen-annual herb systems appear to be near steady state for nutrients, but accumulating material at a very slow rate. Hay (1973) has reported similar results for diamorpha ecosystems. Although these soil-island systems are stages in primary succession (Burbanck and Platt 1964, Shure and Ragsdale 1977), for short-term, i.e., annual, nutrient studies they can be assumed to be in steady state. The driving force of succession appears to be the accumulation of sediment and the exfoliation of underlying rock, but these processes are extremely slow. This conclusion becomes more evident if we look at replacement times for the four study ecosystems. Assuming granite depressions were emptied, it would require 303, 539, 128, and 76 years, respectively, for inputs of bed load sediments to replenish soil volumes.

Crossley et al (1975) and others have characterized these lichen-herb ecosystems as accumulator systems. They observed that these systems accumulated fallout radionuclides, and some of these nuclides, such as ^{90}Sr and ^{137}Cs, are metabolized by mechanisms that are similar to those for nutrient elements, such as Ca and K. This accumulation phenomenon by island ecosystems results from the great affinity of lichens to absorb heavy radioactive elements (Tuominen and Jaakkola 1973) and the deposition pattern of bed load sediment in the systems. Lichens exhibit a high efficiency for the retention of ^{137}Cs and other heavy radioactive elements. Lichens accumulate ^{137}Cs much more efficiently than ^{40}K; the contribution of ^{40}K to the natural radioactivity of lichens was only 2-5% of the total β activity (Tuominen and Jaakkola 1973). Lichens act as a substantial reservior of ^{137}Cs for a long period of time because of their longevity and the long half-life of Cesium-137. The lichen, Parmelia, which is common on the rock surface of outcrops, retains nearly all of the ^{137}Cs intercepted because of its large surface area per unit weight. Plummer (1969) and Plummer and Helseth (1965) reported Parmelia becomes the most radioactive plant present on the outcrop following a fallout contamination. Fragments of Parmelia thalli and rock debris, many with thalli fragments attached are produced by weathering processes and are washed into island ecosystems as suspended and bed load sediment. These sediments accumulate at the upslope edges of the systems. The lichen thallus with its radionuclides is incorporated into the soil. This explains why McCormick and Cotter (1964) and Plummer and Helseth (1965) found greater levels of radioactivity at the upper and outer edges of island systems. Systems closer to the outcrop base accumulated greater radioactivity because they generally have larger watershed areas than systems near the top. Vascular plants which grow near system edges, primarily Diamorpha, show the greatest bioaccumulation of radioisotopes of any plant species in island communities (McCormick and Cotter 1964). In summary, accumulation of radioactive fallout by island ecosystems is largely a function of the molecular weight of the radioisotope, the presence of the lichen, Parmelia, which is particularly absorptive, and geomorphology.

These lichen-annual herb ecosystems can be characterized as open systems (Odum 1971). Nutrient budgets are tied closely to the pattern of precipitation. Outputs are highly dependent on inputs and both inputs and outputs of most cations were related to rainfall amount. Nutrient inputs and outputs are large; about 10 times larger than inputs to nearby forested areas (Krebs and Golley 1977, Swank and Henderson 1976). Most of this increased input comes from drainage from rock upslopes. Nutrient input by direct precipitation is similar to nearby forested areas. It should be emphasized that most soil-island ecosystems have considerable larger watershed upslopes than the systems in this study, and consequently greater material flows per unit area.

Annual inputs of Na, K, Mg and Ca in dissolved and suspended solids exceeded amounts of those nutrients bound in system biomass. The ratio of elemental standing crop to throughput ranged from 0.9 for K in E2, to <0.05 for Na; ratios for Mg averaged 0.7 and Ca was 0.1. Ratios of nutrient standing crops to nutrient throughput in forest systems are much greater than 1.

Large percentages of the standing crop of nutrients, especially potassium and magnesium, in lichen-annual herb ecosystems are held by the vegetation subsystem rather than in the soil (Table 10). These patterns are like those of tropical rain forests (Golley et al. 1975, Odum 1971), and Meyer (1972) has shown a similar apportionment in annual perennial herb ecosystems. The large amount of water moving through these small biomass systems is probably the major factor in creating these patterns. Nutrients not bound tightly will be easily leached from these systems. Tropical forests prevent large losses of scarse nutrients and maintain their high productivity by rapid recycling from litter back to plant. Herrera et al. (1978) have demonstrated direct transfer of phosphorus from litter to roots by fungi, a more or less direct recycle path that reduced loss from the system by leaching. Granite outcrop systems have apparently not evolved any such "shortened" recycle mechanism, probably because of severity of edaphic factors and lack of large litter accumulation. Accordingly, outcrop communities have low productivity. Vegetation growth must be accomplished largely with nutrients available at the brief periods of time when moisture conditions are favorable.

Lichen-annual systems are largely limited by abiotic factors. Nutrient flow and moisture availability, which influence growth and density of several biotic components, are strongly limited by precipitation amount and frequency. Moisture stress during the spring and early summer of 1977 reduced soil water content (P_W) to less than 10% (Fig. 13) during April and caused large decreases in the density of vascular plants, arthropods, and soil microflora (Fig. 15).

Nutrient uptake by nonvascular plants occurs directly from precipitation and/or watershed inflow. Between precipitation events they dry quickly and there is little or no uptake from soil. Regardless of low standing crop to throughput ratios, uptake and release of cations by nonvascular plants was evident in ecosystem nutrient budgets. For example, nonvascular plants in E1 accumulated Na, K, Mg, and Ca from January to May 1977 and then began releasing them in June. These elemental gains and losses can be independently seen in nutrient budgets for E1 (Fig. 10).

Uptake by vascular plants is probably largely localized at the soil/outcrop interface or below it. Vascular plants appeared to develop deep root systems. Root mats were discovered beneath exfoliations in this study and _Diamorpha cymosa_ sets thick mats against the granite base of depression (Wiggs and Platt 1962). This stratification differs from situations in deciduous forest ecosystems where root systems are located near the soil surface (McGinty 1976) or in tropical rain forests where a conspicuous root mat covers the surface soil (Witkamp and Ausmus 1976, Herrera et al. 1978). As in desert ecosystems, outcrop species find it advantageous to maintain a deep root system, relatively speaking, to avoid moisture depletion at the surface, and take advantage of trapped water reserved at the base of the rock depressions. This intimate association of roots and granite surface suggests that direct transfers from rock to roots could take place, although appreciable transfers of this sort have not been demonstrated.

Meyer (1972) reported large reductions in soil nutrient pools underlying _V. porteri_ in annual perennial herb ecosystems betwen June and September due to its rapid growth. Rapid uptake by growing vegetation has been observed as net gains or reduced losses in nutrient budgets (Likens et al. 1977), but was seen infrequently in these ecosystems. In fact, some of the largest net losses of K and Ca occurred from June to August (Fig. 10 and 11).

These data suggest that Na, K, Mg and Ca were probably not limiting to plant growth in lichen-annual systems or in any of the other outcrop systems described by Burbanck and Platt (1964). A similar conclusion for annual-perennial ecosystems was reported by Meyer et al. (1975).

Yet, vascular plant density and standing crop was low in these systems compared to others (Shure and Ragsdale 1977). Soil depth, which determines total moisture capacity, doubtlessly limits growth of vascular plant populations. Average soil depth for the study ecosystems is 2.8 cm, about half as deep as 10 lichen-annual herb systems studied by Shure and Ragsdale (1977). Average maximum soil depth (7.7 cm) is at the lower range for lichen-herb systems (7-15 cm) studied by Burbanck and Platt (1964). Shallow soils lower moisture availability which inhibits germination, stunts growth, and increases mortality of many vascular plant species (Sharitz and McCormick 1973, McCormick et al. 1974).

Average standing crop of above-ground plant biomass in the study ecosystems was 1014±86 g dry wt/m^2 and similar to standing crops in old field vegetation and frequently reach average heights of more than 100 cm, while nonvascular plants dominate these outcrop systems whose average vertical stratification is about 15 cm. The lower mean water content of outcrop vegetation allows a much greater concentration of dry weight. In addition, net primary production in old fields exceeds standing crop (Odum 1971) in contrast to outcrop communities where annual growth is probably much less than standing crop.

Average densities of insects and spiders in the study systems ranged from 1800±310 ind/m^2 (N = 3) in February 1977 to 470±360 ind/m^2 in May 1977. Numbers of microarthropods varied from 122000±30000 ind/m^2 (January 1977) to 20000±4000 ind/m^2 (June 1977). These values were higher than expected considering the harsh environmental conditions of rock outcrop systems. Densities of both insect groups were similar to values reported for old fields, and microarthropod numbers were within the range of densities measured in mesic hardwood forests of the Southeast US (Best et al. 1978, McBrayer et al. 1977, Odum 1971). Densities were substantially greater than values reported for various hot deserts (Edney et al. 1976), but so was soil moisture availability. Soil water content (% wet wgt.) of the three island systems not treated with insecticide averaged 24±3% during the study compared to 5±1% for a similar period (Nov. - Jun.) at a desert site in Nevada (Edney et al. 1976). Regardless of the difference in densities, fluctuations in densities of both faunas appeared to be influenced by changes in soil moisture.

Arthropod populations of island ecosystems are probably frequently augmented during favorable moisture regimes by immigrations from forest stands surrounding the outcrop. Collembola swarms were frequently observed on the outcrop from November through March both years of the study period, and probably originate in the forest stands.

Microbial standing crop, indicated by ATP concentration, were similar to those at a desert site in Utah. Skujins (1976) measured concentrations from 0.010 to 1.174 μg ATP/g dry soil, which are similar to values for lichen-annual herb ecosystems (Fig. 15). The highests average concentration measured in this study in June 1977 was 27000 μg ATP/m^2 and is at the lower end of values reported for litter and soil (to 10 cm) of a mesic hardwood forest: 625000 to

25000 $\mu g/m^2$ (Ausmus 1972). The microflora standing crop is apparently substantially reduced in soil-island ecosystems much of the time.

The average adenylate energy charge ratio, 0.62±0.02 (N = 7), also demonstrated that soil microflora were in a stationary growth state much of the time. Microbial growth must occur rapidly over short periods of time when conditions are optimal. Highest EC ratios were measured in February 1977 when they approached 0.8, the point at which normal growth occurs (Chapman et al. 1971). Early spring must be a period of optimal temperature and moisture conditions for microflora populations in outcrop ecosystems.

Changes in soil water pH, exchangeable H^+, base saturation were generally correlated with fluctuations in the chemical content of precipitation and watershed inflow. The large amount of exchangeable hydrogen in incoming water has reduced soil pH and base saturation of lichen-annual herb systems (Table 8). Average soil pH was similar to that of inflow (3.92 versus 4.03) and average base saturation was 4.5±0.6% (N = 4). Thomas et al. (1964) have characterized these soils as relatively infertile. Indeed, these sandy soils have lower pH, CEC, and base saturation, but greater amounts of organic matter than nearby agricultural soil (USDA 1959).

Decomposition also appeared to be largely controlled by abiotic factors with soil organisms playing a minor role. Disappearance rates for cellulose, 10%/yr, agree well with rates for balsa wood strips, 9%/yr, (Bostick 1970). Bostick also reported litter breakdown rates of about 15%/yr for vascular plants in lichen-annual herb ecosystems. This value is about half the rate measured in this study for Polytrichum, 29%/yr, and Cladonia, 38%/yr. Bostick concluded that litter disappearance was generally a distintegration and leaching process.

Decay rates remained linear throughout this study, regardless of changes in density of microarthropods (Fig. 14) or soil microflora (Fig. 15). The relatively low decay rates for litter in lichen-annual herb ecosystems is probably the result of reduced microbial activity by edaphic factors. Microflora effect most of the decomposition of organic material (Odum 1971, Witkamp and Ausmus 1976). The most important factors controlling microbial decomposers are moisture and temperature (Witkamp 1966, 1971) and both are frequently limiting in the study systems. During summer, soil moisture levels fluctuate widely and daily soil temperatures fluctuate from about 33°C to 25°C (Shure and Ragsdale 1977).

