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Abstract

We measured aboveground plant biomass, aboveground net primary productivity (ANPP), detritus accumulation, and nitrogen and phosphorus uptake by aboveground vegetation in six *Metrosideros polymorpha* stands on the windward slopes of Mauna Loa, Hawai'i, USA. Our objective was to quantify the effects of elevation (primarily temperature) on ecosystem properties during primary succession, as a key to understanding ecosystem–climate interactions. Four study sites were on 111- to 136-yr-old lava flows at elevations of 290, 700, 1130, and 1660 m. Two additional sites on 3400-yr-old lava were at 700 and 1660 m elevations. All sites were on solid pahoehoe (smooth or ropy-textured) lava substrates with gentle relief, were free of significant human disturbance, received abundant precipitation, and had similar vegetation composition. Total aboveground biomass, soil organic matter mass, and aboveground net primary production (ANPP) were all greater in the old sites than in young sites. Differences between young and old sites in aboveground live biomass, detrital mass, and ANPP all supported the conclusion that ecosystem development proceeded relatively faster at 700 m elevation than at 1660 m. However, aboveground biomass in the old sites (81 Mg/ha at 1660 m elevation and 123 Mg/ha at 700 m) was low in comparison with other wet tropical forests. Accumulations of N and P in live biomass and detritus followed the same trends as were observed for organic matter. Rates of soil carbon accumulation over the first 3400 yr of succession averaged 2.1 $g{\cdot}m^{-2}{\cdot}yr^{-1}$, similar to other reported soil chronosequences. Observed rates of N accumulation ranged from 0.1 to 0.6 $g{\cdot}m^{-2}{\cdot}yr^{-1}$ over the first 136 yr of succession. There were no monotonic elevational trends among young sites with respect to live biomass, detritus mass, or total N or P accumulation. Foliar nitrogen concentrations in the young sites were among the lowest reported from any tropical forests and tended to decline with increasing elevation. The growth and biomass of individual plant species varied in distinctive ways along the elevational gradient. Nevertheless, among young sites there was a direct, linear relationship between total ANPP and mean annual temperature of the site, with a similar pattern in the two old sites. For each 1°C increase in mean annual temperature, total ANPP increased by 54 $g{\cdot}m^{-2}{\cdot}yr^{-1}$. Community-level ANPP also was directly correlated with rates of N and P uptake by the vegetation, regardless of site age or elevation.

Disciplines

Biogeochemistry | Ecology and Evolutionary Biology | Environmental Monitoring | Natural Resources and Conservation | Natural Resources Management and Policy | Terrestrial and Aquatic Ecology

PRIMARY PRODUCTIVITY AND ECOSYSTEM DEVELOPMENT ALONG AN ELEVATIONAL GRADIENT ON MAUNA LOA, HAWAI'I

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Abstract. We measured aboveground plant biomass, aboveground net primary productivity (ANPP), detritus accumulation, and nitrogen and phosphorus uptake by aboveground vegetation in six *Metrosideros polymorpha* stands on the windward slopes of Mauna Loa, Hawai'i, USA. Our objective was to quantify the effects of elevation (primarily temperature) on ecosystem properties during primary succession, as a key to understanding ecosystem–climate interactions. Four study sites were on 111- to 136-yr-old lava flows at elevations of 290, 700, 1130, and 1660 m. Two additional sites on 3400-yr-old lava were at 700 and 1660 m elevations. All sites were on solid pahoehoe (smooth or ropy-textured) lava substrates with gentle relief, were free of significant human disturbance, received abundant precipitation, and had similar vegetation composition. Total aboveground biomass, soil organic matter mass, and aboveground net primary production (ANPP) were all greater in the old sites than in young sites. Differences between young and old sites in aboveground live biomass, detrital mass, and ANPP all supported the conclusion that ecosystem development proceeded relatively faster at 700 m elevation than at 1660 m. However, aboveground biomass in the old sites (81 Mg/ha at 1660 m elevation and 123 Mg/ha at 700 m) was low in comparison with other wet tropical forests. Accumulations of N and P in live biomass and detritus followed the same trends as were observed for organic matter. Rates of soil carbon accumulation over the first 3400 yr of succession averaged 2.1 g·m^{-2}·yr^{-1}, similar to other reported soil chronosequences. Observed rates of N accumulation ranged from 0.1 to 0.6 g·m^{-2}·yr^{-1} over the first 136 yr of succession. There were no monotonic elevational trends among young sites with respect to live biomass, detritus mass, or total N or P accumulation. Foliar nitrogen concentrations in the young sites were among the lowest reported from any tropical forests and tended to decline with increasing elevation. The growth and biomass of individual plant species varied in distinctive ways along the elevational gradient. Nevertheless, among young sites there was a direct, linear relationship between total ANPP and mean annual temperature of the site, with a similar pattern in the two old sites. For each 1°C increase in mean annual temperature, total ANPP increased by 54 g·m^{-2}·yr^{-1}. Community-level ANPP also was directly correlated with rates of N and P uptake by the vegetation, regardless of site age or elevation.

Key words: biomass; elevational gradient; Hawai'i; Histosols; Mauna Loa; Metrosideros polymorpha; *net primary productivity; nitrogen; nutrient cycling; phosphorus; primary succession; temperature.*

INTRODUCTION

Jenny (1941, 1980) proposed that the attributes of ecosystems, soils, or vegetation could be understood best by isolating and investigating the effects of any one of several predominant controlling variables, the most important of which he identified as climate, organisms, relief, parent material, and time. Ideally, the influence of any one of these factors can be determined by keeping all the others constant. Practically, this is rarely possible; even individual factors such as "climate" are themselves multivariate, and interactions among these factors abound in nature. Nevertheless, Jenny's conceptual approach provides a foundation

upon which investigations of ecosystem processes can be evaluated.

Mauna Loa, an active volcano on the Island of Hawai'i in Hawaii, USA, provides an environment that is uniquely well suited to the investigation of environmental controls over ecosystem properties (Vitousek et al. 1988, 1992, 1995). Individual lava flows frequently extend from above the treeline to near sea level, and the locations and ages of surface flows have been mapped (Lockwood et al. 1988; J. P. Lockwood, *personal communication*). Because the ages of substrates are known, side-by-side flows differing in age can be compared (e.g., Drake and Mueller-Dombois 1993) and ecosystem properties can be studied on individual flows that extend across broad elevational gradients (e.g., Vitousek et al. 1992, Aplet and Vitousek 1994).

The extreme isolation of Hawaii has resulted in a

TABLE 1. Characteristics of the six study sites on windward Mauna Loa, Hawai'i, USA.

Elevation (m)	Age (yr)	Tree density† (no./ha)	Basal area (m²/ha)	Canopy height (m)	Tree-fern density‡ (no./ha)	Species richness‖
Young flows						
290	110	1610	5.1	9.4	4	24
700	136	425	1.2	4.7	80	24
1130	136	930	2.3	5.3	50	27
1660	136	62	0.1	2.7	40	26
Old flow						
700	3400	715	17.5	14.1	1790	38
1660	3400	1760	17.6	11.6	90	40

† Includes all tree stems ≥10 cm in circumference at breast height.

‡ All *Cibotium* spp. with visible aboveground stems.

‖ The number of vascular plant species found within one 0.5-ha plot.

flora and fauna that is both unique and species-poor (Carlquist 1980, Kitayama and Mueller-Dombois 1992, 1994). Hence, both young and old lava flows are frequently dominated by the same, few plant species, and these same species dominate sites at a wide variety of elevations. Mauna Loa is built of recent lava flows, and its long, gentle slopes provide a uniform relief at all elevations. Rising 4167 m in the face of the prevailing northeasterly trade winds, the windward slopes of Mauna Loa generate abundant orographic precipitation. Within this rainy belt, moisture availability is high year-round.

Hence, by appropriate site selection, Jenny's state factors of climate, organisms, relief, parent material, and time can all be considered, ruled out, or investigated individually with a minimum of confounding variables. We utilized the well-defined environmental matrix of windward Mauna Loa to investigate the effects of elevation—primarily the effects of temperature—on rates of biomass accumulation, plant productivity, and nutrient cycling in undisturbed forest stands on parallel, young vs. old lava flows that extended over an elevational gradient from 290 to 1660 m.

STUDY SITES

Six study sites were located on the eastern, windward slopes of Mauna Loa, at about 19°45′ N and 155°15′ W on the Island of Hawai'i. All six sites (Table 1) were on pahoehoe lava, which is solid with an undulating surface interspersed with cracks and with occasional tumuli. Roots of the developing vegetation were unlikely to penetrate to buried soil horizons.

