The Mauna Loa environmental matrix: foliar and soil nutrients

Peter M. Vitousek[1], Gregory Aplet[1,*], Douglas Turner[1], and John J. Lockwood[2]

[1] Department of Biological Sciences, Stanford University, Stanford, CA 94305, USA
[2] U.S. Geological Survey, Hawaii Volcano Observatory, Volcano, HI 96718, USA

Summary. The accumulation of total carbon, nitrogen, and phosphorus in soils, available soil nutrients, and foliar nutrients in the native dominant *Metrosideros polymorpha* were determined across a wide elevational range on 9 lava flows on Mauna Loa, Hawai'i. The flows included a young (<140 y) and an old (>2800 y) 'a'a (rough surface texture) and pāhoehoe (smooth) flow on the wet east and dry northwest side of the mountain. Soil element pools and nutrient availability increased with flow age independent of climate. The dry sites accumulated organic matter and nutrients more slowly than comparable wet sites, but relative nutrient availability to plants (as indicated by soil assays and foliar nutrients) was greater in the dry sites. Accumulation of soil organic matter and nutrients occurred most rapidly in lower-elevation sites on the young flows, but the largest accumulations occurred at higher elevations on old flows. The range of sites sampled represents a complete and largely independent matrix of major factors governing ecosystem structure and function.

Key words: Primary succession – Ecosystem structure – Hawaiian Islands – *Metrosideros polymorpha* – Soil carbon

Jenny (1941, 1980) identified the major "state factors" controlling soils and ecosystems as climate, relief (or topography), organisms, parent material, and time, and this framework has provided a widely used conceptual model for examining the ultimate controls on ecosystem structure and function. The active Hawaiian volcano Mauna Loa supports an extraordinarily broad array of systems for which the influence of these controls can be evaluated directly. Mauna Loa is a 4168 m tall shield volcano built up of frequent and rather fluid lava flows;

it has little local topography. Its climate is highly variable, from lowland tropical to alpine and from very wet (>6000 mm/y) to very dry (<250 mm/y) (Giambelluca et al. 1986), but that variation is predictable as a function of elevation and exposure to the prevailing northeast trade winds. Due to the extreme isolation of Hawai'i, its native flora lacks diversity (Carlquist 1980), and one woody species (*Metrosideros polymorpha* in the Myrtaceae) is a dominant component of communities across much of the very broad range of environments on Mauna Loa.

The surface lava flows of Mauna Loa have been well mapped and dated (Lockwood et al. 1988). Their chemistry is nearly invariant within flows and little different between them (Wright 1971, Wright and Helz 1987); standard elemental composition (as oxides) is approximately 52% Si, 14% Al, 1% Fe, 7% Mg, 11% Ca, 2.3% Na, 0.37% K, and 0.21% P, with most variation in the fraction contributed by olivine (magnesium silicate) (Wright 1971). Flows differ substantially in surface texture from 'a'a (rough clinker lava) to pāhoehoe (with a massive, smooth, ropy surface), but this variation is not associated with any systematic difference in chemistry. Each flow therefore represents a single-age, single-substrate transect from above treeline towards, and often to, the sea. Adjacent flows on the same aspect of the mountain differ in age, while flows on different aspects may be similar in age but differ substantially in the amount and/or timing of precipitation.

Consequently, ecosystems on Mauna Loa can be viewed as a matrix of sites in which topography, organisms, and the chemistry of parent material are relatively constant, while substrate age, temperature, precipitation, and parent material texture vary substantially – but predictably and largely independently. The influence of the factors that vary can then be analyzed in a way that is impossible in – but useful to the understanding of – more complex continental ecosystems.