The faster disappearance of lichen (Cladonia) litter could be the result of saprophagous arthropods. Most of the Collembola and many of the Acari are regarded as saprophages (Wallwork 1976) and could feed directly on lichen since they are composed largely of fungal hyphae.

Changes in nutrient content of Polytrichum and Cladonia in the litter decay study were similar to results of the leaching study. Sodium and potassium were lost in large amounts initially, followed by increases in Ca and Mg concentration. While losses of Na and K occurred during the first 45 days then stopped, Ca and Mg were accumulated throughout the 335 day study by Cladonia. This increase in concentration was not due entirely to leaching of Na and K because dead Cladonia in the litter study accumulated more Ca and Mg than live Cladonia in the leaching study. The dead lichen probably retained its ability to accumulate selected cations after death. Witkamp and Frank (1967) demonstrated that Cladonia subtenuis lost only 4-8% of its ability to accumulate cesium-137 after death.

A large portion of the nutrients held by vascular plants are readily leachable following death. For example, Hypericum gentianoides lost 62% of Na, 98% of K, 93% of Mg, and 89% of Ca within 120 days following death. Similar leaching rates were observed for Andropogon. Large losses of nutrients from D. cymosa, A. uniflora, and V. porteri after death have been reported by Myer (1972). Following death, leaching occurs during rainfall events, which bring large amounts of through-flow.

Remaining nutrients in vascular plant skeletons can be lost by blowout, especially for Virguiera. Isolated V. porteri plants, common in this outcrop, become brittle after having been leached and dried; and can be easily broken by a gust of wind and carried out of the system. This occurred to the single large V. porteri in E1. By April 1978, no trace of it could be found. Hypericum stems are much more fibrous, eventually are bent over and can remain in the system for several years. If density of vascular plants is large enough, their branches become intertwined and form a mat resistant to wind gusts.

Internal cycling of nutrients requires stable surface conditions permitting litter to fall in place and remain, ameloration of temperature and moisture stresses for growth of microflora and microarthropods, and close association of debris with roots to complete the transfer from remineralization to plant uptake. One or more of these factors is usually missing or limiting in granite outcrop ecosystems. Greatest plant densities occur in fall (Oct. or Nov.). After death, rapid plant regrowth does not begin until the following spring. In the meantime, rainfall amounts during winter months allow many nutrients lost from vegetation to be easily washed out of the system by throughflow.

Meyer (1972) suggested that one aspect of internal cycling in annual-perennial herb ecosystems was the inward movement of dissolved nutrients during storms that did not fill the basin storage to capacity. He indicated that this would occur in his study system during the storms with less than 5 mm rainfall. This phenomenon occurred in the lichen-herb systems of this study with rainfalls less than 2.6 mm. The proportion of storms 2.6 mm or less was only 10%. Thus, inward movement and concentration of nutrients is probably not important because of its low frequency of occurrence.

Insecticide perturbation had no observable affect on concentration of nutrients in discharge, output of suspended particulate matter, loss of sediment, or nutrient budgets. Arthropod populations were reduced about 91% in the experimental system during the course of the study. Populations in the untreated system were eventually reduced 75% by moisture stress (Fig. 13) late in the treatment phase. In addition, the presence or absence of microarthropods had no effect on litter decay rates. Accordingly, the hypothesis, stated earlier, that destruction of one or more biotic compartments of an outcrop ecosystem will increase nutrient loss is false for arthropod biophages and saprophages.

Arthopod populations are not a major reserve for essential cations in these systems, which is not surprising considering their small biomass. In this study, standing crop of calcium in arthropod populations was less than 0.2 dg/m^2. Arthropods, likewise, provide only a small storage component for nutrients in deciduous forests (Franklin 1973, Gist and Crossley 1975) and tropical rain forests (Golley et al. 1975, Odum and Pigeon 1970). McBrayer (1978) argued that crypozoan invertebrates have no direct effect on release rates for essential cations in deciduous forests.

In fact, elimination of arthropod populations would more likely delay rather than increase elemental release, and thus retard nutrient cycling rates. Indirect effects of arthropods may be more important than their direct effects of feeding. Biophages may kill trees, cause breakages, transmit disease, and cause foliage disturbances (Franklin 1973). Indirect effects of arthropod saprophages include fragmentation of litter, inoculation of organic debris with microbes, selective grazing of microflora, and preventing senescence of microflora populations (Burges and Raw 1967, Crossley 1977, Wallwork 1976). Arthropod elimination from litter with naphthalene has resulted in significant reductions in litter decay and nutrient loss (Kurcheva 1960, Witkamp and Crossley 1966, Williams and Wiegert 1971, Cromack 1973). Weary and Merriam (1978) significantly reduced litter decomposition and initiated an increase in litter standing crop of a red maple woodlot by applying a carbamate insecticide at recommended rates.

Recovery of arthropod populations appeared rapid. Numbers of arthropods extracted from litter bags from the treated system 120 days after cessation of treatment were similar to densities in bags from the other study ecosystems.

The herbicide treatment significantly increased nutrient loss from the lichen-annual herb ecosystem, but did not greatly accelerate cation loss. The dominant vegetation showed great resistance to the herbicide. The mosses, Polytrichum and Grimmia had to be repeatedly sprayed before being killed. The herbicide (ROUNDUP^R) has greater sensitivity the faster the photosynthic rate, since it acts as a biochemical block to aromatic amino acid synthesis (Hilton 1974). Slow growth rates of moss probably allowed hericide to be leached out before death. The lichen, Cladonia, never seemed affected. Nonvascular plant species accumulated cations through May, before accelerated losses occurred in June (Fig. 12).

Sodium and calcium concentrations in discharge (Fig. 8) were increased the greatest by the devegetation experiment, but significant difference with the undisturbed eocsystem, E4, could only be demonstrated at P = 0.06. However, significant budgetary losses were documented for Na, K, Mg and Ca.

Monthly net losses of potassium differed from the other cations. Greater amounts of Na, Mg and Ca were lost over the whole range of monthly output amounts relative to its control, E4. Potassium losses from E3 were greater at the lower range, and smaller at the upper range of losses from E4. It appeared that a greater amount of easily leached potassium was available, but it was limited. After rapid flushing by a small amount of precipitation, further precipitation produced diminished losses. Elemental losses primarily resulted from direct leaching of vegetation by water throughflow during storm events. Other system components and processes seemed to respond to moisture stress rather than the destruction of the vegetation.

Why weren't nutrient losses accelerated? One reason is that my results indicated that vegetation decomposition rates were low. A year after cessation of spraying, Polytrichum and Grimmia patches, though dead, were still largely intact. Decomposition rates for standing dead material are probably lower than indicated by the litterbag study. Material in the litterbags had to be laid horizontal which produced compaction, not observed in standing dead material. Microflora and saprophagous arthropods were retarded from invading and breaking down standingdead material because of the interaction of high temperature and moisture stress. Soil temperatues of lichen-annual herb ecosystems are significantly higher (≈6°C in August) than ambient air temperature (Shure and Ragsdale 1977).

One year after forests at Hubbard Brook had been cut, annual cation losses of 130 kg/ha were measured which was almost the amount recycled annually, 171 kg/ha, by the ecosystem before cutting. Losses were attributed to remineralized organic matter, and shifts in the microflora component to nitrifiers who producted H^+ replacing cations on cation exchange sites in soil. Unlike Hubbard Brook ecosystems, there was no intrasystem recycling of large amounts of cations to disrupt in outcrop systems. Each component appeared to act largely independent of the others. Inter-connectiveness apparently is minimized because of harsh abiotic factors. Thus, synergism and interaction, so characteristic of more biologically controlled communities, are almost entirely lacking.

Losses of suspended particulate matter and bed load sediment were unaffected by vegetation destruction. Diamorpha and Polytrichum play important roles in maintaining the physcial integrity of lichen-annual herb ecysostems. For example, in E3, many Grimmia patches in the center of the system observed to float when water was added from the system edge. Yet, in spite of large amounts of throughflow, it remained intact. The anchoring effect of vascular plant stems, especially Diamorpha around the edges, many growing through Grimmia moss, is the major factor. Low decay rates allow dead stems to remain for several years. Attachments are fragile, though, and can be easily broken by a bird, a small mammal, or man. Effect of this type of disruption has been reported earlier. Rapid invasion of Diamorpha into disturbed portions of the system, observed in E3, also contributes to the stability of these systems and is an aspect of resilience to physical perturbations.

Once Polytrichum moss invades, physical stability increases greatly. Polytrichum rhizoids hold soil together very tightly, and also protect the soil surface from erosive force of raindrops and throughflow. Polytrichum also increases vegetation height and creates conditions for greater moisture retention for the germination and growth of vascular plants (McCormick et al. 1974).

The results of this study seem to have a bearing on the interesting and often controversial concept of stability. The nutrient cycles of lichen-annual herb ecosystems demonstrated a high resistance component of relative stability for chemical perturbations, but lower resistance to severe drought.

Relative stability has been conceptualized as being a function of resistance, a system's ability to absorb stress and oppose displacement, and resilience, the time for a system to recover to its original state (Webster et al. 1975, Leffler 1977). Stability evaluations are highly dependent on the variable monitored, the type of perturbation and its timing (Jordan et al. 1972, Harwell et al. 1977, Leffler 1977). Nutrient output showed low resistance, but high resilience to drought conditions. Output nutrient concentration and amounts quickly reflected changes in input mediated by rainfall. They are similar to aquatic microcosms and streams, which usually show low resistance but high resilience (Leffler 1977, Webster 1975). Like streams and aquatic microcosms, island ecosystems lack any large abiotic reserves, recycling is minimal, or absent, and they are subject to large nutrient throughput. They differ from decidous forest watersheds which demonstrate high resistance (Monk et al. 1977). Island ecosystems lack the homeostatic ability to regulate nutrient output because they lack any large biotic or abiotic storage compartment to buffer changing input: standing crops of biomass and their uptake are low, and soils are sandy and shallow. Large storage has been related to resistance by Webster et al. (1975). Island ecosystems would probably show low resistance, but high resilience to additions of soluble fertilizers. Nutrients would quickly be washed out of the system by the large throughflows characteristic of these systems. The vegetation, on the other hand, showed high resistance to drought. Beyers (1962), Cooke (1970) and Peterson (1975) have shown that system stability results from the relative contributions of its components.

Resistance and resilience to herbicide treatment were high. Repeated applications of herbicide were required before vegetation death, and losses of nutrients were small compared to losses from deforestation (Likens et al. 1970).

Resistance to perturbation was generated through the dominant vegetation which are probably inherently resistant to disturbances by chemical additions, and through the physical structure and persistence of dead plant parts. Low decay rates retarded the destruction of community structure. The abiotic matrix thus held maintained the integrity of the island ecosystem. Vegetation resiliency was mediated by Diamorpha, a less resistant member of the producer compartment to herbicide treatment. Rapid reinvasion by this winter annual helps restore community structure and reestablishes new connections with the abiotic matrix. Diamorpha appears to have a role in lichen-annual herb ecosystems analogous to the pin cherry in northern hardwood ecosystems (Marks 1974, Marks and Bormann 1972). Recovery time for the dominant vegetation types, mosses and lichens, will be much longer due to their slow growth rates.

Ecosystem stability to physical disturbance appears low. Systems have little resistance to disruptions by birds or mammals (or motorcycles), which could produce large losses of structural material. Restoration of lost soil through geologic processes could take many years.

Several advantages of utilizing field mesocosms (Odum et al. 1978) over laboratory microcosms are evident from this study. The importance of environmental fluctuations in mediating system response to an experimental perturbation may be evaluated. Abiotic factors may enhance or suppress, as in this study, system response. Biotic phenomena might assume exaggerated roles in determining a system's response under constant environmental conditions, when abiotic stresses are dominant in the field.

Microcosms are better adapted to measuring the resistance component of stability. Laboratory microcosms prevent the reinvasion of species eliminated in an experimental disturbance. Leffler (1977) found that system recovery was sometimes impossible with the loss of species during perturbation, and admitted that resilience stability results would probably be altered if microcosms had been open to invasion. Field microcosms allow for invasion and therefore greater resiliency.