Four sites were located on young flows of documented ages. Three of these were located on the 1855 flow, at elevations of 700, 1130, and 1660 m above mean sea level. An additional young site was located on the 1881 flow at 290 m elevation (Table 1). The other two sites were situated on an old lava flow at elevations of 700 and 1660 m, near sites on the younger flows, but far enough from flow edges that there was no discernible effect of the flow edge on the vegetation. The old flow was similar in texture and relief to the young flows; it is described as being on the Punahoa flow, dated at 3388 ± 28 yr (mean $\pm$ 1 SE) before present (Rubin et al. 1987, Lockwood 1995). All lavas emanating from Mauna Loa are mineralogically similar (Clague and Dalyrymple 1987, Wright and Helz 1987).

All six sites had overstories dominated by *Metrosideros polymorpha* (Myrtaceae), the most widespread tree on the Hawaiian Islands, and the communities had few species (Table 1). Understories in the sites were dominated by *Dicranopteris linearis* (N. L. Burm.) Underw. (Gleicheniaceae), *Machaerina angustifolia* (Cyperaceae) and, at the highest-elevation young flow, *Coprosma ernodeoides* (Rubiaceae) and *Vaccinium reticulatum* (Ericaceae). The nitrogen-fixing canopy tree *Acacia koa* (Fabaceae) was present in the old sites. Angiosperm nomenclature follows Wagner et al. (1990).

The soils in all six sites are Histosols overlying pahoehoe bedrock; those in the old sites were classified as Lithic Tropofolists by Sato et al. (1973). They are acid, very dark brown, friable, slightly sticky, slightly plastic, and strongly smeary mucks overlying pahoehoe bedrock. They have very high water-holding capacities, with moisture contents frequently exceeding 500% of dry mass.

The prevailing climatic characteristics of the study sites are documented for the period September 1991 through August 1993, and long-term mean monthly rainfall has been determined (Juvik and Nullet 1994). Mean annual temperatures on windward Mauna Loa decline linearly from 23.6°C at 10 m elevation to 13.1°C at 1640 m (Fig. 1). Mean monthly temperatures during the summer average 4–6°C higher than winter minima (Fig. 2). Mean annual rainfall increases from
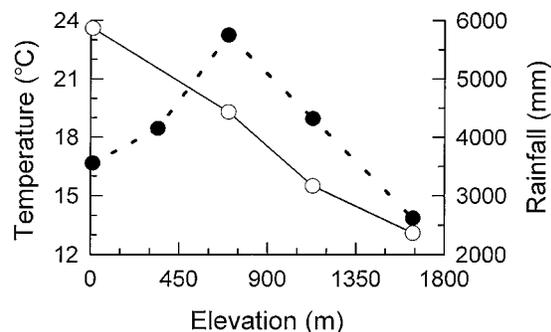
FIG. 1. Average annual climatic characteristics of windward Mauna Loa, Hawai'i. Air temperatures (○) are based on 2 yr of continuous measurements by Juvik and Nullet (1994). Rainfall data (●) represent long-term averages as reported by Juvik and Nullet (1994). Data for 342-m elevation are from weather station number 88.1, courtesy of the Commission on Water Resource Management, Department of Land and Natural Resources, State of Hawaii, USA.

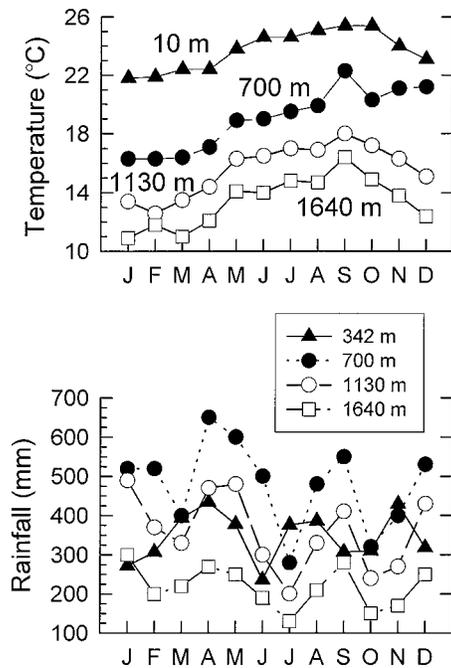FIG. 2. Mean monthly air temperatures (top) and rainfall (bottom) on windward Mauna Loa, Hawai'i. Air temperatures are based on 2 yr of continuous measurements by Juvik and Nullet (1994). Rainfall data are as reported by Juvik and Nullet (1994). Data for 342-m elevation are from weather station number 88.1, courtesy of the Commission on Water Resource Management, Department of Land and Natural Resources, State of Hawaii, USA.

3560 mm at an elevation of 10 m to 5750 mm at 700 m elevation, and then declines at higher elevations (Fig. 1). Mean monthly rainfall (Fig. 2) exceeds mean monthly evaporation during all months of the year (Juvik and Nullet 1994). In addition, there is an unmeasured input of cloudwater that increases with elevation within the range of this study (Juvik and Nullet 1993).

METHODS

A single 50 × 100 m plot was established in each site, within which all sampling utilized a stratified random design. Field studies of biomass and productivity extended from January 1991 through July 1992, except that tree growth measurements extended through July 1993.

Live and dead biomass

Tree biomass.—Aboveground tree biomass was determined with forest inventory and regression techniques. We inventoried all trees in the young site at 1660 m, where there were few trees, and inventoried a single 20 × 100 m transect contiguous to the old site at 700 m, which had an extraordinarily dense understory. In the other four sites we measured the circumference and height of all living tree stems ≥10 cm in circumference at breast height in 6–12 randomly selected, 10 × 10 m plots. Tree circumferences at breast

height were measured to the nearest 1.0 mm. Heights of trees ≤10 m tall were measured to the nearest 0.1 m with an extension pole, and taller trees were measured with a clinometer.

Regressions of total aboveground tree mass, total aboveground wood mass, and tree leaf mass (Table 2) were derived from a cumulated data set of all harvested *Metrosideros* trees from windward Hawai'i (total $n = 44$ trees, maximum basal diameter = 38.3 cm, maximum height = 19.4 m). Both diameter at breast height (dbh) and basal diameter of a large number of trees were measured to determine site-specific tree tapers for biomass regressions (Table 2). Allocation of total wood mass (total mass − leaf mass) to twig, branch, and bolewood components was based on the mean proportions of each found in the harvested trees. *Metrosideros* trees of different sizes did not differ consistently in their allocation patterns: aboveground woody mass averaged 4% leafy twigs, 14% branches ≤1 cm diameter, and 82% in boles and branches >1 cm diameter. At each site samples of live *Metrosideros* leaves, leaf-bearing twigs, branches, and bolewood were collected from 2–5 trees for nutrient analysis.

Tree species other than *Metrosideros* were important only in the old site at 700 m elevation. To estimate their total biomass and allocation patterns we utilized the biomass-regression equations and original harvest data of Aplet and Vitousek (1994), matching species as closely as possible. Biomass regressions for *Psidium cattleianum* (Table 2) were determined independently by harvesting six individuals of different sizes. We collected samples of leaves, branches, and bolewood from three individuals of each of three additional tree species in this site to estimate tree nutrient content. To estimate the biomass of large *Acacia koa,* some >1 m dbh, we utilized the wet forest equation of Brown and Iverson (1992).

Sapling biomass.—In each site a single 5 × 50 m transect was randomly selected, and the heights of all *Metrosideros* saplings within this transect were measured. Saplings were defined as all seedlings and saplings <3.2 cm dbh. The biomass of each sapling was estimated using biomass–height relationships of small harvested trees (Table 2).

Understory and litter biomass.—In each site three or four 1 × 3 m plots were randomly located, and all aboveground live vegetation (sorted by species), all standing dead plants (sorted by species), and all woody and non-woody surface litter were harvested and weighed (excluding *Metrosideros* saplings and all trees). We did not harvest roots because an unknown proportion penetrated the lava cracks, from which they were impossible to remove. Well-mixed subsamples were used to determine dry masses (oven dried at 105°C) and nutrient content (oven dried at 70°C).

Soils.—Soil mass was sampled in three locations in each of the 3–4 understory-biomass plots by selecting a pit location with a stratified random design. In the

TABLE 2. Regression equations utilized to estimate the biomass of individual trees and tree parts in the six study sites on Mauna Loa volcano, Hawai'i, USA. n = the number of trees sampled.