Portions of the Mauna Loa environmental matrix have been examined in studies of soil sequences (Sherman and Ikawa 1968; Yost et al. 1982), plant coloniza-

* *Present address:* Department of Forestry Sciences, Colorado State University, Fort Collins, CO 80523, USA

Offprint requests to: P.M. Vitousek

tion in early succession (Skottsberg 1941; Eggler 1948), community dynamics (Jacobi et al. 1983; Mueller-Dombois 1987), nutrient cycling (Vitousek et al. 1983; Vitousek et al. 1989), and ecophysiology (Stemmermann 1983; Vitousek et al. 1990); most of these studies have emphasized the importance of substrate age. An earlier study by Vitousek et al. (1988) evaluated interactive effects of age and temperature on ecosystem characteristics by examining variation in soil carbon and nutrient pools and foliar nutrients with elevation on a young (1855) and an old (ca 3400 y) pāhoehoe flow on Mauna Loa's wet east flank. They concluded that soil carbon and nutrients accumulate most rapidly at low elevation, but that element pool sizes ultimately reach their maximum values at high elevation on the old flow where cool temperatures reduce decomposition to a greater extent than production. Trees on both flows had lower foliar nitrogen and phosphorus concentrations at high elevation, but the old flow supported trees with substantially higher foliar nitrogen concentrations than the young flow at intermediate and low elevations. The difference in foliar nitrogen with soil age reflects an increase in nitrogen availability during primary succession.

In this study, we extend the analysis of foliar and soil nutrients to a complete matrix of Mauna Loa lava flows differing in precipitation (the wet east versus the dry northwest flank of Mauna Loa) and parent material texture ('a'a versus pāhoehoe lava) as well as age and elevation. In addition to using a much larger set of flows to test the generality of earlier conclusions concerning soil age/temperature interactions, we use this matrix of sites to evaluate predictions that: 1) soil organic matter and nutrients accumulate more slowly on dry than on wet sites; 2) foliar nutrient levels, particularly those of nitrogen, are higher on wet than dry sites because water limitation impedes decomposition, delays nutrient cycling, and thereby reduces nutrient availability in dry

sites (Pastor and Post 1988); 3) soil organic matter and nutrients accumulate more rapidly and to higher levels, and foliar nutrient concentrations are higher, on 'a'a than pāhoehoe flows because of the former's greater surface area for rock weathering and more protected sites for plant colonization.

Sites

Study sites were selected across the elevational range from near treeline (2450 m on Mauna Loa) to the lower limit of native vegetation on 9 Mauna Loa lava flows. The flows were selected to represent a young (<140 y) and an old (>2800 y) pāhoehoe and 'a'a flow on both the wet east and the dry northwest flank of Mauna Loa. An additional young pāhoehoe flow was sampled on the east flank. The flows and the elevational range across which samples were collected are summarized in Table 1, and the locations of the sites are summarized in Fig. 1. Where a particular flow had been wholly covered by younger flows at a given elevation, we collected samples from a different but comparably-aged flow as described in Table 1. While most of the flows are clearly identified and dated (Lockwood et al. 1988) (Fig. 1), the old, dry pāhoehoe flow is relatively poorly known; it may represent a collection of two or more such flows.

Climates of the sites were estimated by interpolation from weather stations. Temperature on the island of Hawai'i varies with elevation at an environmental lapse rate of 5.8° C/1000 m (Atlas of Hawaii 1983); mean annual temperature averages 24° C at sea level and 10° C at treeline on Mauna Loa. On the wet east flank of Mauna Loa, precipitation increases from 3200 mm/y at sea level to over 6000 mm/y at 650 m (Fig. 1) (Giambelluca et al. 1986); it then drops gradually to approximately 2000 mm/y at 2000 m. At higher elevation, sites

Table 1. Sites sampled on 9 flows on the Mauna Loa environmental matrix. Values are the elevation (in m) of the site actually sampled within each elevation class (column on extreme left) on each flow; only the elevation class is reported on subsequent tables. Where no sample was collected in a given elevation class, a "–" is reported; where a comparable flow was substituted, the substitution is footnoted