A series of similar field mesocosms, each with a species diversity greater than can be maintained in a microcosm, can be selected with a high probability that they will remain similar. Odum and Lugo (1970) identically seeded a series of microcosms to simulate some properties of a tropical rainforest floor. After a year of acclimation on the forest floor, each microcosm was dominated by a different herb species and the soil animals compartments were different in each.

The current interest in microcosms for ecological assessment leads one to ask if the island ecosystems in this study could by used, for example, by the Environmental Protection Agency to test releases of toxic materials. While toxicity to various ecosystem components and functions could be evaluated, information about a substance's effect on, for example, the recycling mechanisms of forested ecosystems, or material transfer through vertebrate food chains, especially, to man would be minimal. In addition, island ecosystems could probably not be utilized on a large scale. The EPA is responsible for testing thousands of toxic substances.

Although there are numerous outcrop systems available, they are widely dispersed, privately owned, and subject to vandalism. Endemic plant and animal species could be threatened with extinction, and some system components which are slow to recover could prevent their use for a second perturbation experiment.

Indeed, it would probably not be practical for the EPA to test all suspected toxic substances in field mesocosms or microcosms. A series of laboratory screening tests would be valuable in detecting those substances which require further ecological testing.

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Table 1. Characteristics of four lichen-annual herb ecosystems.

Character	Ecosystem			
	E1	E2	E3	E4
Dimensions (m^2)				
Island ecosystem	4.44	3.81	2.72	4.63
Upslope watershed	46.2	41.4[a]	58.1	108.3
Community watershed	16.5	19.5	11.1	7.9
Total watershed	62.7	60.9	69.2	116.2
Ecosystem Characteristics				
Soil depth[b] (cm)				
Average	2.7	3.5	2.3	2.7
Maximum	7.0	9.5	6.4	7.8
Soil volume (cm^3)	120840.	121608.	62285.	107226.
Cover type[b] (%)				
Grimmia	3.5	10.8	27.7	19.2
Polytrichum	46.4	30.5	3.6	17.8
Cladonia	46.0	32.6	53.7	27.8
Andropogon virginicus	2.1	1.2	0.0	0.0
Bare soil	1.4	16.1	10.5	20.3
Rock fragments	0.0	8.2	3.7	14.3
Wood fragments	1.0	0.0	0.0	0.0

[a] Contains a lichen-annual herb community (8.95 m^2).

[b] Results of mapping done 26-28 July 1976.

Table 2. Average evapotranspiration (E_t) rates for lichen-annual herb ecosystems.

Season	E_t Rate ($1/m^2 \cdot da$)	Authority
Summer		
(Jun, Jul, Aug)	1.72	McCormick et al. (1974)
Spring-Fall		
(Mar, Apr, May) (Sep, Oct, Nov)	0.90[a]	Ragsdale (1969)
Winter		
(Dec, Jan, Feb)	0.48	Estimated

[a] Estimated from a graph.

Table 3. Average inflow from rock upslopes (WSI), precipitation (P), evapotranspiration (E_t), and discharge (Q) for the four experimental ecosystems, expressed in millimeters of water.

Month	WSI	P	E_t	Q
January, 1976	1880	102	11	1971
February	1023	59	10	1072
March	5313	276	28	5562
April	407	26	23	410
May	3820	200	18	4002
June	1715	95	50	1761
July	2193	117	40	2269
August	1094	61	46	1110
September	547	35	30	552
October	2522	134	21	2635
November	2376	126	26	2476
December	2479	132	9	2602
January, 1977	2296	123	13	2406
February	955	53	13	996
March	3383	180	18	3545
April	1198	66	19	1244
May	454	30	29	454
June	753	50	50	753
July	2252	120	30	2343
August	1352	76	32	1396
September	1699	93	24	1769
October	1764	93	24	1833
Annual, 1976	25369	1363	312	26422

Table 4. Relationship between cation concentration (mg/l) of system discharge and discharge volume (l) expressed by the regression model: $Y = a_o + a_1 \ln X$, where Y = concentration, and X = volume.

System		H^+	Na^+	K^+	Mg^{2+}	Ca^{2+}
E1	a_o	0.342	1.303	1.723	0.608	3.400
	a_1	-0.033	-0.138	-0.194	-0.072	-0.412
	r^2	0.39***	0.38***	0.31***	0.51***	0.47***
	N	80	84	83	83	81
E2	a_o	0.302	1.194	1.380	0.386	2.548
	a_1	-0.027	-0.120	-0.144	-0.043	-0.305
	r^2	0.23***	0.32***	0.24***	0.59***	0.61***
	N	75	80	80	80	79
E3	a_o	0.368	1.408	1.866	0.493	2.766
	a_1	-0.034	-0.151	-0.221	-0.057	-0.331
	r^2	0.12*	0.36***	0.44***	0.51***	0.47***
	N	78	80	79	79	77
E4	a_o	0.296	1.357	1.553	0.511	2.732
	a_1	-0.026	-0.130	-0.166	-0.055	-0.296
	r^2	0.29***	0.22***	0.23***	0.46***	0.38***
	N	87	89	87	88	87

Table 5. Weighted annual cation concentration (mg/l) of discharge from control ecosystems during 1976.

Ecosystem	H	Na	K	Mg	Ca
E2	0.099	0.239	0.217	0.048	0.226
E4	0.089	0.234	0.152	0.046	0.272

Table 6. Average annual[a] input and output of cations as dissolved (D), suspended particulates (S), and bed load sediment (S) for the study ecosystems. Data are expressed as dg/m^2 and percent of D+S+B element total.

Element	Total D+S+B dg/m^2	Dissolved dg/m^2	Dissolved %	Suspended Particulate dg/m^2	Suspended Particulate %	Bed Load dg/m^2	Bed Load %
				Input			
Na	54.00± 7.72	53.96± 7.72	99.9	0.037±0.018	<0.1	0.005±0.001	<0.1
K	43.00± 5.62	41.67± 5.76	96.9	1.233±0.475	2.9	0.095±0.043	0.2
Mg	10.09± 1.41	9.68± 1.43	95.9	0.389±0.165	3.9	0.026±0.003	0.3
Ca	49.56± 5.79	48.88± 6.00	98.6	0.585±0.241	1.2	0.091±0.027	0.2
				Output			
Na	54.75± 8.79	54.71± 8.79	99.9	0.028±0.004	<0.1	0.011±0.004	<0.1
K	45.48± 2.97	44.27± 2.89	97.3	1.085±0.201	2.4	0.126±0.055	0.3
Mg	11.69± 1.46	11.33± 1.44	96.9	0.312±0.058	2.7	0.051±0.023	0.4
Ca	58.84±10.99	58.16±11.11	98.8	0.492±0.076	0.8	0.192±0.094	0.3

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[a] Dissolved and suspended particulate amounts are for 1976; bed load sediments are for the period 13 May 1976 to 12 May 1977.

Table 7. Mean (N = 14) above-ground nonvascular plant biomass and below-ground biomass (dg/m^2) in each lichen-annual herb ecosystem from 21 November 1976 to 26 June 1977.

	Ecosystem			
	E1	E2	E3	E4
		Above-ground biomass		
Nonvascular				
<u>Grimmia</u>	509± 300	2083± 790	3795±516	3089±823
<u>Polytrichum</u>	5573±1115	6195±1792	353±257	2781±718
<u>Cladonia</u>	4791± 791	3789± 514	4625±554	2622±554
Total	10873±1081	12067±1234	8773±512	8492±558
		Below-ground biomass		
Rhizoids				
<u>Grimmia</u>	0	3± 3	33± 24	19± 19
<u>Polytrichum</u>	1813± 574	989± 330	174±151	838±259
Roots	19± 9	38± 14	9± 5	14± 4
Total	1832± 570	1030± 325	216±146	871±254

Table 8. Means of selected soil parameters for each study ecosystem. Litter, organic matter, cation exchange capacity (CEC), and bulk density are means of 14 samples from 21 November 1976 to 26 June 1977; soil pH and base saturation are means of 2 samples for 21 November 1976.

Parameter	Unit	Ecosystem E1	E2	E3	E4
Litter	dg/m^2	464 ±76	418 ±119	578 ±137	543 ±150
Organic matter	%	8.2 ± 0.5	4.6 ± 0.4	7.3 ± 0.7	5.1 ± 0.5
Soil pH	pH	3.86	3.87	3.98	4.00
CEC	meq/hg	6.4 ± 0.34	4.1 ± 0.20	3.4 ± 0.29	4.2 ± 0.24
Base saturation	%	3.1 ± 0.2	3.3 ± 0.5	2.2 ± 0.4	3.3 ± 1.0
Bulk density	g/cm^3	1.33± 0.18	1.36± 0.15	1.17± 0.14	1.50± 0.17

Table 9. Average weight loss of <u>Polytrichum</u> moss, <u>Cladonia</u> lichen, and cellulose from litter bags in the study ecosystems during 1976 and 1977. This relationship was expressed by a linear regression model: $Y = a_o + a_1X$, where Y = the proportion of litter remaining at time t, $a_1 = k$, the rate of decay (Olson 1963), and X = time (t) in years. % R = percent weight remaining after one year; r = correlation coefficient. Sample size (N) of each regression is 32.

Litter Type	% R	k	r
<u>Polytrichum</u>	74.9	-0.29	0.96**
<u>Cladonia</u>	68.6	-0.38	0.89**
Cellulose	90.4	-0.10	0.66**

Table 10. Average nutrient distribution in lichen-annual herb ecosystems. Data are expressed in terms of dg/m^2 and percent of total nutrient amount.

Component	Na		K		Mg		Ca	
	dg/m^2	%	dg/m^2	%	dg/m^2	%	dg/m^2	%
Vegetation	0.9	37	29.2	81	7.8	79	6.2	44
Litter	0.03	1	0.4	1	0.3	3	1.0	7
Soil	1.4	62	6.6	18	1.7	18	6.7	48
Total	2.3	100	36.2	100	9.8	100	13.9	100

Fig. 1. A generalized island ecosystem (E) and surrounding rock upslopes. A weir collection system (I) samples inputs from the rock watershed area (IWS) to the ecosystem (E), and a second weir system (O) samples ecosystem outputs. Inputs from the community watershed area (CWS) were estimated from IWS data. Measuring devices include: a standard rain gauge (R), polyethylene precipitation collector (P) and thermometer (T).