Species	Equation	n	r^2
Taper equations			
Metrosideros polymorpha			
Young flow, 290 m	$D = 0.83 + 1.11 \cdot dbh$	65	0.98
Young flow, 700 m	$D = 1.30 + 1.11 \cdot dbh$	63	0.93
Young flow, 1130 m	$D = 1.28 + 1.07 \cdot dbh$	52	0.96
Young flow, 1660 m	$D = 3.62 + 1.13 \cdot dbh$	32	0.69
Old flow, 700 m	$D = 1.75 + 1.07 \cdot dbh$	33	0.95
Old flow, 1660 m	$D = 0.86 + 1.06 \cdot dbh$	39	0.99
Antidesma plicata	$D = 0.26 + 1.29 \cdot dbh$	46	0.90
Cheirodendron trigynum	$D = 0.18 + 1.22 \cdot dbh$	11	0.99
Coprosma spp.	$D = 0.82 + 1.16 \cdot dbh$	4	0.99
Hedyotis spp.	$D = -0.90 + 1.99 \cdot dbh$	6	0.80
Ilex anomala	$D = 0.66 + 1.13 \cdot dbh$	25	0.90
Melicope clusiifolia	$D = 0.99 + 1.08 \cdot dbh$	15	0.95
Psidium cattleianum	$D = 0.29 + 1.43 \cdot dbh$	10	0.99
Biomass equations			
Metrosideros polymorpha			
dbh <3.2	$\ln(T) = 2.95 + 1.76 \cdot H$	23	0.59
dbh >3.2	$T = 2930 + 22.5 \cdot D^2H$	44	0.95
	$W = 2450 + 21.9 \cdot D^2H$	44	0.95
	$L = 374 + 14.1 \cdot BBA$	38	0.94
Cheirodendron trigynum†	$\ln(T) = 2.956 + 1.068 \cdot \ln(D^2H)$		
	$L = -77.3 + 25.8 \cdot BBA$	10	0.89
Coprosma spp.†	$\ln(T) = 3.450 + 0.914 \cdot \ln(D^2H)$		
	$L = 47.9 + 10.8 \cdot BBA$	8	0.95
Ilex anomala†	$\ln(T) = 3.497 + 0.959 \cdot \ln(D^2H)$		
	$L = 29.3 + 38.4 \cdot BBA$	7	0.96
Psidium cattleianum	$\ln(T) = 3.936 + 0.739 \cdot \ln(D^2H)$	8	0.90
	$L = -42.4 + 18.9 \cdot BBA$	6	0.99
Other trees <20 cm dbh	$\ln(T) = 3.783 + 0.849 \cdot \ln(D^2H)$	42	0.91
	$L = 47.7 + 21.0 \cdot BBA$	33	0.81
Other trees >20 cm dbh‡	$T = 21297 - 6953 \cdot dbh + 740 \cdot (dbh)^2$		

Key: BBA = basal area of tree at base (cm²); D = basal diameter of tree (cm); dbh = diameter at breast height (cm); H = total tree height (m); L = total tree leaf mass (g); T = total aboveground tree mass (g); W = total aboveground wood mass (g).

† From Aplet and Vitousek (1994).

‡ From Brown and Iverson (1992).

young sites the pits were 50×50 cm each except at the highest elevation, where all soil within the 1×3 m plot was collected. In the old sites each pit measured 25×25 cm. Within each pit all soil was removed to the surface of the lava, and any loose lava rocks were removed to expose soil beneath them. Soil depth was measured at each corner and at the center of each pit, and sieved (5-mm mesh) soil was weighed. Subsamples were oven-dried at 105°C to determine dry mass, and at 70°C for elemental analysis.

Dry subsamples were then sieved (2-mm mesh) to remove gravel (i.e., small pieces of lava covered with organic-matter skins). The 2-mm material was sorted into three fractions: plant litter, soil, and fine roots (diameters <2 mm). Determination of total soil C required that C in both the soil (<2 mm) and gravel (2–5 mm) fractions be considered. Ash-free dry masses were determined by combustion at 500°C for 4 h, and the relationship between percentages of ash-free dry mass (AFDM) and soil C content were determined on 22 samples, with soil C being measured with a Carlo–Erba elemental analyzer:

$$C = 0.51 \times AFDM - 1.2$$

($n = 22$, $r^2 = 0.93$, $P < 0.001$). Soil C:N was determined on subsamples of soil from each pit (three per plot) using a Carlo-Erba elemental analyzer, after grinding to pass through a 0.25-mm sieve.

Aboveground net primary productivity

Aboveground net primary productivity (ANPP) was measured as the sum of increases in aboveground standing crop of live vegetation plus litter production. Losses due to herbivory were not measured, but are typically <10% of ANPP in forest ecosystems (e.g., Reichle et al. 1973, Whittaker 1975, Boring et al. 1981, Proctor et al. 1989) and may be even lower in these sclerophyllous ecosystems. Total ANPP in each site was determined by independently sampling trees, saplings, understory herbs, grasses, the climbing fern *Dicranopteris linearis,* and overstory litterfall. We used the same spatial and temporal sampling schemes and the same measurement techniques in all six sites unless otherwise noted.

Biomass increments.—Annual increments in aboveground biomass were determined as the sum of the individual increments in the overstory, sapling, and understory strata.

Tree growth was measured directly in each site. Every tree measured in our biomass study was tagged with a unique number and the location of the circumference measurement was marked. Tree circumferences and heights were measured every one or two years for 1.2–2.3 yr total. Growth was calculated for each tree based on its initial and final biomass. All positive increments were summed within plots to estimate total tree growth.

The mean annual biomass increment of the understory vegetation was estimated by dividing total aboveground live understory biomass by the age of the underlying lava. This method assumes that mean annual biomass increments were constant over the lifespan of the sites. The net growth of *Metrosideros* saplings was estimated in the same way.

Litter production.—Rates of litter production by the entire plant community were determined as the sum of overstory litterfall and measured aboveground production by herbs, grasses, and *Dicranopteris*.

The productivity of understory herbs and ferns (excluding *Dicranopteris*) was measured in ten 1×1 m quadrats in each young-flow site. Quadrats were delineated with polyvinyl chloride (PVC) plastic frames within which all rooted plants were monitored monthly. Whenever a leaf, ramet, or branch died it was harvested, oven-dried at 70°C, weighed, and ground for later nutrient analysis. Quadrats were relocated within sites after 6 mo to minimize impacts on the sampled sites; mortality of herbs was monitored for a total of 1 yr. We did not monitor herbaceous production in the old sites because their understories were completely dominated by *Dicranopteris*.

The annual production of grasses, principally *Andropogon virginicus,* was estimated from maximum aboveground standing crop (late summer). In each young site all grass was harvested from twelve 1-m² quadrats, and sorted into live green, newly dead, and old dead grass. Annual production was presumed to equal the mass of live green and newly dead grass.

Annual production by *Dicranopteris linearis* was determined by measuring all aboveground tissue production over a 13-mo period. In five of the six sites, ten 1-m² quadrats were randomly selected and framed with PVC. In the young site at 1660 m the population was so small that the entire population of the 0.5-ha study plot could be monitored. *Dicranopteris*'s morphology is unusual in that the frond is a single indeterminate leaf arising from an underground rhizome (the true stem). We measured production at the lowest unit of accounting, the leaf segment, defined here as the analog of an internode on a stem and all attached pinnae. Every month all new leaf segments that had passed the fiddlehead (emerging leaf) stage within the quadrat were tagged and counted. Tagged segments that died over the 13-mo period were harvested and weighed. At the end of 13 mo, all the tagged leaf segments were harvested, separated by components (leaves and stems), dried at 105°C, and weighed. Subsamples were dried at 70°C, ground, and analyzed for nutrients.

Litter production by overstory trees and shrubs, including leaf shedding by treeferns (*Cibotium* spp.), was measured monthly with ten 0.5×1.0 m litter traps in each site. The collected litter was oven dried at 70°C and weighed, and subsamples were ground for nutrient analysis. Trap locations within sites were changed after 6 mo, and litter production was monitored for one full year. In the high-elevation young site a total of 20 litterfall traps were used, 10 in the open and 10 beneath tree canopies. Litter production in this site was based on the mean of collections from open and from beneath-canopy locations, each mean weighted in proportion to the area of its habitat.