Elevation (m)	Wet					Dry			
	Young			Old		Young		Old	
	pāhoehoe		'a'a	pāhoehoe[1]	'a'a[2]	pāhoehoe	'a'a	pāhoehoe[3]	'a'a[4]
	1881	1855	1852	Punahoa		1859	1859		Kaniku
<100	80	–	–	–	–	–	–	–	–
300	305	–	–	–	–	305	305	305	305
750	610	760	–	760	610[5]	700	700	700	700
1200	1170	1220	1160	1220	1200	1160	1160	1150	1180
1600	1740	1710	1760	1590	1760	1600	1600	1600	1600
2000	2040	2040	2070	2010[6]	2070	1950	2010	2010	2010[7]
2400	2410	2480	–	2350[6]	2410	–	–	–	–

[1] The old wet-side pāhoehoe flow has been ^{14}C-dated at ~3400 y
[2] The old wet-side 'a'a flow's age has been estimated at ~3000 y by context
[3] The old dry-side pāhoehoe flow is not as well defined as the others; the sites below 1600 m are from a single ~4000 y old flow, but the others may represent other old pāhoehoe flows
[4] The old dry-side 'a'a flow has been dated at ~2800 y

[5] A different flow of approximately the same age was sampled in place of the 3000 y old aa flow at 610 m
[6] A slightly younger pāhoehoe flow was sampled in place of the 3400 y old flow above 2000 m
[7] A slightly older (undated) flow was substituted for the 2800 y old flow at the highest elevation
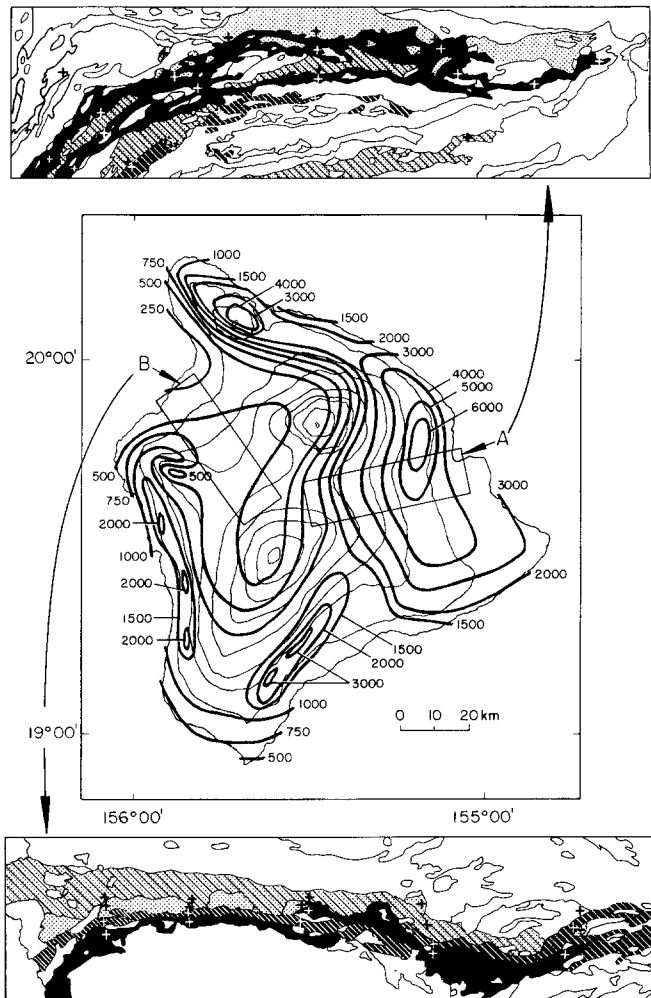
Fig. 1. The central section is a mean annual rainfall/topographic map of the Island of Hawai'i, redrawn from Giambelluca et al. (1986). Precipitation (darker lines) is in mm, and elevation contours are at 500 m intervals. Above the island map is a lava flow age-class map of rectangle *A*, and below is a similar age-class map of rectangle *B* (both from Lockwood et al. 1988). The darker shading represents the young flows sampled, and the lighter shading the older flows. 'A' a flows are indicated with diagonal lines. Sites where soil was sampled are marked with a cross (+); sites where foliage alone was sampled are not marked