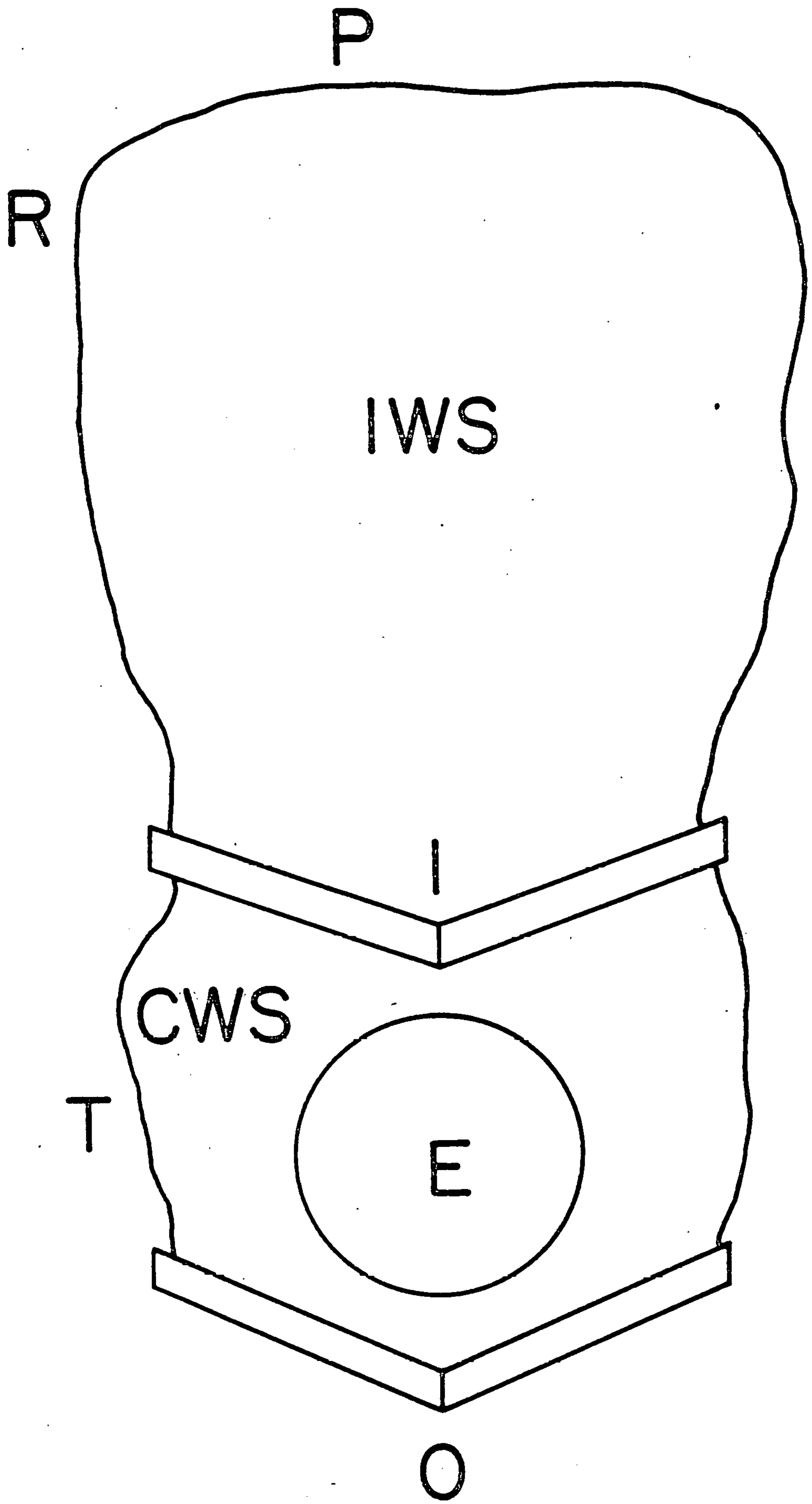

P
R
IWS
I
CWS
T
E
O

Fig. 2. Modified V-notch weir mounted in ISOFOAM® dam. Nylon netting stretched over rod frame is in the flow splitter. Tubing leading to a proportional sampler can be seen leaving the base of the flow splitter. Plexiglass tubing used to measure peak water levels is in the foreground.

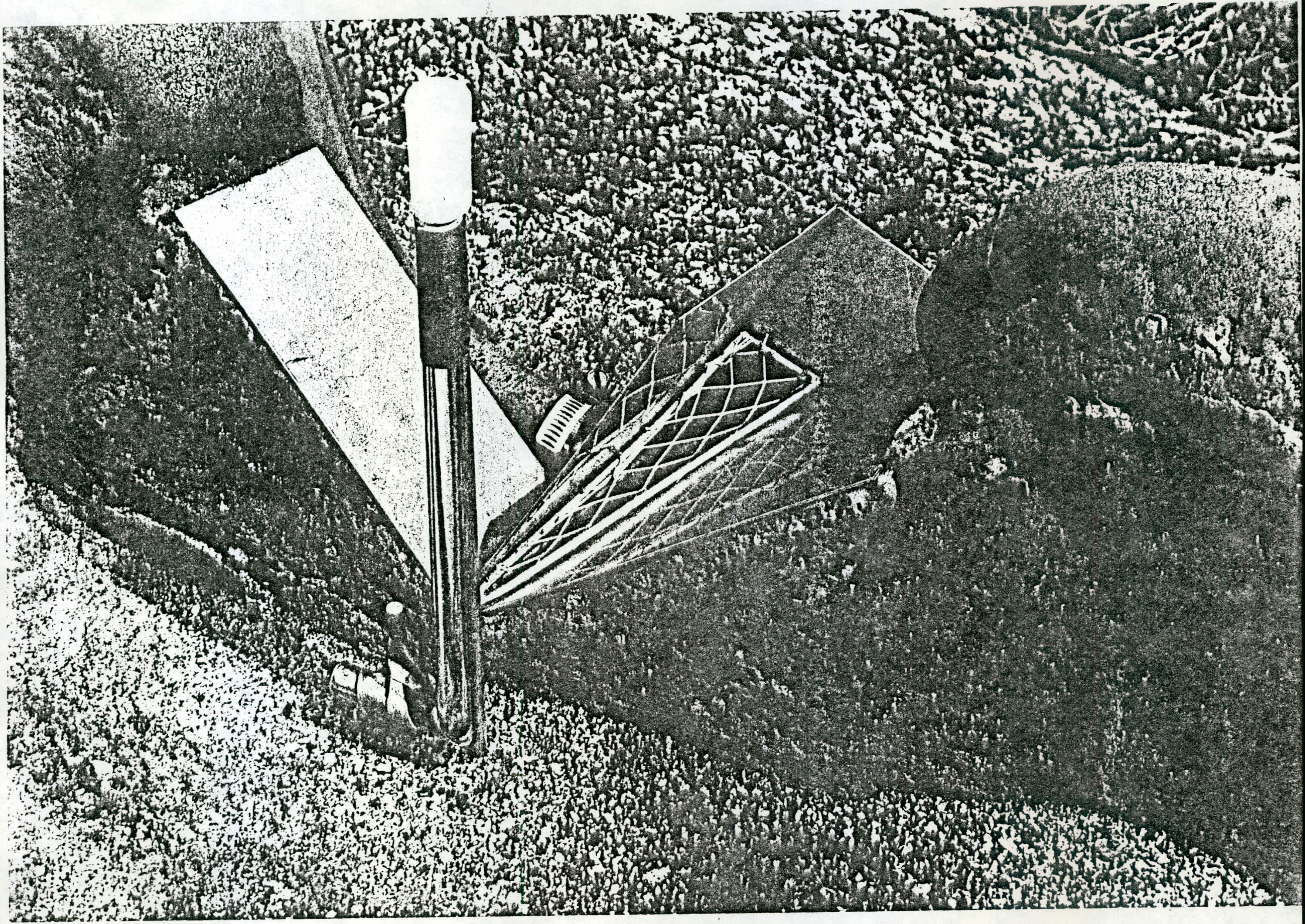


Fig. 3. Proportional sampler mounted on the rock surface. The cover has been removed to show the inside. Diverted flow from the weir enters through the cover. Tubing leaving the sampler enters collection bottles.

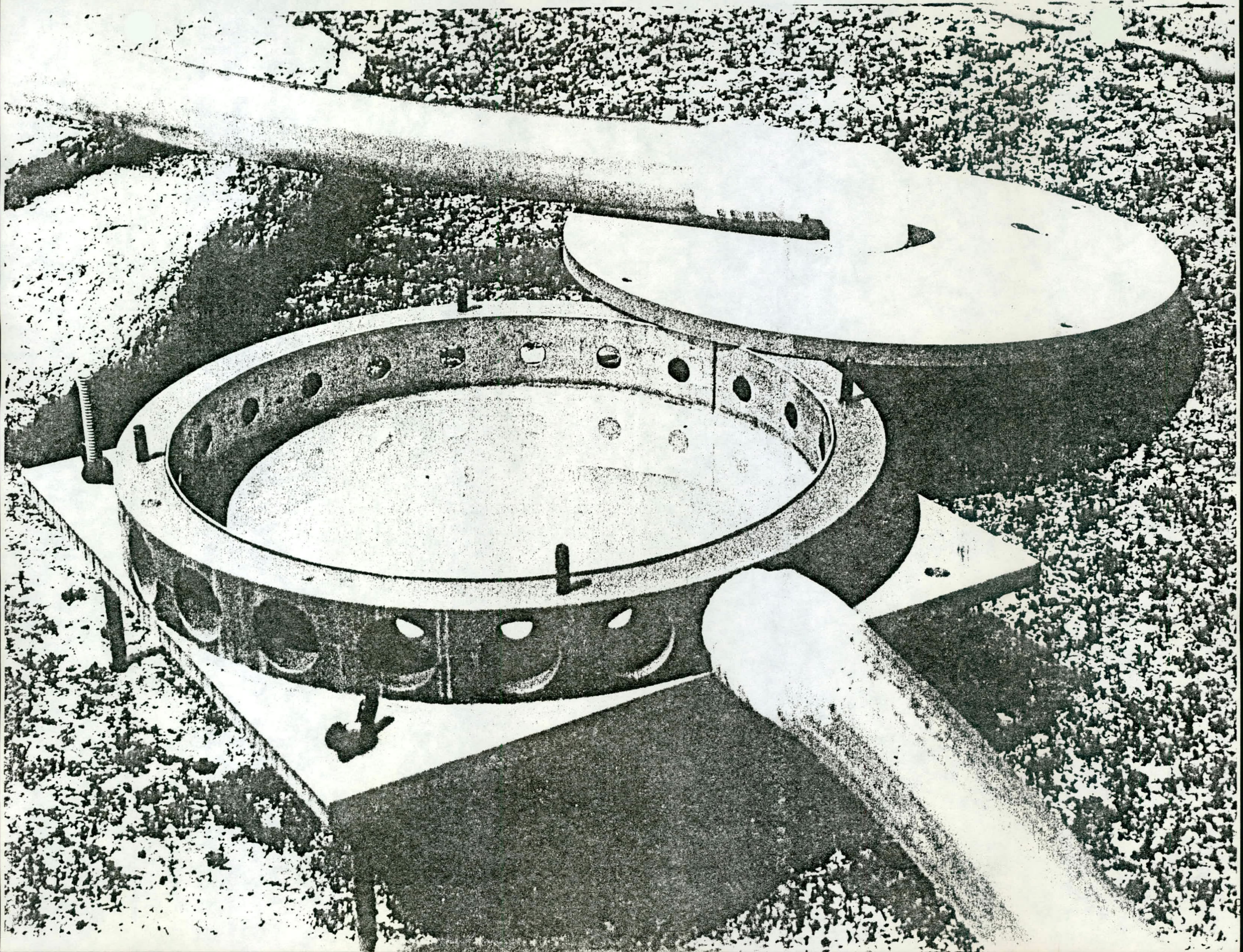


Fig. 4. Mean (N = 2) amount of potassium (μg) leached from a gram (air dry wt) of irradiated (0) and nonirradiated (0) *Polytrichum*. Bars indicate ±SE.