Nutrient analyses

Plant tissues for nutrient analysis were ground to pass through a 1.0-mm mesh sieve. Mature live leaves and newly senesced leaves were analyzed to independently determine nutrient standing crops and uptake requirements. Nutrient analyses followed the methodologies used by Vitousek et al. (1988).

Basic soil chemical and physical characteristics were determined on composite samples from each biomass-harvest plot, weighted by the soil mass per pit. Samples of the 2-mm fraction were digested in 0.2 mol/L HNO_3 with mild heating. This digest was found to extract organic P but not the mineral P present in the lava particles. Elemental compositions of the digest were determined using plasma emission spectroscopy (Isaac and Johnson 1985). These analyses were conducted by the Agricultural Diagnostic Service Center, University of Hawaii at Manoa. Soil pH was determined in a 2:1 water : soil slurry of three freshly collected surface-soil samples per site.

Nutrient fluxes

Plant nitrogen and phosphorus uptake.—Nutrient-uptake requirements for net growth of the understory plants and *Metrosideros* saplings were estimated by dividing the total N and P content of the aboveground live understory and sapling biomass by the age of the underlying lava. Nutrient uptake by trees, understory herbs, grasses, and *Dicranopteris* were individually determined by multiplying their measured productivities by the nutrient concentrations of newly senesced tissues (e.g., Cole and Rapp 1981). Nutrient-uptake requirements for overstory litter production were derived from nutrient concentrations of litterfall components multiplied by their mass fluxes. We did not measure N or P fluxes in water cycling through the sites, and therefore may have underestimated nutrient uptake slightly.

Nitrogen mineralization and soil P availability.—

TABLE 3. Mean characteristics of the soils of the Mauna Loa study sites. Values are based on a minimum of three samples per site. An ''n.d.'' indicates no data.

Characteristic	Young sites				Old sites	
	290 m	700 m	1130 m	1660 m	700 m	1660 m
Soil age (yr)	110	136	136	136	3400	3400
Soil depth (cm)	5	8	n.d.	<1	22	15
Soil mass† (kg/m²)	3.3	2.4	5.1	1.2	22.6	22.0
pH (in H_2O)	4.9	4.7	4.9	5.1	4.8	5.0
Soil C (g/m²)	2480	985	2260	257	6990	7360
C:N	27.4	25.2	30.9	20.6	16.7	18.1
Nitrate-N (μg/g)	0.1	1.3	2.4	0.3	10.8	1.0
Ammonium-N (μg/g)	29.9	19.2	35.0	16.2	20.1	17.8
Available P‡ (μg/g)	11.6	6.1	9.4	12.2	2.2	1.3
Total P‖ (mg/g)	0.6	0.4	0.3	0.9	1.1	0.9
Extractable‖ Al (mg/g)	2.0	1.9	2.1	0.3	4.0	5.4
Extractable B (μg/g)	10	18	11	5	16	22
Extractable Ca (mg/g)	3.1	1.7	1.9	1.5	1.4	1.8
Extractable Cu (μg/g)	20	29	22	41	37	46
Extractable Fe (mg/g)	0.8	4.4	1.0	5.6	14.2	9.5
Extractable K (mg/g)	0.3	0.2	0.2	0.4	0.4	0.2
Extractable Mg (mg/g)	0.9	0.9	0.8	1.3	0.6	0.5
Extractable Mn (μg/g)	83.5	96.8	34.0	67.2	159	129
Extractable Na (mg/g)	0.3	0.4	0.3	0.9	0.6	0.5
Extractable Zn (μg/g)	155	175	185	33	146	34

† Includes the 2-mm fraction only, for the entire soil volume.
‡ Ammonium fluoride extraction.
‖ As extracted in 0.25-mol/L HNO_3 with mild heating.

Laboratory measurements of soil net nitrogen mineralization were made using the surface 5 cm of soil collected from 16–20 random locations per site in February 1991, May 1992, and July 1992. Soils were kept on ice until being extracted (within 24 h) with 2.0 mol/L KCl for NO_3-N and NH_4-N (Keeney and Nelson 1982), and with acid fluoride for PO_4-P (Olsen and Sommers 1982). At the same time, paired soil samples were watered to near their field capacity, covered, and stored at room temperature for 2 wk. At the end of this incubation period NO_3-N and NH_4-N were extracted. All extracts were refrigerated and shipped to Stanford, California, for colorimetric analysis with an autoanalyzer.

Data analysis

Within each site we quantified variables on 2–20 randomly selected samples to estimate within-site variance and to test for differences among site means. Sample sizes were small, and hence assumptions of normal distributions and homogeneous variances could not be tested adequately. Therefore, we used the Kruskal-Wallis test, a nonparametric one-way ANOVA by ranks (Daniel 1990), to test for significant differences among young-flow sites. All Kruskal-Wallis tests conducted were based on four groups (young sites) and three degrees of freedom; the stated sample size refers to the total number of measurements or samples contributing to the result.

To determine if observed differences among young-flow sites were significantly correlated with elevation, linear regression was applied. We used the mean flux or mass estimate for each of four young sites as a single unbiased estimate of the flux or mass of interest at that site's elevation. Because only two old sites were included in this study, we did not test for elevational relationships on the old flow.

We tested for differences between young and old sites at the same elevation using the Mann-Whitney two-sided test. This required that all samples within sites be considered true replicates. Similar analyses were used to identify differences between the two old-flow sites.

RESULTS

Soil properties

All sites had acid soils, with pH ranging from 4.7 to 5.1. Overall, the surface soils of all sites had comparable characteristics (Table 3). However, the old sites had lower soil C:N ratios, consistent with a greater accumulation of decomposed organic matter, and lower concentrations of available P. Soils of the old sites also had higher A1, Fe, and Mn concentrations than did those of the young sites, suggesting greater weathering of the lava bedrock in the older sites.

Biomass

Overstory biomass.—Our sites were dominated by *Metrosideros polymorpha,* which comprised >95% of the tree biomass in five of the six sites. *Metrosideros* made up 40% of the tree biomass in the old site at 700 m elevation, where four large *Acacia koa* trees (3% of the measured stems) comprised more than half the aboveground tree biomass. Tree biomass was substantially greater in both of the old sites than in the young

TABLE 4. Biomass of aboveground vegetation and detritus in the six study sites on Mauna Loa in Hawai'i, USA. Shown are means ± 1 SE for all data with $n > 1$, where n = number of quadrats or plots sampled.

	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6
Site age (yr)	110	136	136	136	3 400	3 400
Elevation (m)	290	700	1 130	1 660	700	1 660
Tree biomass (g/m²)						
Leaves	167 ± 25	44 ± 6	89 ± 10	7	239	371 ± 23
Total	2 130 ± 430	360 ± 50	793 ± 100	51	10 800	6 750 ± 710
n	8	12	6	1	1	10
Sapling biomass (g/m²)						
Leaves	46	46	149	13	1	256
Total	124	136	431	45	3	699
n	1	1	1	1	1	1
Understory biomass (g/m²)						
Ferns†	430 ± 67	133 ± 27	232 ± 34	0 ± 0	1 500 ± 415	451 ± 53
Herbs	160 ± 120	308 ± 58	276 ± 40	18 ± 10	17 ± 17	66 ± 55
Shrubs	101 ± 65	0 ± 0	174 ± 144	206 ± 68	0 ± 0	111 ± 88
Bryophytes	105 ± 28	426 ± 63	317 ± 93	221 ± 141	0 ± 0	22 ± 13
Total	796 ± 185	867 ± 31	998 ± 185	445 ± 198	1 520 ± 427	649 ± 109
n	3	4	3	4	4	4
Total aboveground live biomass (g/m²)						
	3 050	1 370	2 220	542	12 300	8 100
Detritus (g/m²)						
Litter‡	1 150 ± 38	826 ± 168	1 450 ± 313	154 ± 30	5 780 ± 867	2 360 ± 442
Soil OM	2 920 ± 977	1 940 ± 595	4 450 ± 1 440	509 ± 128	13 800 ± 1 760	14 500 ± 7 210
n	3	4	3	4	4	4

Notes: Sapling biomass includes all *Metrosideros* <3.2 cm dbh. Lichens are included with bryophtyes.

† Includes treeferns.