often encounter the very dry air above the trade-wind inversion, and precipitation decreases and evaporation increases dramatically (Juvik et al. 1978). The dry northwest flank of Mauna Loa is in the rain shadow of neighboring Mauna Kea, and precipitation varies from <250 mm/y at sea level to approximately 600 mm/y at 1000 m, then declines gradually with further increases in elevation (Fig. 1) (Giambelluca et al. 1986).

Sites were selected for soil sampling at intervals of approximately 450 m elevation on each flow (Fig 1). Foliar samples often were collected at more frequent intervals.

Methods

Sampling and analytical methods were identical to those of Vitousek et al. (1988). Briefly, five soil samples were collected in a

stratified random design (one in each 10 m increment) along each of 5 50 m transects in each site. Samples were 6 cm diameter cores to the lava surface, which ranged up to 25 cm deep on older flows. An unknown amount of soil had worked its way into cracks in pāhoehoe flows and into the interstices of 'a'a flows and could not be collected with these methods. Soils were sorted to remove rocks and large roots, and composited by transect. Where little soil was present in a site, samples from all of the transects were pooled in a single composite.

In the laboratory, a 20 g subsample of each composite was extracted in 2 N NaCl within 24 h of collection; the extract was analyzed for ammonium, nitrate, calcium, magnesium, and potassium. Another 3 g subsample was extracted in acid fluoride for available phosphorus determinations (Olsen and Sommers 1982). Finally, a large subsample was oven-dried at 105° C for moisture content, then used for determinations of total carbon, nitrogen, and phosphorus. All dry-side soils were sampled in September 1988; various wetside samples were collected in March 1987, December 1987, September 1988, and September 1990.

For foliar sampling, 8–10 mature leaves of *Metrosideros polymorpha* were collected from sunlit positions on 5 trees in each site. In sites where soil sampling was carried out, leaves from each tree were analyzed separately; at other sites, they were composited into a single sample per site. Pubescent and glabrous varieties of *Metrosideros polymorpha* occur together in several sites (Dawson and Stemmermann 1990); these were collected, composited (in appropriate sites), and analyzed separately where they co-occurred. Leaf area was measured on fresh leaves using a Delta-T leaf area meter on the day of collection; leaves were then oven-dried for at least 3 days at 70° C for determination of leaf mass per area (LMA).

Both plant and soil samples were acid-digested using a peroxide/persulfate procedure for total nitrogen and phosphorus (Technicon Instrument Systems 1976). Samples for foliar cation analyses were dry-ashed at 500° C for 4 h, then dissolved in nitric acid and analyzed using atomic absorption spectrophotometry.

Ammonium and nitrate were determined colorimetrically with an autoanalyzer, and exchangeable cations were analyzed by atomic absorption. Soil carbon was calculated using a linear regression of the carbon content measured on 15 samples with a LECO induction furnace against loss on ignition (4 h at 500° C); the regression yielded a slope of 0.54 and an r^2 of 0.99 (Vitousek et al. 1983).

Results

Soils

Results for soil mass are summarized in Table 2, and results for total soil carbon, nitrogen, and phosphorus are summarized in Table 3. Soils on the wet east flank of Mauna Loa were highly organic, averaging 35–48% C by mass at lower elevations, while soil on the dry northwest flank contained more mineral material.