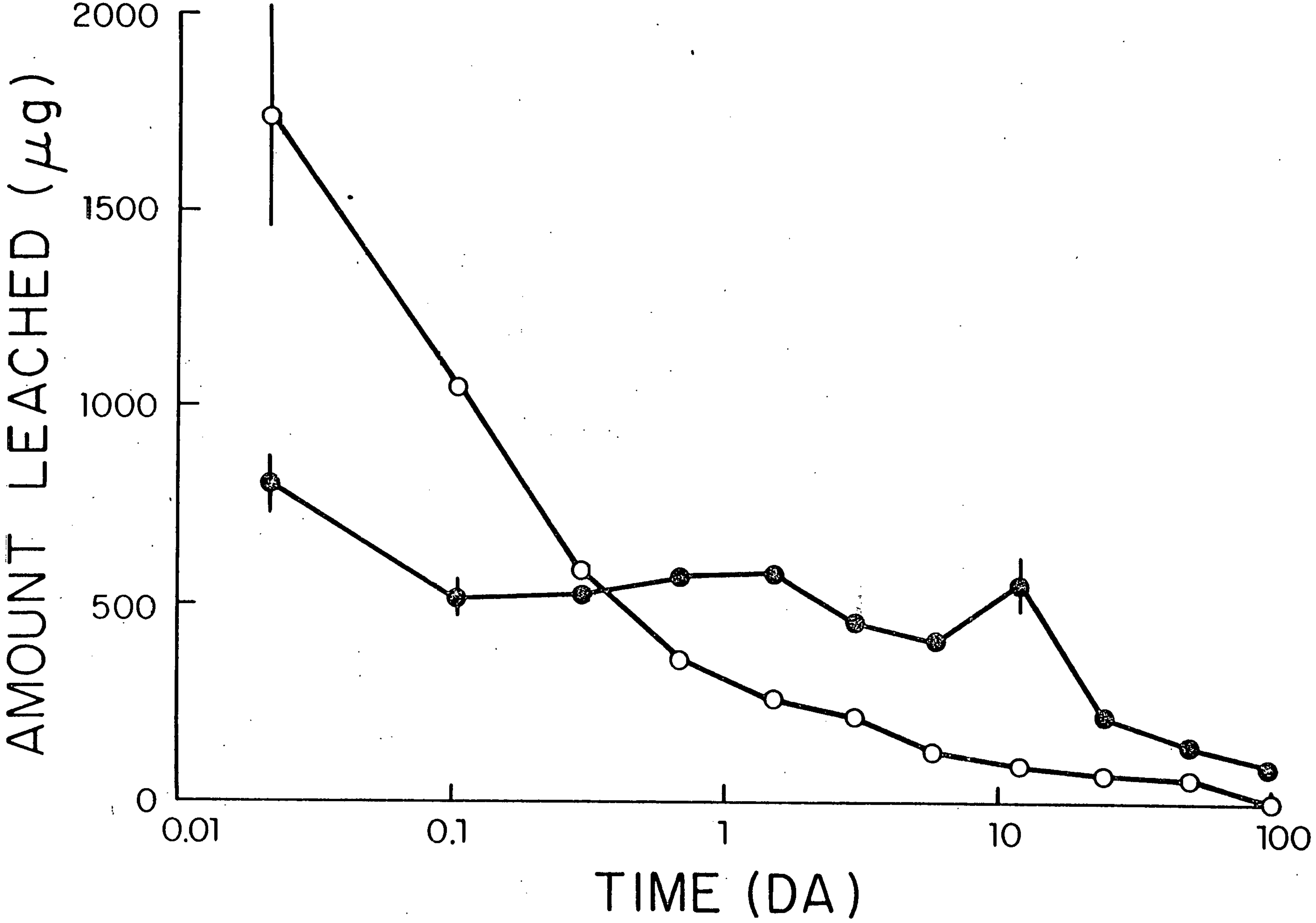

AMOUNT LEACHED (μg)
2000
1500
1000
500
0
0.01
0.1
1
10
100
TIME (DA)

Fig. 5. Mean (N = 2) average (Δ), maximum (O), and minimum (O) monthly air temperatures (59 cm above rock surface) for the study area during Dec. 1975 - Oct. 1978.

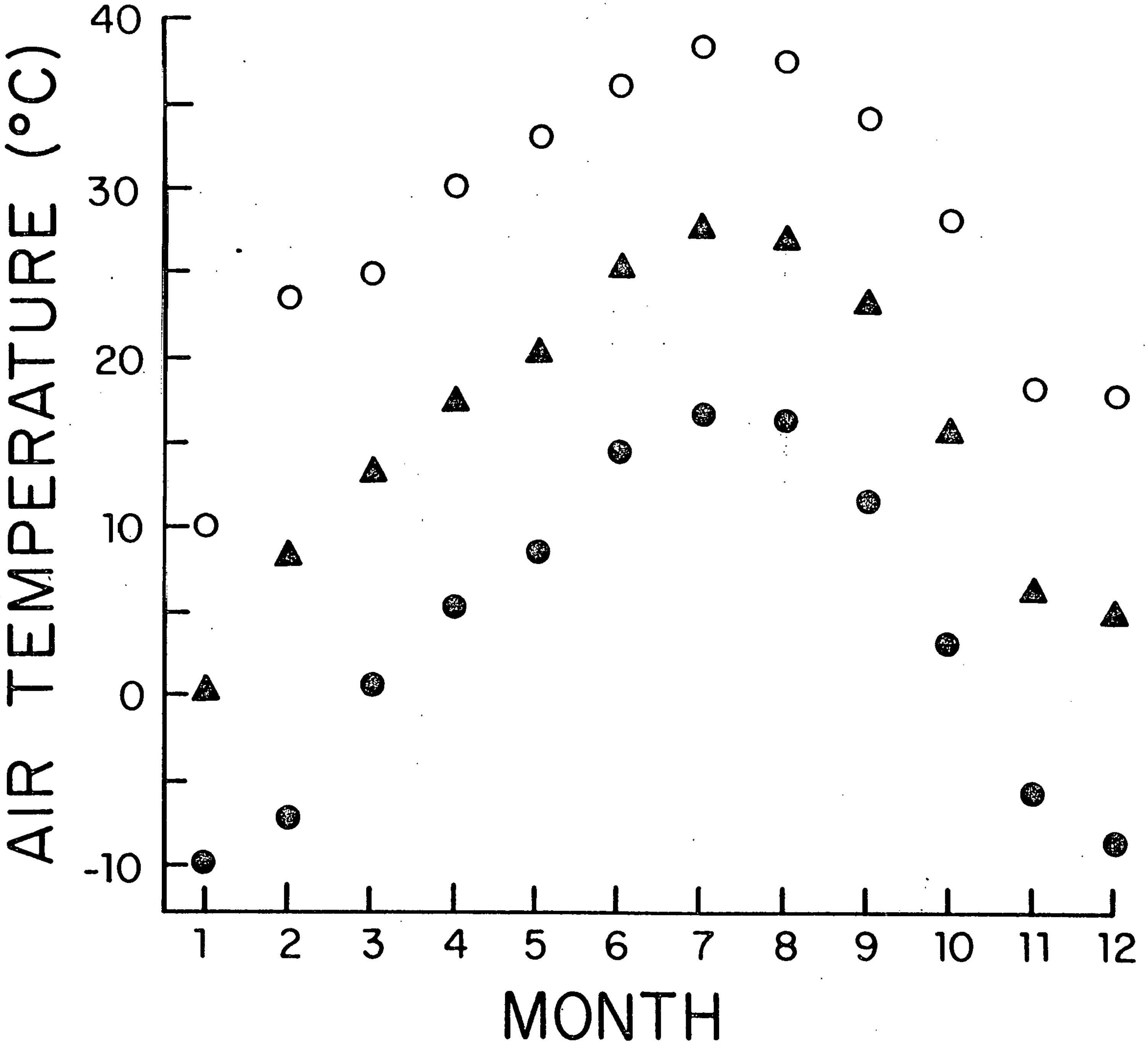

AIR TEMPERATURE (°C)
40
30
20
10
0
-10
1
2
3
4
5
6
7
8
9
10
11
12
MONTH

Fig. 6. Average (N = 4) weighted monthly concentrations of H^+, Na^+, K^+, Mg^{2+}, and Ca^{2+} in precipitation.

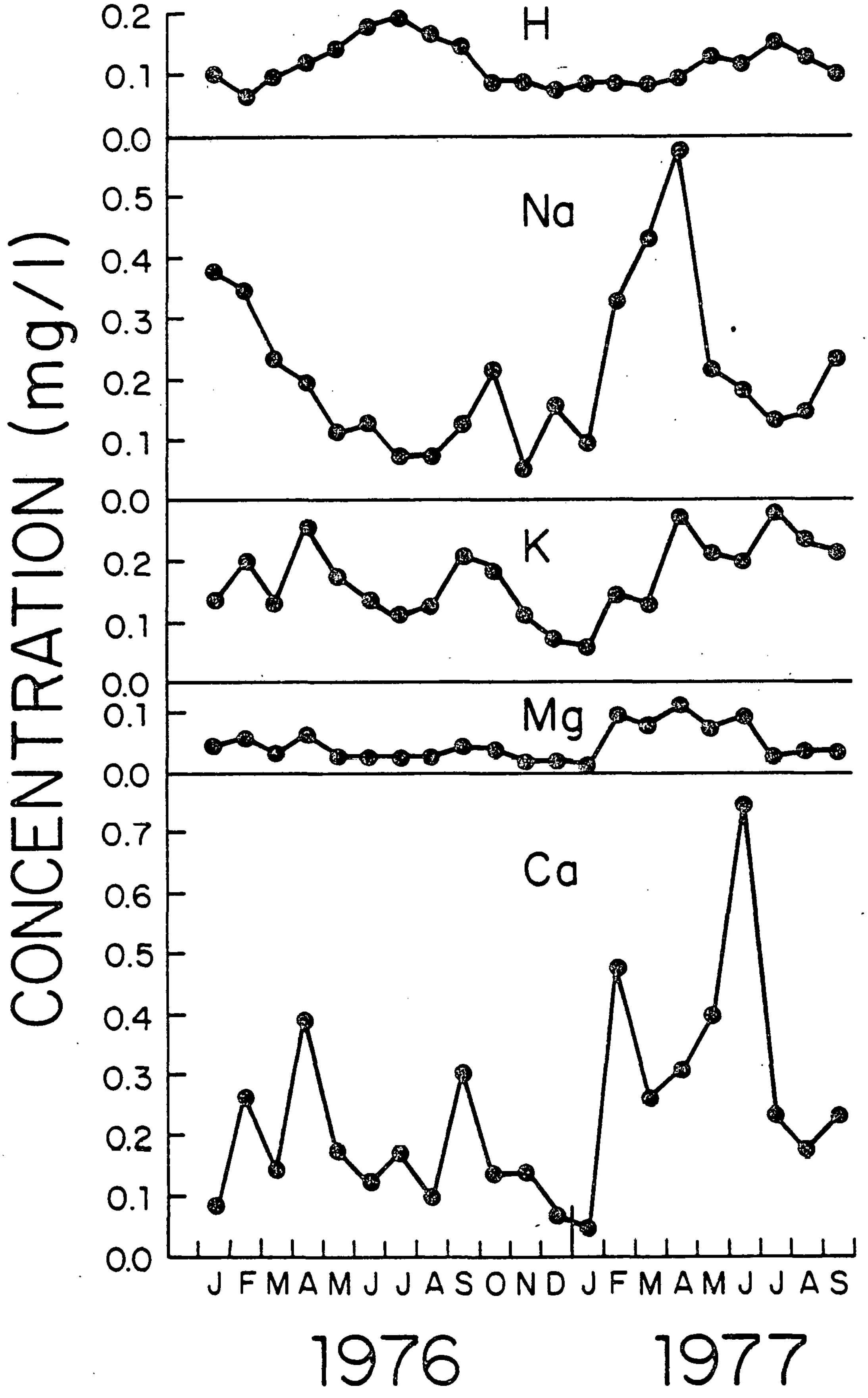

CONCENTRATION (mg/l)
H
Na
K
Mg
Ca
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
J F M A M J J A S O N D J F M A M J J A S
1976
1977

Fig. 7. Average (N = 4) weighted monthly concentrations of H^+, Na^+, K^+, Mg^{2+}, Ca^{2+} in inflow from rock upslopes.