‡ Includes dead treefern stems. Excludes standing and fallen tree boles and branches >5 cm diameter, which were not sampled.

sites (Table 4). Aboveground tree biomass differed significantly among young sites (Kruskal-Wallis test, H = 21.3, n = 55 plots, $P < 0.001$), but was not significantly correlated with elevation (linear regression, n = 4 sites, $P = 0.19$) due to the relatively high biomass at the 1130-m site. *Metrosideros* saplings were abundant in most sites, and their biomass was unrelated to elevation (Table 4).

Understory biomass.—Ferns, particularly *Dicranopteris linearis* and *Cibotium* spp., composed >50% of the understory biomass in both old sites and in the lowest-elevation young site (Table 4). Shrubs composed >40% of the understory biomass in the highest elevation young site, but <20% in all other sites. The biomass of nonvascular plants (i.e., mosses, liverworts, and lichens) was >100 g/m² in all of the young sites, but <30 g/m² in both old sites (Table 4). Total understory biomass did not differ significantly among young-flow sites, nor between young and old sites.

Detritus.—We combined all surface litter and standing dead understory vegetation into a single category hereafter referred to as litter (Table 4), which included dead and rotting treefern stems, but excluded coarse woody debris >5 cm diameter, which was not measured. There was significantly more litter in the old sites than in the young sites at both 700 m and 1660 m elevations (Mann-Whitney test, n = 8 plots, $P < 0.03$). Differences among young sites were also sig-

nificant (Kruskal-Wallis test, H = 9.3, n = 14 plots, $P = 0.025$) due to the low litter mass present in the young site at 1660 m elevation (Table 4). The large amounts of litter in the old site at 700 m were due mainly to accumulations of dead ferns, which comprised >60% of the litter mass.

Most of the detritus present in all six sites was comprised of soil organic matter (OM). Mean pools of soil organic matter were similar in the two old sites, although spatial variability in soil OM pools was large (Table 4). There was almost an order of magnitude more soil organic matter present in the old sites than in the young sites (Table 4). Soil OM pools varied significantly among young sites (Kruskal-Wallis test, $P = 0.011$), again due to a very low mass of soil OM at the highest elevation (Table 4).

Nutrient accumulation

Foliar nutrient concentrations of the dominant plant species in our sites were low (Fig. 3 and 4). In general, foliar N concentrations declined with increasing elevation, whereas minimum foliar P levels were found at intermediate elevations (Fig. 3). However, only *Metrosideros* foliage varied significantly in N content among sites (Kruskal-Wallis test, $P < 0.05$). Foliar P varied significantly among sites for both *Dicranopteris* ($P = 0.05$) and *Machaerina* ($P = 0.08$), but not for *Metrosideros.* Foliar N concentrations of *Metrosideros*
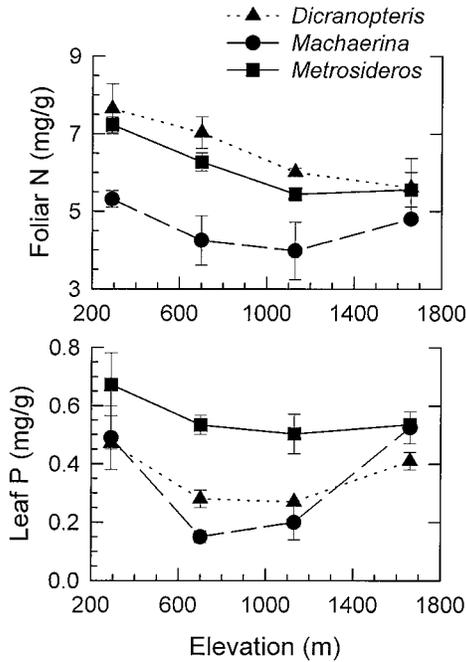
FIG. 3. Foliar nitrogen and phosphorus concentrations of three species in four young sites on windward Mauna Loa, Hawai'i. Data are based on well-mixed samples of live leaves from entire plant canopies. Shown are means ±1 SE based on 2–5 samples per species and site.
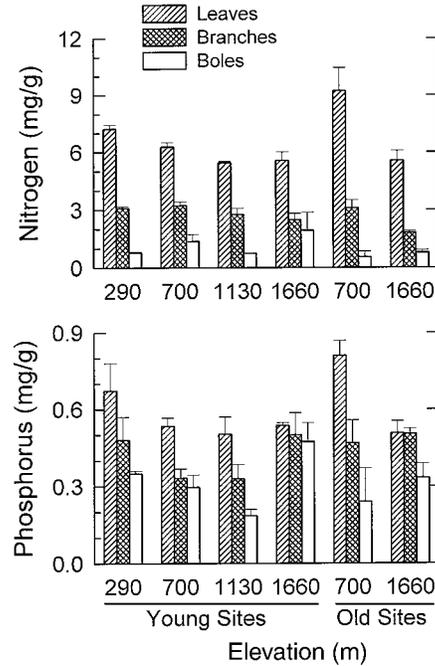

FIG. 4. Nitrogen and phosphorus concentrations in *Metrosideros polymorpha* leaves, branches, and boles in study sites on windward Mauna Loa, Hawai'i. Branches included are ≤1 cm in diameter; boles include larger branches. Shown are means ±1 SE based on 2–5 sample trees per site.

(and *Dicranopteris,* Russell 1996) were consistently greater in the old site at 700 m than in any other site (Fig. 4).

Nutrient concentrations within other plant tissues also varied among sites, but without clearly identifiable patterns. As a result, nutrient accumulation in total living and dead biomass in our various sites reflected very closely the accumulation of organic matter (cf. Tables 4 and 5). The single largest pool of nutrients sampled was soil organic matter, which contained >75% of the N and >55% of the P in all six sites (Table 5).

Aboveground net primary productivity

The ANPP of individual species responded to the elevational gradient in unique ways. Overstory litterfall and *Dicranopteris* production (Table 6) both declined significantly with increasing elevation on the young flows (linear regressions, $n = 4$ sites, $r^2 = 0.99$, $P < 0.001$ and $r^2 = 0.83$, $P < 0.06$, respectively). Mortality in the herb layer and grass production (Table 6) also varied significantly among young sites (Kruskal-Wallis test, H values = 14.9–18.6, $n = 40–41$ quadrats, df = 3, $P < 0.01$) but was not significantly correlated with elevation. Understory herbs such as *Machaerina angustifolia* and *Palhinhaea cernua* had their maximum productivities at intermediate elevations, while other species were measurably productive only in the highest-elevation young site. *Andropogon virginicus* was common only in the young site at 700 m, and the in-

vasive orchid *Arundina graminifolia* was most productive at 290 m.

Despite this variation among species, community-level ANPP (in grams per square meter per year) in the young sites declined monotonically and significantly with increasing elevation (ELEV, in meters) according to: ANPP = $670 - 0.36 \times$ ELEV ($n = 4$, $r^2 = 0.99$, $P = 0.002$) (Fig. 5). Biomass accumulation in the understory, sapling, and tree strata together contributed <18% of the total ANPP in all sites.
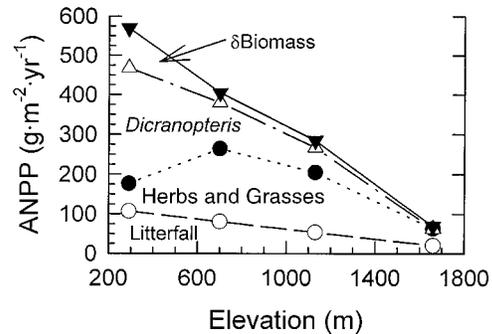

FIG. 5. Total community aboveground net primary productivity (ANPP) along an elevational gradient of young sites on windward Mauna Loa, Hawai'i. δBiomass is the sum of biomass increments in the understory, sapling, and tree layers. The topmost line (▼—▼) indicates the total community ANPP; lower lines separate the contributions of individual components.

TABLE 5. Nutrient pools in aboveground vegetation and detritus in the six study sites on Mauna Loa in Hawai'i, USA. Shown are means ± 1 SE, where nutrient concentrations were determined on a plot-level basis.