Soil carbon pools are summarized graphically in Fig. 2. Overall, carbon pools were much greater on the wet than the dry sites for most elevation/age combinations. The 1881 and 1855 flows on the wet side were very similar, with the slightly younger 1881 flow supporting slightly less soil carbon (Fig. 2). Soil carbon accumulated most rapidly at low elevation on young flows on the wet side. On the dry side, the largest carbon pools on young flows were at intermediate elevation. Soil carbon pools were greater on both young and old 'a'a than on comparable pāhoehoe flows on the wet east side (despite the likelihood that more soil was missed during sampling on 'a'a flows), but the opposite was true on the dry northwest (Table 3, Fig. 2).

Table 2. Soil mass above the lava flow surface for 9 lava flows on the Mauna Loa environmental matrix. When no soil was encountered during sampling, a "0" is reported. Values reported are means of 5 transects per site (±standard errors); where no errors are reported the value is derived from a composite sample

Elevation (m)	Wet					Dry			
	Young			Old		Young		Old	
	pāhoehoe		'a'a	pāhoehoe	'a'a	pāhoehoe	'a'a	pāhoehoe	'a'a
	1881	1855	1852	Punahoa		1859	1859		Kaniku
Mass of Soil (g/m²)									
<100	1920 (590)	–	–	–	–	–	–	–	–
300	2540 (250)	–	–	–	–	83	0	4190 (2400)	110
750	2075 (470)	2630 (370)	–	3900 (370)	13,320 (3010)	280 (200)	1880 (1290)	7900 (2000)	260 (230)
1200	1440 (460)	2320 (750)	4390 (300)	8200 (790)	22,210 (3900)	190	4620 (2600)	4030 (1440)	2060 (640)
1600	240 (80)	620 (300)	450 (180)	7170 (1030)	16,099 (1540)	20	0	7760 (6400)	600 (200)
2000	3	43	405	3490 (1610)	2,060 (510)	0	660	7490 (2550)	3760 (1960)
2400	0	0	–	5600 (1370)	300	–	–	–	–

Table 3. Soil carbon, nitrogen, and phosphorus contents for 9 lava flows on the Mauna Loa environmental matrix. Values are means of 5 transects per site, with standard errors in parentheses. Symbols as in Table 2

Elevation (m)	Wet					Dry			
	Young			Old		Young		Old	
	pāhoehoe		'a'a	pāhoehoe	'a'a	pāhoehoe	'a'a	pāhoehoe	'a'a
	1881	1855	1852	Punahoa		1859	1859		Kaniku
Soil Carbon (g/m²)									
<100	880 (300)	–	–	–	–	–	–	–	–
300	1120 (50)	–	–	–	–	8	0	1210 (780)	5
750	950 (230)	1220 (180)	–	1830 (210)	3621 (857)	39 (28)	19 (17)	2230 (490)	110 (100)
1200	690 (230)	900 (320)	2100 (120)	2890 (330)	6475 (1017)	46	13 (9)	840 (340)	760 (240)
1600	47 (11)	49 (27)	130 (5)	2850 (430)	5240 (570)	0.2	0	1770 (1250)	180 (80)
2000	0.5	1.4	166	830 (333)	551 (145)	0	1.4	2290 (720)	920 (750)
2400	0	0	–	590 (170)	120	–	–	–	–
Soil Nitrogen (g/m²)									
<100	29 (10)	–	–	–	–	–	–	–	–
300	28 (1)	–	–	–	–	0.4	0	56 (35)	0.2
750	27 (7)	34 (5)	–	53 (4)	169 (41)	3 (2)	2 (1)	160 (44)	5 (4)
1200	19 (6)	21 (8)	50 (5)	113 (12)	279 (46)	3.0	3 (2)	60 (28)	37 (14)
1600	1 (0.2)	3 (2)	3 (0.1)	99 (16)	340 (5)	0.01	0	77 (46)	8 (3)
2000	0.03	0.09	2.4	34 (14)	19 (5)	0	0.04	160 (52)	26 (21)
2400	0	0	–	23 (7)	4	–	–	–	–
Soil Phosphorus (g/m²)									
<100	1.7 (0.7)	–	–	–	–	–	–	–	–
300	1.9 (0.1)	–	–	–	–	0.2	0	12 (7)	0.1
750	1.0 (0.2)	1.0 (0.2)	–	3.1 (0.4)	13.4 (3.3)	0.7 (0.6)	1.2 (0.9)	28 (8)	0.4 (0.4)
1200	0.7 (0.2)	0.7 (0.3)	2.9 (0.2)	9.2 (1.3)	33.0 (6)	0.5	1.7 (1)	13 (5)	4.1 (1.5)
1600	0.05 (0.01)	0.1 (0.03)	0.09 (0.03)	6.0 (1.1)	18.0 (2)	0.01	0	11 (9)	1.2 (0.4)
2000	0.01	0.01	0.08	2.5 (1.1)	1.8 (0.5)	0	0.1	10 (3)	2.3 (1.3)
2400	0	0	–	3.8 (1.1)	0.3	–	–	–	–