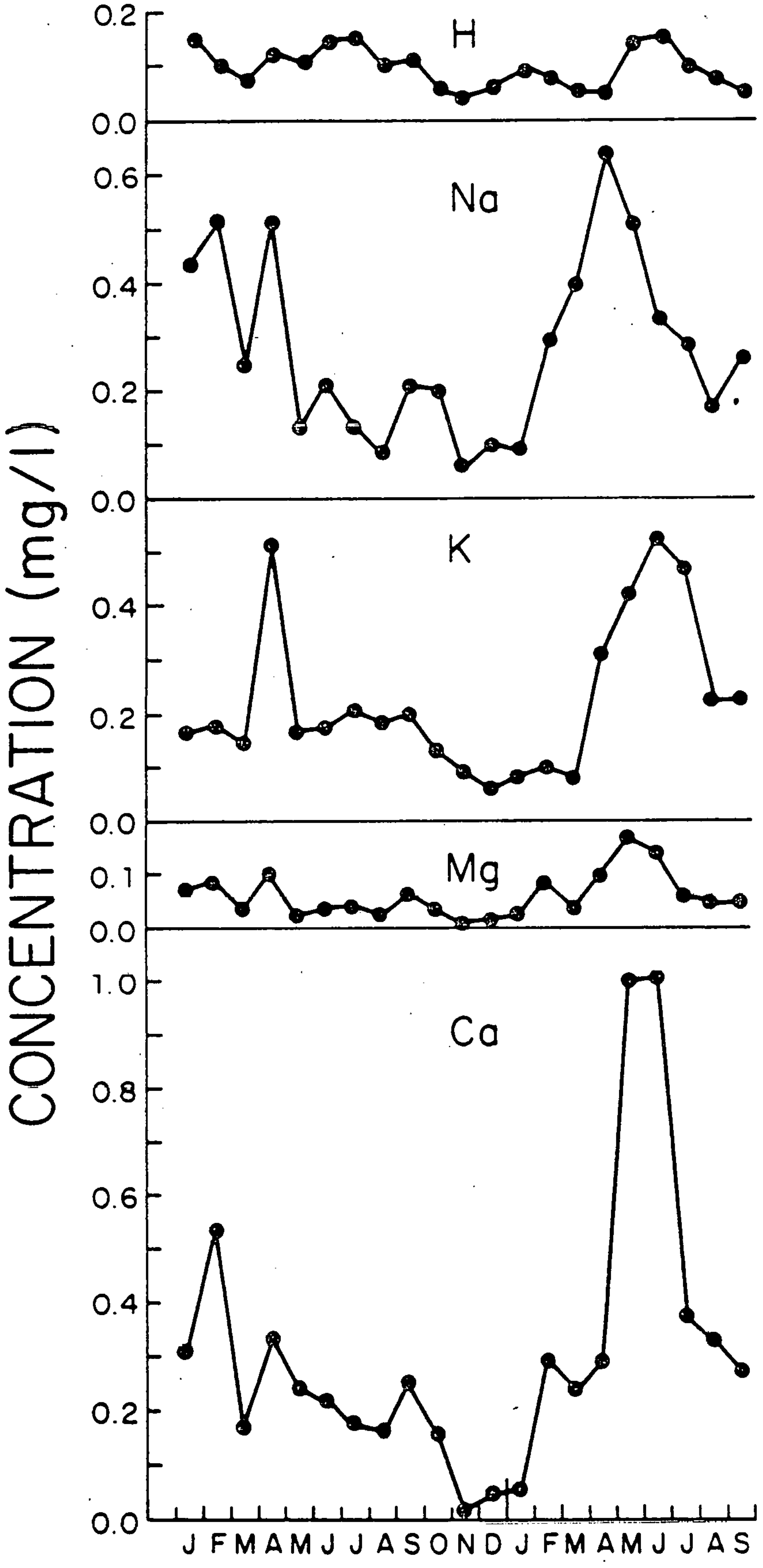

CONCENTRATION (mg/l)
H
0.2
0.0
Na
0.6
0.4
0.2
0.0
K
0.4
0.2
0.0
Mg
0.1
0.0
Ca
1.0
0.8
0.6
0.4
0.2
0.0
J F M A M J J A S O N D J F M A M J J A S
1976
1977

Fig. 8. Monthly weighted concentrations (mg/1) of H^+, Na^+, K^+, $Mg2^+$, and Ca^{2+} in discharge from E3 (0) and E4 (0). Arrows mark the initiattion of the herbicide treatment of E3.

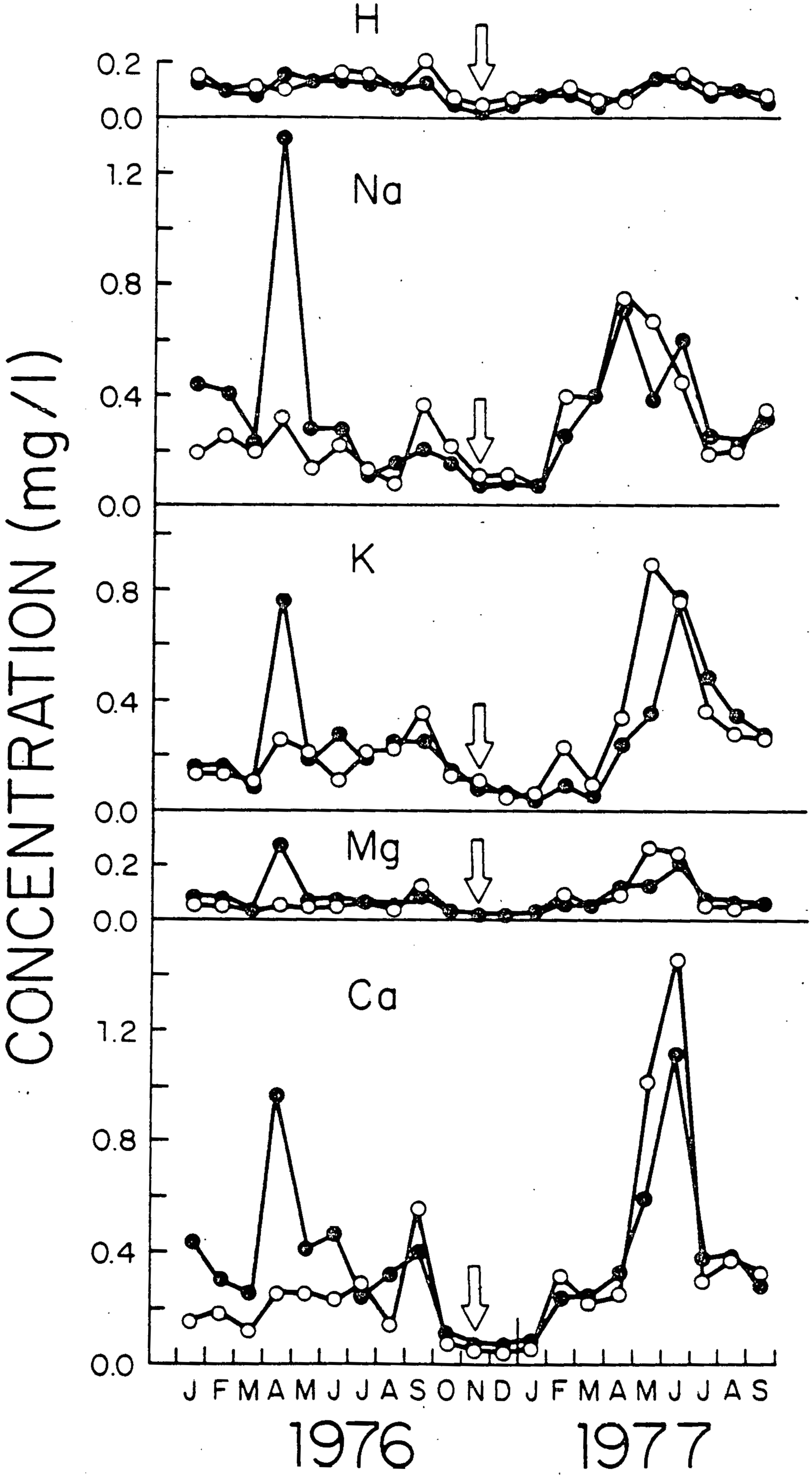

H
Na
K
Mg
Ca
CONCENTRATION (mg/l)
0.0
0.2
0.4
0.8
1.2
J F M A M J J A S O N D J F M A M J J A S
1976
1977

Fig. 9. Monthly flow of cations for perturbed ecosystem E3. The arrow indicates initiation of herbicide treatment. Input (0) and output (0) are given in dg/m^2.

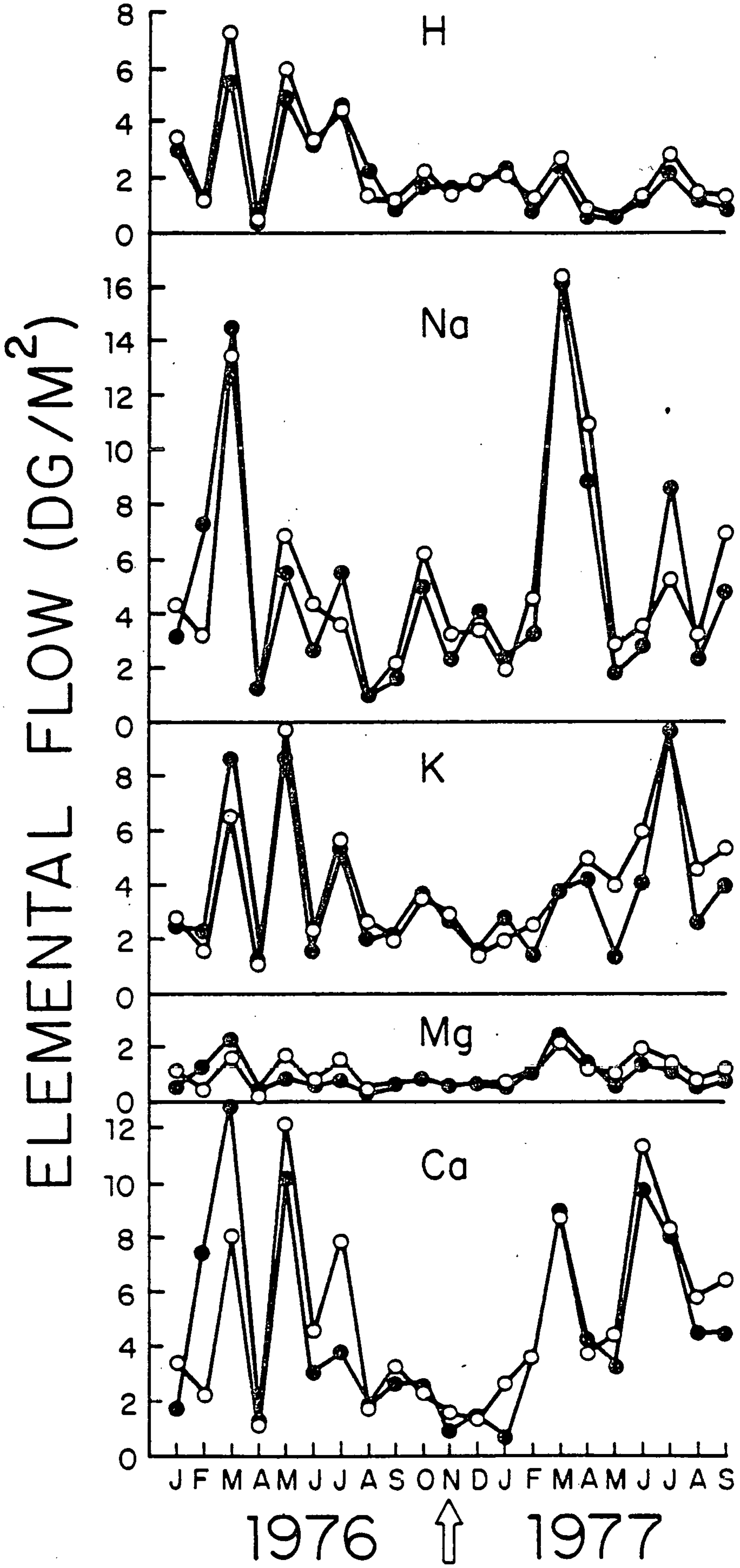

ELEMENTAL FLOW (DG/M^2)
H
Na
K
Mg
Ca
8
6
4
2
0
16
14
12
10
8
6
4
2
0
8
6
4
2
0
2
0
12
10
8
6
4
2
0
J F M A M J J A S O N D J F M A M J J A S
1976 ⇧ 1977

Fig. 10. Monthly net gains and losses (dg/m^2) of cations from the ecosystem treated with insecticide, E1 (O), and its undisturbed control system, E2 (0). The arrow indicates initiation of insecticide treatment in E1.