	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6
Site age (yr)	110	136	136	136	3400	3400
Elevation (m)	290	700	1130	1660	700	1660
Tree biomass (g/m^2)						
Total N	3.7	0.8	1.3	0.1	35.8	8.6
Total P	0.87	0.12	0.20	0.03	2.29	2.54
Sapling biomass (g/m^2)						
Total N	0.4	0.5	1.2	0.1	<0.1	1.9
Total P	0.06	0.05	0.14	<0.01	<0.01	0.29
Understory biomass (g/m^2)						
Total N	3.9 ± 0.9	4.6 ± 0.3	5.1 ± 0.8	2.9 ± 1.4	6.5 ± 1.5	2.9 ± 0.5
Total P	0.30 ± 0.10	0.19 ± 0.01	0.29 ± 0.08	0.18 ± 0.08	0.38 ± 0.11	0.21 ± 0.05
Total aboveground live biomass (g/m^2)						
Total N	8.0	5.9	7.6	3.2	42.4	13.3
Total P	1.22	0.36	0.63	0.21	2.67	3.05
Detritus (g/m^2)						
Litter N	5.3 ± 0.6	3.2 ± 0.8	4.6 ± 0.5	0.8 ± 0.2	31.9 ± 4.8	11.3 ± 1.9
Soil N	54.2 ± 17.8	39.1 ± 11.9	73.2 ± 15.3	12.5 ± 3.8	418 ± 42	408 ± 235
Litter P	0.18 ± 0.03	0.13 ± 0.04	0.17 ± 0.07	0.05 ± 0.01	1.14 ± 0.15	0.64 ± 0.15
Soil P	1.83 ± 0.79	0.82 ± 0.21	1.54 ± 0.78	0.48 ± 0.15	15.2 ± 4.7	14.1 ± 7.2

TABLE 6. Aboveground plant productivity and nutrient fluxes in the six study sites on Mauna Loa in Hawai'i, USA. Shown are means ± 1 SE where estimates were determined on a plot-level basis.

	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6
Site age (yr)	110	136	136	136	3400	3400
Elevation (m)	290	700	1130	1660	700	1660
Tree growth (g·m^{-2}·yr^{-1})						
Biomass	94 ± 18	18 ± 3	7 ± 2	2	59	90 ± 18
N uptake	0.1	<0.1	<0.1	<0.1	0.1	0.1
P uptake	0.04	0.01	<0.01	<0.01	0.02	0.03
Litterfall (g·m^{-2}·yr^{-1})						
Biomass	108 ± 31	81 ± 28	54 ± 28	21 ± 8	175 ± 20	229 ± 47
N uptake	0.4 ± 0.2	0.3 ± 0.1	0.2 ± 0.1	0.1 ± 0.0	1.6 ± 0.2	0.9 ± 0.2
P uptake	0.03 ± 0.01	0.03 ± 0.02	0.02 ± 0.01	0.01 ± 0.00	0.07 ± 0.01	0.07 ± 0.02
Dicranopteris (g·m^{-2}·yr^{-1})						
Biomass	291 ± 29	116 ± 16	62 ± 11	<1	658 ± 69	263 ± 36
N uptake	0.8	0.3	0.2	<0.1	2.4	1.2
P uptake	0.04	0.01	<0.01	<0.01	0.12	0.06
Herb layer (g·m^{-2}·yr^{-1})						
Biomass	67 ± 84	153 ± 75	151 ± 68	43 ± 19	trace†	trace†
N uptake	0.2	0.4	0.3	0.2	trace†	trace†
P uptake	0.02	0.04	0.03	0.02	trace†	trace†
Grasses (g·m^{-2}·yr^{-1})						
Biomass	2 ± 2	30 ± 9	0 ± 0	0 ± 0	trace†	trace†
N uptake	<0.1	0.1	<0.1	0	trace†	trace†
P uptake	<0.01	0.01	<0.01	0	trace†	trace†
Understory biomass increment (g·m^{-2}·yr^{-1})						
Biomass	7	6	7	3	<1	<1
N uptake	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1
P uptake	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01

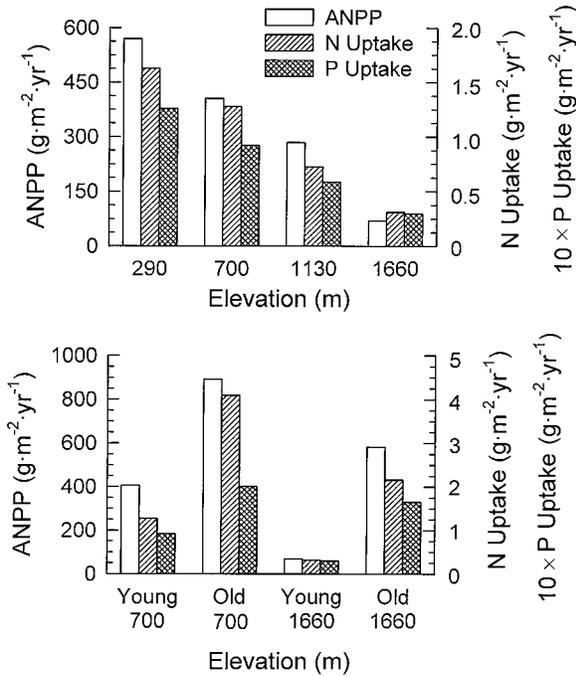† Not measured: uncommon in the study sites.

FIG. 6. Total aboveground net primary productivity (ANPP), N uptake, and P uptake by aboveground vegetation in: (top) young flows at four elevations and (bottom) paired young and old sites at two elevations.

Understories in the old-flow sites were completely dominated by *Dicranopteris linearis.* This fern grew so densely that understory herbs and grasses did not contribute to the measured ANPP in either old site. *Dicranopteris* growth (Table 6) was significantly greater in the old than in the young site at each of the two elevations (Mann-Whitney test, $n = 20$ quadrats, $P = 0.0001$), and was greater at the lower than at the higher elevation on the old flow (Mann-Whitney test, $n = 20$ quadrats, $P = 0.0001$).

Total ANPP in the old flows could not be statistically compared with ANPP on the young flows because only a single estimate of total ANPP exists for each of the sites. Given this constraint, our data suggest that ANPP on the old flow followed an elevational pattern similar to that found on the young flows. Total ANPP declined from 890 $g·m^{-2}·yr^{-1}$ at 700 m elevation to 580 $g·m^{-2}·yr^{-1}$ at 1660 m, for an average of -0.32 $g·m^{-2}·yr^{-1}$ per 1-m increase in elevation. This corresponds with the mean slope of -0.36 found in the young sites. Overall, ANPP on the 3400-yr-old flow was ≈ 500 $g·m^{-2}·yr^{-1}$ greater than it was on similarly situated sites on the 136-yr-old flow.

Nutrient cycling

Nitrogen and phosphorus uptake by the aboveground vegetation (Table 6) varied among sites in direct proportion to ANPP (Table 6, Fig. 6). As was the case with ANPP, both N and P uptake (in grams per square meter per year) declined linearly with increasing elevation on the young flows (linear regression, $n = 4$, $r^2 = 0.99$, $P < 0.01$). In the young-flow sites total ANPP, N uptake, P uptake, and elevation all were correlated with one another with Pearson's correlation coefficients $r > 0.98$.

Concentrations of inorganic N and P in the soil (Table 7) varied among sampling dates, so statistical comparisons were done individually for each of the three measurements. All sites had similar soil NH_4-N concentrations on all sampling dates. Concentrations of NH_4-N consistently exceeded those of NO_3-N (Wilcoxon's signed-ranks test, $n = 16$–20 samples per site and date, $P < 0.01$), except in the old site at 700 m elevation on two of three dates. Soil NO_3-N concentrations differed significantly among sites on all three dates (Kruskal-Wallis test, $H = 24.1$–56.4, $n = 77$–95, df $= 3$–5, $P < 0.001$), and were typically greater in the old site at 700 m than in any other site. Concentrations of available P, in contrast, were consistently lower in the old sites than in the any of the young sites (Kruskal-Wallis test, $H = 37.0$–51.7, $n = 77$–95, df $= 3$–5, $P < 0.001$).

Nitrogen mineralization rates also varied significantly among sites (Kruskal-Wallis test, $H = 17.6$–42.7, $n = 77$–95, df $= 3$–5, $P < 0.002$) due to very high mineralization rates on the old flow at 700 m. Mineralization rates were similar among young-site soils, and were consistently lower in soils from 1660-m than from 700-m elevation on the old flow (Table 7). Both net nitrification rates and soil NO_3-N concentrations were very low in all sites and on all three dates, except in the 700-m old site (Table 7).

TABLE 7. Inorganic N and P concentrations and fluxes in soils from the six Mauna Loa study sites in Hawai'i, USA. Mineralization rates are based on laboratory incubations over a 2-wk period. Values shown are means $\pm$ 1 SE based on 2–3 replicated experiments per site. For each experiment, $n = 16$–20 samples per site.