Pools of nitrogen and phosphorus followed a pattern similar to that of carbon (Table 3). Carbon:nitrogen ratios were much narrower on the dry than the wet sites; N:P ratios were also narrower, although that could reflect the greater proportion of mineral material in the dry-side soils. On the wet side, there was a tendency for carbon:nitrogen ratios to narrow with increasing soil age, especially on 'a'a flows.

Soil cation concentrations are summarized in Table 4. The variable amounts of soil (Table 2) and differences in the admixture of organic and mineral material make it difficult to interpret these results directly. However, it is clear that soil calcium and magnesium concentrations on old flows were higher on the dry than the wet side. Potassium concentrations decreased with increasing elevation on most flows, but calcium and magnesium had no consistent pattern of variation with elevation.

The concentrations of available nitrogen and phosphorus are summarized in Table 5. As for cations, variation in the amount of soil (Table 2) and its mineral fraction complicates the interpretation of these results; moreover, these concentrations were measured at only
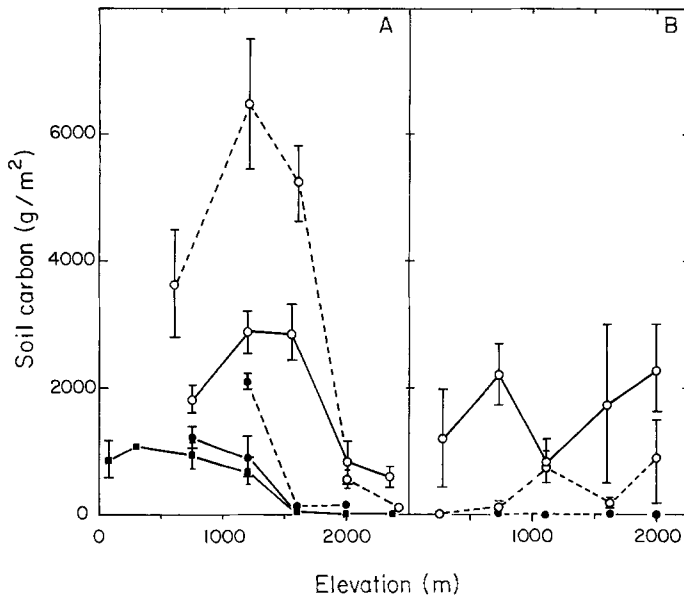
Fig. 2A, B. Soil carbon content as a function of elevation on Mauna Loa lava flows. The solid symbols denote young (<140 y) and the hollow symbols old (>2800 y) lava flows; the solid lines represent pāhoehoe and the dashed lines 'a'a lava flows. A. Flows on the wet east flank; the solid squares represent the 1881 lava flows (see Table 1). B. Flows on the dry northwest flank

one time, and they can vary rapidly. However, the lack of nitrate in most of the wet-side sites and its presence in most dry-side sites is striking. Vitousek et al. (1988) found no nitrification in laboratory incubations of the wet-side sites they sampled, while substantial rates of nitrification were observed in soil collected on the two old flows at 700 m on the dry side (unpublished data). Extractable phosphorus generally declined with increasing elevation on most of the flows, and very high concentrations (but very little soil) were observed at low elevation on the old, dry-side 'a'a flow.