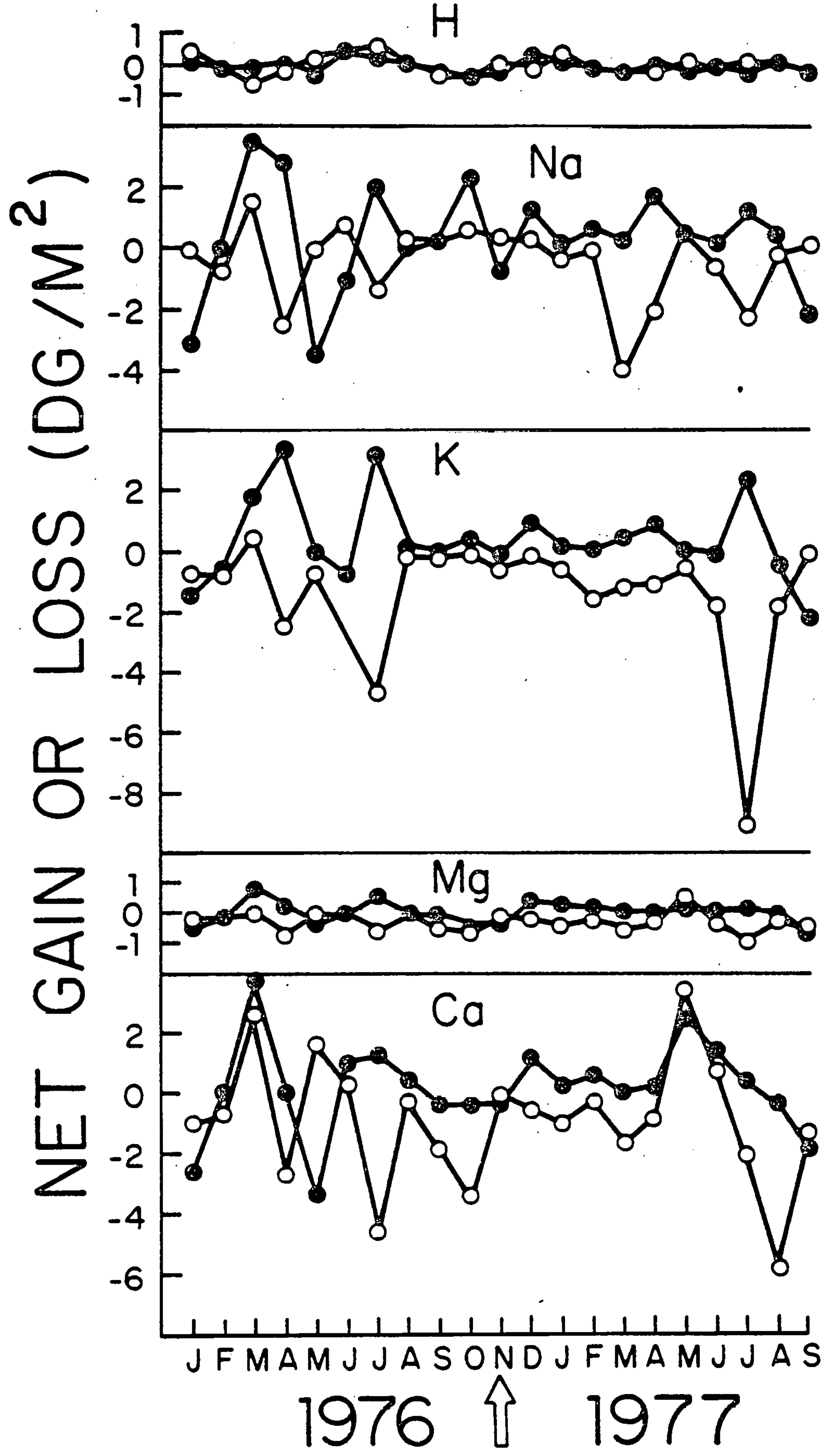

H
Na
K
Mg
Ca
NET GAIN OR LOSS (DG/M^2)
1
0
-1
2
-2
-4
-6
-8
J F M A M J J A S O N D J F M A M J J A S
1976
1977

Fig. 11. Monthly net gains and losses (dg/m^2) of cations from the ecosystem treated with herbicide, E3 (0), and its undisturbed control system, E4 (◍). The arrow indicates initiation of herbicide treatment.

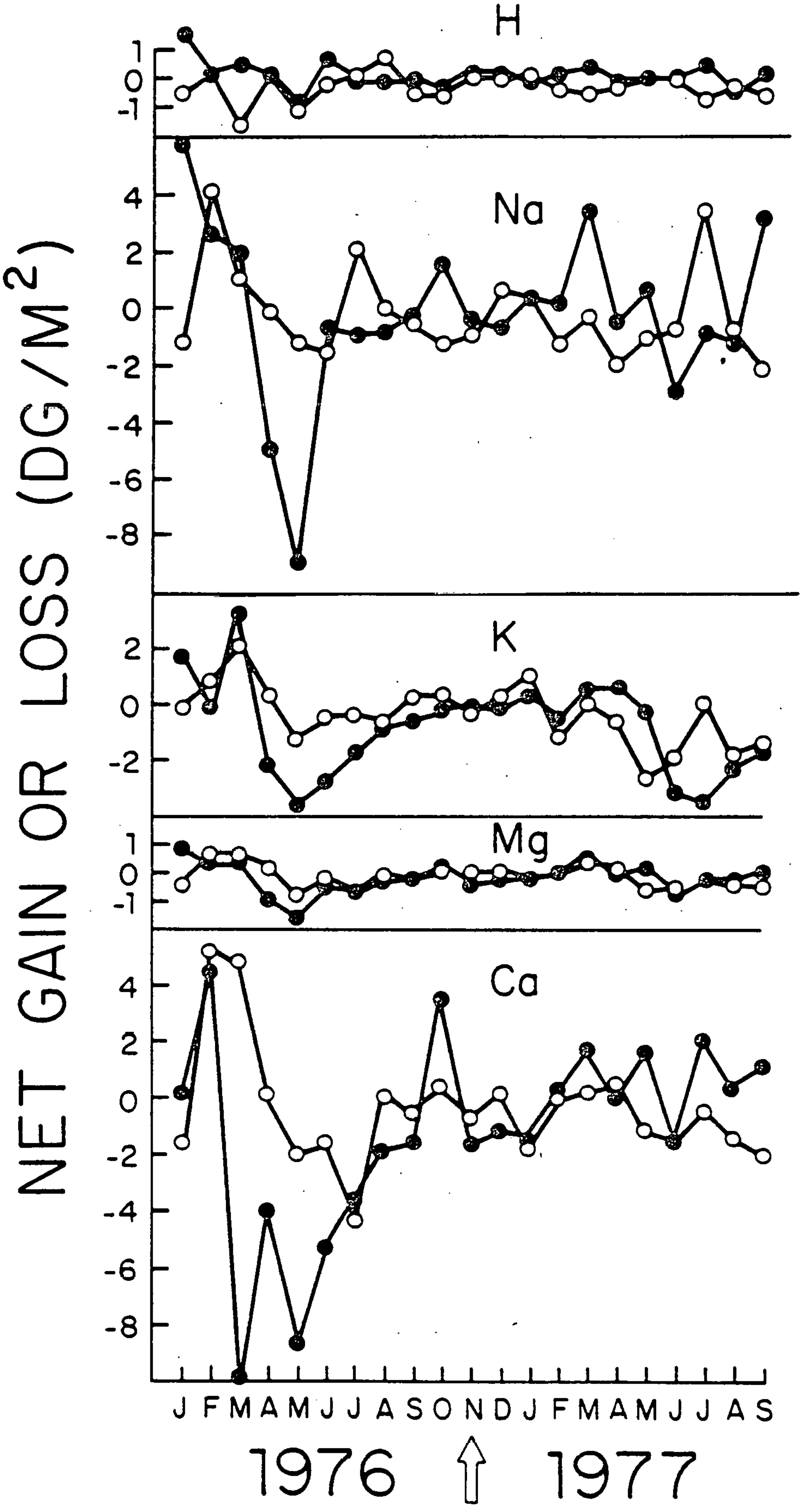

H
1
0
-1
Na
4
2
0
-2
-4
-6
-8
K
2
0
-2
Mg
1
0
-1
Ca
4
2
0
-2
-4
-6
-8
NET GAIN OR LOSS (DG/M^2)
J F M A M J J A S O N D J F M A M J J A S
1976
1977

Fig. 12. Elemental concentrations in Polytrichum moss from the disturbed ecosystem, E3 (O), and the control ecosystem, E4 (0). Initiation of herbicide treatments is indicated by the arrow.