Soil inorganic nutrient concentrations

Age (yr)	Elevation (m)	NO_3-N ($\mu g/g$)	NH_4-N ($\mu g/g$)	Bray's P ($\mu g/g$)
110	290	0.1 ± 0.1	29.9 ± 12.9	11.6 ± 6.4
136	700	1.3 ± 1.8	19.2 ± 9.5	6.1 ± 1.1
136	1130	2.4 ± 2.2	35.0 ± 1.4	9.4 ± 2.4
136	1660	0.3 ± 0.2	16.2 ± 4.4	12.2 ± 6.0
3400	700	10.8 ± 7.5	20.1 ± 9.6	2.2 ± 0.6
3400	1660	1.0 ± 1.0	17.8 ± 6.7	1.3 ± 0.6

Net nitrogen mineralization rates

Age (yr)	Elevation (m)	Nitrification ($\mu g·g^{-1}·mo^{-1}$)	Mineralization ($\mu g·g^{-1}·mo^{-1}$)
110	290	0.3 ± 0.7	51.3 ± 64.7
136	700	1.7 ± 7.0	23.0 ± 44.7
136	1130	−2.6 ± 2.8	13.1 ± 63.1
136	1660	0.0 ± 1.0	32.0 ± 20.3
3400	700	91.3 ± 37.5	204 ± 92.3
3400	1660	4.0 ± 3.0	31.5 ± 44.5

DISCUSSION

All six of our study sites contained similar plant species, had similar substrates and reliefs, received abundant precipitation, and were free of significant human disturbance. Hence, the four young sites represented a well-defined elevational transect, with few confounding variables. The two old-flow sites similarly represented the net effects of 3400 yr of ecosystem development at two elevations, where we paired them with nearby young sites. Hence, young–old comparisons provide insights into the long-term development of ecosystems on pahoehoe lava on windward Mauna Loa, Hawai'i.

Long-term ecosystem development

Based on our comparisons of 136- and 3400-yr-old sites at 700 m and 1660 m elevations, aboveground live biomass was much greater in the old sites than in the young sites at both elevations (Table 4), a typical feature of forest successions (e.g., Kira and Shidei 1967, Odum 1969, Bormann and Likens 1979, Aplet and Vitousek 1994). However, aboveground biomass of mature wet tropical forests is usually at least two times greater than the 123 Mg/ha found in our lower-elevation site (Brown and Lugo 1980, 1982, Tanner 1980, Scatena et al. 1993). Brown and Lugo (1982) observed that tropical forest biomass generally increased with increasing moisture, but tended to decline in very wet tropical forests. The relatively low biomass of our old-forest sites may be due in part to the high rainfall they receive, and to their relative lack of soil development.

An additional factor in these sites is occasional canopy-level dieback (Jacobi 1983, Jacobi et al. 1983, Mueller-Dombois 1985, 1986, 1987, Hodges et al. 1986). The old site at 700 m elevation had clearly gone through a significant dieback phase as evidenced by its very open canopy and abundant fallen, dead trees. In contrast, there was no evidence of previous or ongoing dieback at 1660 m elevation, where there was very little coarse woody debris.

Detritus accumulation was also substantially greater in the 3400-yr-old sites than in the paired 136-yr-old sites (Table 4). The average long-term rate of soil C sequestration (excluding litter) in our sites was 2.1 $g \cdot m^{-2} \cdot yr^{-1}$ ($n = 2$ sites), which is very similar to rates reported in comparable studies (mean $\pm$ 1 SE = 2.4 $\pm$ 0.7 $g \cdot m^{-2} \cdot yr^{-1}$, $n = 16$, Schlesinger 1990). Detritus accumulation represents a balance between organic matter production by live vegetation and its decomposition and consumption by soil heterotrophs. Vitousek et al. (1994) found that decomposition rates declined logarithmically with increasing elevation on windward Mauna Loa, whereas we found that detritus production (i.e., ANPP) declined linearly. The increasing disparity between the production and decomposition of detritus with increasing elevation (Fig. 7) likely
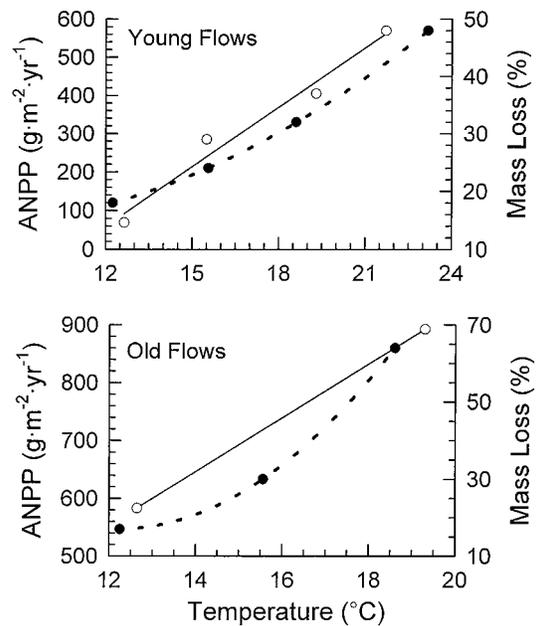

FIG. 7. Aboveground net primary productivity (○) and decomposition rates (●) in relation to temperature on windward Mauna Loa, Hawai'i. Mass loss refers to the percentage of *Metrosideros* leaf mass lost during the first year of decomposition in situ, based on Vitousek et al. (1994). ANPP data are from *Results: Aboveground net primary productivity.*

explains why soil OM pools were similar in our two old-flow sites (Table 4), despite differences in their rates of aboveground production (Table 6).

Rates of N accumulation in our sites provided minimum estimates of rates of N inputs from precipitation and fixation, as N is not present in the lava substrates. At 700 m elevation, rates of total N accumulation in detritus and aboveground live vegetation averaged 3.5 $kg \cdot ha^{-1} \cdot yr^{-1}$ over the first 136 yr of succession, and 1.4 $kg \cdot ha^{-1} \cdot yr^{-1}$ over the first 3400 yr. At 1660 m, N-ac-
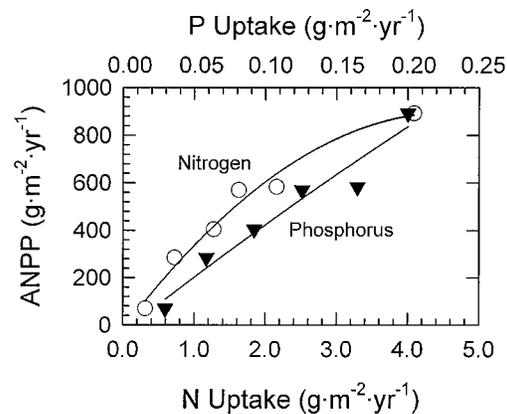

FIG. 8. Aboveground net primary productivity (ANPP) shown in relation to N and P uptake by vegetation in six study sites on windward Mauna Loa, Hawai'i. The curves show the best-fit second-order regressions between ANPP and uptake.

TABLE 8. Ratios of mass and productivity between young and old sites at elevations of 700 and 1660 m. Each value represents the young : old ratio for that quantity at that elevation (unitless).

	700 m	1660 m
Aboveground live biomass	0.11	0.07
Nonwoody litter mass	0.14	0.07
Soil organic matter mass	0.14	0.04
Aboveground NPP	0.45	0.12

cumulation rates averaged 1.2 kg·ha^{-1}·yr^{-1} over the first 136 yr and 1.3 kg·ha^{-1}·yr^{-1} over the first 3400 yr.

Both biomass and ANPP generally increase asymptotically through time during forest succession (e.g., Kira and Shidei 1967, Odum 1969, Bormann and Likens 1979). Ratios between young-site and old-site biomass or productivity values therefore provide relative measures of ecosystem maturity, as they express the degree to which the young sites have approached the characteristics of more mature stands (Reiners 1992). Ratios between young-site and old-site aboveground vegetation, litter, soil organic matter, and ANPP at both 700 m and 1660 m elevation (Table 8) support the conclusion that ecosystem development proceeds faster at lower elevations, as suggested by Aplet and Vitousek (1994). Our data (Table 8) also imply that rates of net primary production increase relatively more quickly than do biomass pools, as is consistent with general models of forest succession (e.g., Kira and Shidei 1967) and with similar data from Hubbard Brook (Reiners 1992).

None of our sites appeared to be in a phase of rapid biomass aggradation (e.g., Bormann and Likens 1979): net growth was <18% of total ANPP in all of our sites. Most of the ANPP in our sites contributed to the production of detritus, not the development of greater ecosystem structure.

Elevational effects on ecosystem processes

Biomass accumulation.—We did not observe any significant elevational trends in biomass accumulation in our young-flow sites. However, total aboveground biomass and aboveground tree biomass were both greatest at the site with lowest elevation, smallest in the site with highest elevation, and intermediate in the two other young sites (Table 4). Based on a broader survey, Aplet and Vitousek (1994) found that aboveground live biomass declined with increasing elevation on young ʻaʻa (rough, rocky) lava flows of windward Mauna Loa.

Our site at 1130 m elevation had, on average, the largest understory biomass, the largest density and biomass of *Metrosideros* saplings, the largest litter pool, and more soil organic matter than did any other young site (Table 4). There is no obvious way in which the site at 1130 m elevation differs from the other young sites, and we do not know why detrital accumulations

and tree densities at that site do not follow the elevational trends apparent in the other sites.

Aboveground productivity.—Despite species-level differences, total community-level ANPP in the young sites declined linearly with increasing elevation on the young flows (Fig. 5). Unfortunately, we could not measure either root biomass or belowground productivity. These measurements are difficult under the best of circumstances, but are impossible in our sites: roots penetrated cracks in the lava bedrock, from which they could not be extracted. Nevertheless, the magnitude of differences in ANPP among sites is so great that no plausible pattern of belowground allocation could alter any of the conclusions that we have drawn.

Nutrient accumulation and cycling.—Nitrogen and P concentrations in *Metrosideros* leaves decline with increasing elevation on both young and old pahoehoe flows on windward Mauna Loa (Vitousek et al. 1988, 1992). Foliar N and P concentrations on our sites were similar to those reported by Vitousek et al. for similar sites and elevations and, in the young sites above 300 m elevation, approached the minimum levels of N and P that are found in *Metrosideros* foliage (Vitousek et al. 1992).

In fact, foliar N concentrations in plants in all of our young sites (Fig. 3) were extraordinarily low in comparison with other data from tropical moist forests (Grubb 1977, Vitousek and Sanford 1986). Leaves of the dominant plant species *Metrosideros polymorpha, Dicranopteris linearis,* and *Machaerina angustifolia,* all contained <8 mg N/g dry mass in all of our young sites and in the upper-elevation old flow (no data for *Machaerina* at that site). These concentrations are most comparable to leaves in a low caatinga (low bana) forest growing on a nitrogen-poor spodosol in lowland Venezuela (Medina 1984, Cuevas and Medina 1988, Medina and Cuevas 1989). For comparison, mean N concentrations in the mixed foliage of steepland tropical forests average 13.3 mg/g (Scatena et al. 1993), with a minimum of 9.7 mg/g in a mor forest in Jamaica (Tanner 1985). Mean foliar P concentrations of leaves in the dominant species of our young sites (Fig. 3) were within the range of values reported from other tropical forests (Grubb 1977, Vitousek and Sanford 1986, Scatena et al. 1993).

Even our old sites had comparatively very low foliar nutrient concentrations. Concentrations of N and P were highest in the old site at 700 m elevation, where *Metrosideros* leaves averaged 9.2 mg/g and 0.81 mg/g, respectively (Fig. 4), and *Dicranopteris* leaves averaged 9.4 mg/g N and 0.46 mg/g P. Interestingly, foliar N and P levels of *Metrosideros* and *Dicranopteris* foliage did not differ between the young and old sites at 1660 m elevation. To the extent that foliar nutrient concentrations reflect nutrient availability, our data suggest that all of our sites were nutrient poor, and that nutrient supply decreased with increasing elevation on Mauna Loa.

The results of our laboratory soil incubation experiments suggest that there were no substantive differences in the soils' inherent capacity for N mineralization among sites, except for greater rates in the lower-elevation old site. These results must be considered with respect to the different climates and detrital pools present among sites. Soil temperatures significantly influence rates of N mineralization (e.g., Myers 1975, Vigil and Kissel 1995), so in situ rates of N mineralization per gram of soil should be slower at higher elevations. Differences in amounts of soil OM among sites (Table 4) will also lead to differences in total in situ N mineralization among sites.

Integration: elevational effects on ecosystem processes.—Elevation is a complex variable: rainfall, atmospheric humidities, wind speeds and directions, and a variety of other climatic variables vary with elevation on windward Mauna Loa (e.g., Juvik and Nullet 1994). However, none of these factors varies in any direct, monotonic way with elevation. Solar radiation increases with elevation (Juvik and Nullet 1994), and therefore does not explain the decline in ANPP that we observed. Rainfall is abundant year-round in all of the sites, so a lack of moisture availability is not likely to control ecosystem properties in these sites. An excess of moisture could affect ecosystem development, but all of our sites were excessively wet.

Temperature, in contrast, varies directly and monotonically with elevation; mean annual temperatures decline at an average of 6.6°C per 1000-m increase in elevation (Juvik and Nullet 1994). Atmospheric pressure also declines linearly with increasing elevation, resulting in a decline in the partial pressure of CO_2. However, this effect could not explain the dramatic declines in productivity that we observed (Terashima et al. 1995). In our young sites, ANPP (in grams per square meter per year) increased linearly with increasing mean annual air temperatures (T, in degrees Celsius): ANPP $= 54T - 610$; ($n = 4$, $r^2 = 0.99$, $P = 0.002$). Although we had only two old study sites, total ANPP on the old flow followed a similar trend: ANPP increased at an average of 49 g·m^{-2}·yr^{-1} for every 1°C increase in mean annual temperature.

The only directly comparable data are from Weaver and Murphy (1990), who summarized NPP data from wet forest sites at 450, 725, and 1000 m elevation in Puerto Rico. ANPP in these sites was 1050, 760, and 370 g·m^{-2}·yr^{-1}, respectively (Weaver and Murphy 1990), whereas mean annual temperatures average approximately 23.1°, 21.3°, and 18.6°C, respectively (Brown et al. 1983). These data also suggest that ANPP declines linearly with declining temperature ($r^2 = 0.999$, linear regression), albeit at a much faster rate in Puerto Rico than in our pahoehoe-lava sites in Hawai'i.

The simplest explanation for our findings is that temperature controls net primary productivity. However, temperature has multiple effects on ecosystem prop-

erties. It directly influences rates of leaf photosynthesis (e.g., Berry and Björkman 1980, Larcher 1995), thereby potentially driving a correlation between temperature and ANPP. However, the same species occurred in young and old sites, yet their aboveground productivities differed by 500 g·m^{-2}·yr^{-1}. Clearly, factors other than temperature alone are important.

Temperature influences rates of decomposition, soil nutrient mineralization, and nutrient uptake by plant roots (e.g., Swift et al. 1979, Myers 1975, Nye and Tinker 1977) and thereby influences nutrient availability to plants. In our young sites plant productivity increased linearly with increasing temperatures, and a similar trend was apparent in the old sites. In contrast, rates of decomposition, which largely control rates of net N and P mineralization in the soil, increased logarithmically with increasing temperatures (Fig. 7). As a result, soil supply of organic nutrients becomes progressively more limiting, relative to plant demands for available nutrients, as one proceeds toward higher, cooler sites. ANPP in the young sites also was correlated directly with rates of N and P uptake by the vegetation (Pearson's $r > 0.98$, $n = 4$ sites) (Fig. 6). The elevational gradient we investigated is both a temperature and a nutrient-availability gradient.

Time may buffer the effects of temperature because nutrient pools in living and dead biomass increase through time, and this accumulation should increase overall rates of nutrient cycling. We suggest that the different productivities observed in our different sites were likely a consequence of time- and temperature-mediated controls over nutrient availability—particularly the exponential relationship between temperature and decomposition juxtaposed against a linear ANPP : temperature relationship (Fig. 7). We evaluated nutrient limitation experimentally in one site in this matrix; a factorial fertilization study done on the young flow at 1130 m demonstrated that the plant growth at that site was significantly stimulated by additions of either N or P, and that greatest growth occurred in plots receiving both N and P (Raich et al. 1996).

Such interactions between temperature and the balance between production and decomposition (and, hence, between temperature and nutrient availability) have been suggested to be important in the evaluation of the effects of temperature changes on terrestrial ecosystems (e.g., Pastor 1986, McGuire et al. 1992, Schimel et al. 1990). The well-defined environmental matrix of Mauna Loa provides the opportunity to further evaluate and test such interactions with a clarity rarely achievable in field studies.

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