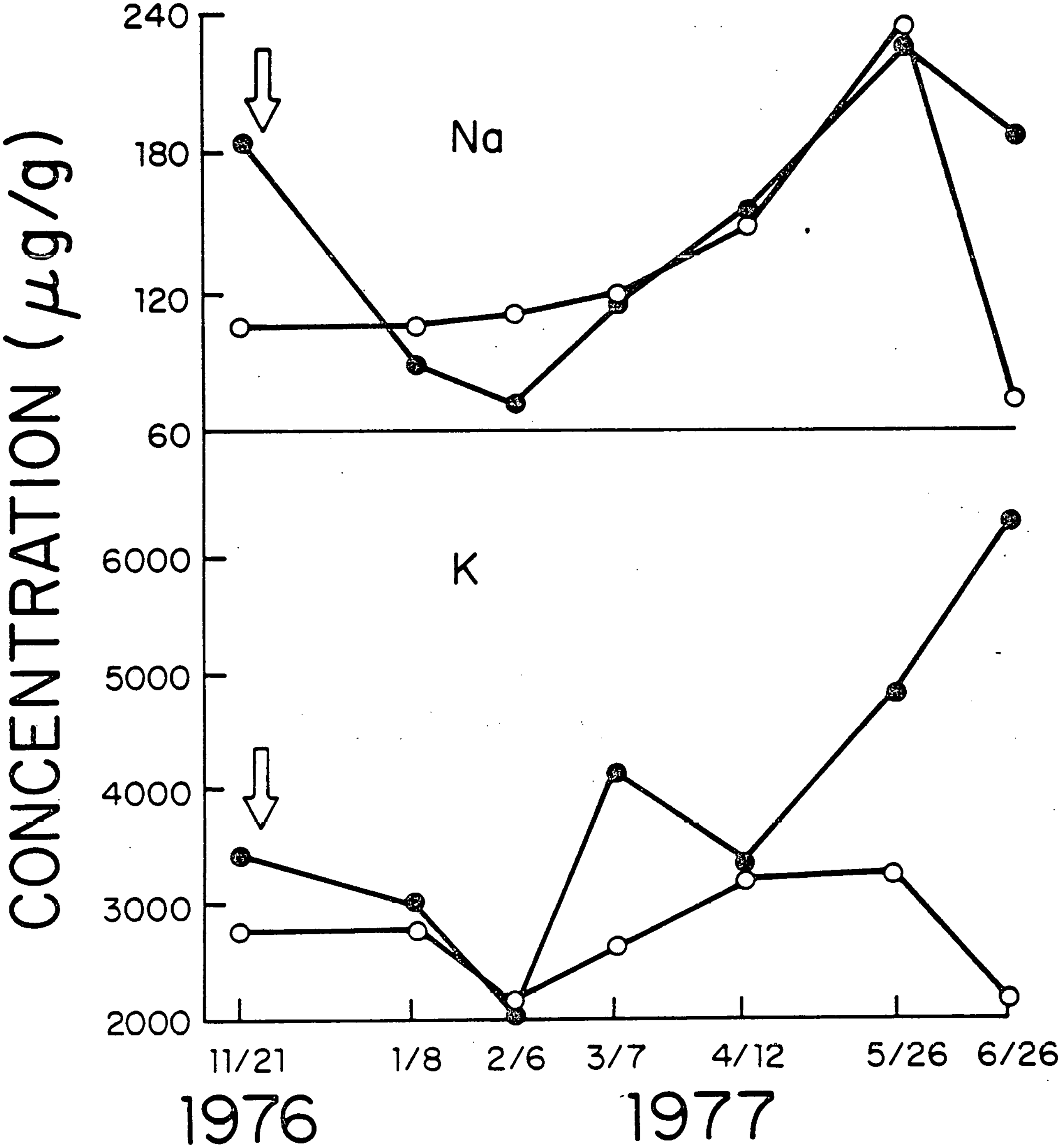
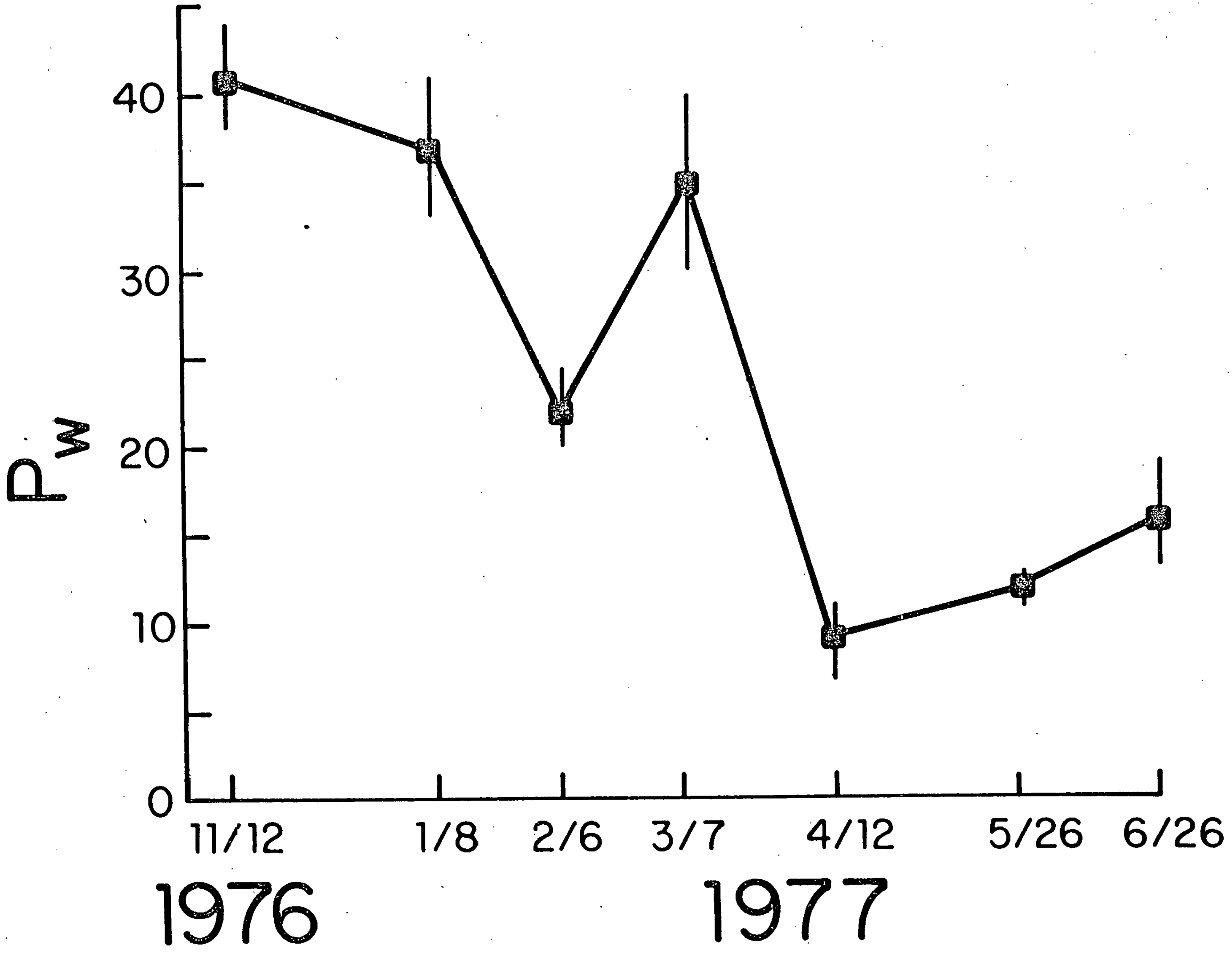
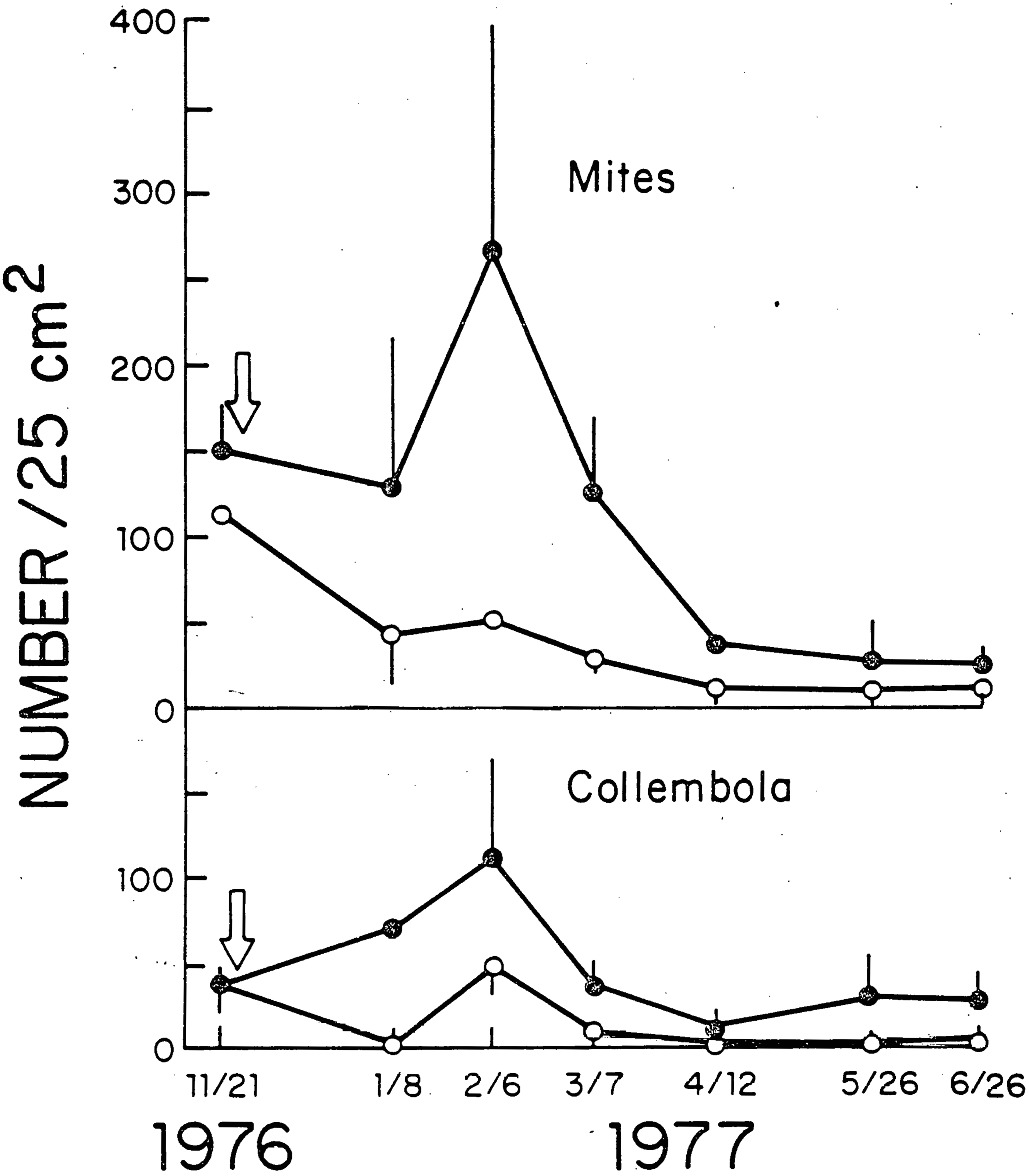

CONCENTRATION (μg/g)
240
180
120
60
Na
6000
5000
4000
3000
2000
K
11/21
1/8
2/6
3/7
4/12
5/26
6/26
1976
1977

Fig. 13. Mean (N = 4) soil water content as wet weight percentage (g water/100g dry soil) of composite soil samples removed from study ecosystems. Bars indicate ±1 SE.



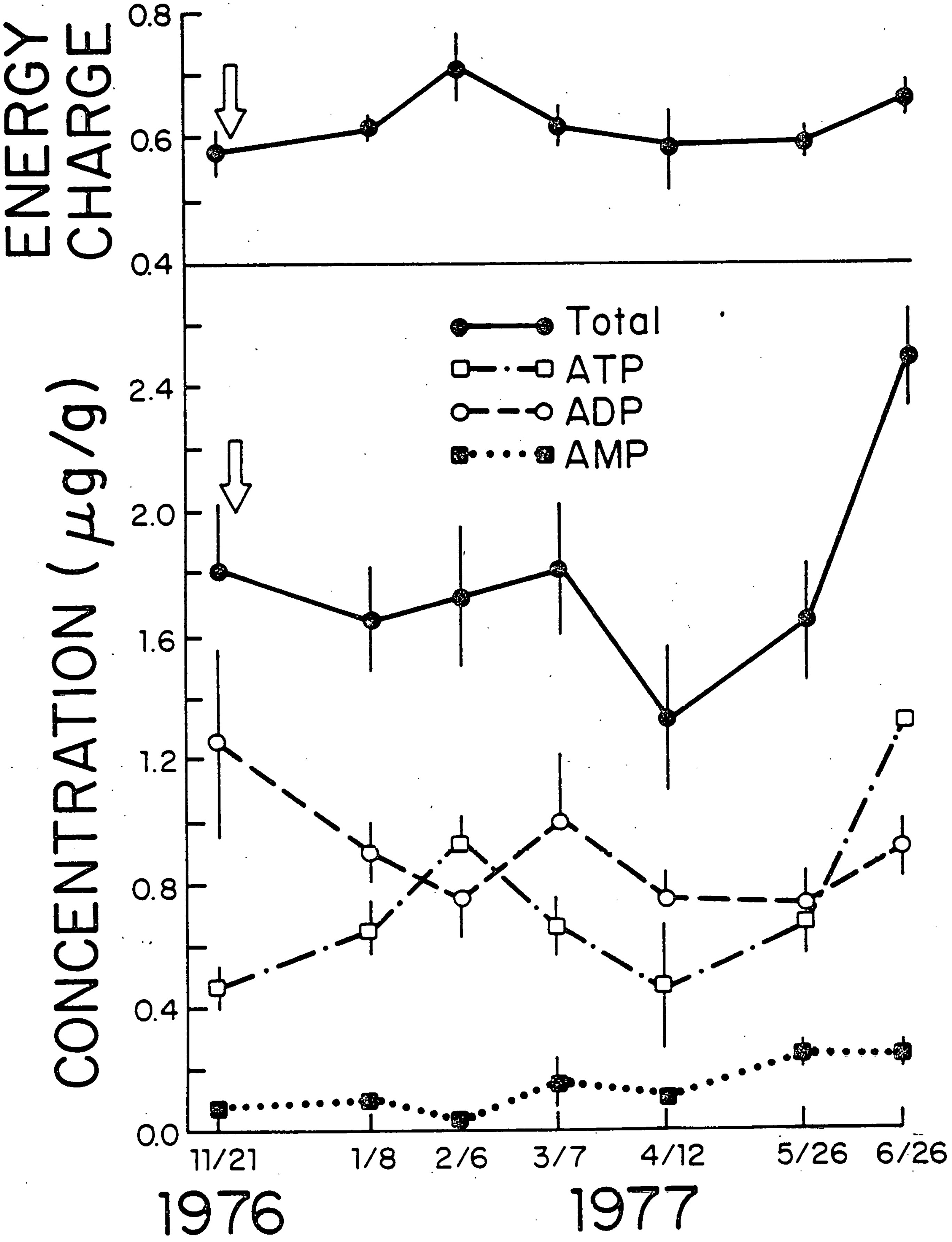
P_w
40
30
20
10
0
11/12
1/8
2/6
3/7
4/12
5/26
6/26
1976
1977

Fig. 14. Mean (N = 2) mite and collembola density fluctuations in the disturbed ecosystem, E1 (0), and the undisturbed system, E2 (0). Initiation of insecticide treatment is indicated by the arrow. Standard error bars extend below the mean values for E1, and above mean values for E2.



NUMBER /25 cm²
400
300
200
100
0
100
0
Mites
Collembola
11/21
1/8
2/6
3/7
4/12
5/26
6/26
1976
1977

Fig. 15. Mean fluctuations in concentration (μg/g dry soil) of adenosine triphosphate (ATP), adenosine diphosphate (ADP), adenosine monophosphate (AMP), and total adenylates; and adenylate energy charge ratio of soil from the study ecosystems. Each point represents the mean of four determinations of a composite soil sample and bars indicate ±SE.


ENERGY CHARGE
0.8
0.6
0.4
CONCENTRATION (µg/g)
2.4
2.0
1.6
1.2
0.8
0.4
0.0
Total
ATP
ADP
AMP
11/21
1/8
2/6
3/7
4/12
5/26
6/26
1976
1977