Foliar nutrients

Foliar nutrient concentrations in *Metrosideros polymorpha* near 1200 m elevation on all flows are summarized in Table 6; results for sites near 1650 m are summarized in Table 7. These results in particular are reported in tables because most of the flows existed and supported *Metrosideros* at those elevations, and because samples from several individual trees were analyzed separately in most of those sites. Foliar characteristics (pubescent versus glabrous forms of *Metrosideros*) are identified in Tables 6 and 7; where both occurred in a site, they are

Table 4. Extractable calcium, magnesium, and potassium concentrations for 9 lava flows on the Mauna Loa environmental matrix. Values are means of 5 transects per site, with standard errors in parentheses. Symbols as in Table 2, with the addition that where insufficient soil was collected for cation extractions, a "+" is reported

Elevation (m)	Wet							Dry			
	Young		'a'a	Old				Young	'a'a	Old	'a'a
	pāhoehoe			pāhoehoe	'a'a			pāhoehoe		pāhoehoe	
	1881	1855	1852	Punahoa				1859	1859		Kaniku
Calcium (μg/g)											
<100	3720 (560)	–	–	–	–			–	–	–	–
300	4640 (620)	–	–	–	–			1320	0	7470 (1400)	590
750	1480 (340)	1690 (300)	–	4400 (370)	1290	(200)		+	144	9530 (650)	4860
1200	2170 (520)	1620 (180)	3770 (380)	2000 (440)	2200	(240)		6420	29 (3)	6660 (540)	11,100 (1150)
1600	1760	1150	280	4200 (670)	8250	(730)		+	0	6990 (740)	9090
2000	+	+	390	6790 (880)	5010	(1510)		0	200	11,100 (1020)	7280 (3230)
2400	0	0	–	720 (250)	8960			–	–	–	–
Magnesium (μg/g)											
<100	740 (110)	–	–	–	–			–	–	–	–
300	760 (50)	–	–	–	–			380	0	1270 (140)	108
750	710 (80)	640 (30)	–	650 (20)	210	(50)		+	11	1620 (130)	3410
1200	590 (70)	530 (30)	700 (60)	390 (20)	120	(15)		890	2 (0.3)	1240 (110)	2150 (160)
1600	140	130	300	320 (40)	680	(40)		+	–	1260 (190)	1250
2000	+	+	150	310 (110)	300	(130)		0	16	1210 (110)	1120 (510)
2400	0	0	–	50 (21)	890			–	–	–	–
Potassium (μg/g)											
<100	430 (40)	–	–	–	–			–	–	–	–
300	580 (40)	–	–	–	–			420	0	380 (30)	221
750	500 (30)	860 (30)	–	910 (50)	140	(30)		+	62	330 (10)	480
1200	380 (32)	850 (120)	430 (20)	430 (60)	180	(20)		260	42 (1)	340 (20)	330 (20)
1600	160	290	120	650 (50)	290	(20)		+	0	250 (20)	250
2000	+	+	100	340 (70)	210	(40)		0	38	250 (30)	200 (70)
2400	0	0	–	120 (10)	220			–	–	–	–

Table 5. Extractable ammonium (NH_4-N), nitrate (NO_3-N), and phosphate (PO_4-P) for 9 lava flows on the Mauna Loa environmental matrix. Values are means of 5 transects per site, with standard errors in parentheses. Symbols as in Table 2, with the addition that where insufficient soil was collected for available nutrient extractions, a "+" is reported

Elevation (m)	Wet					Dry			
	Young			Old		Young		Old	
	pāhoehoe		'a'a	pāhoehoe	'a'a	pāhoehoe	'a'a	pāhoehoe	'a'a
	1881	1855	1852	Punahoa		1859	1859		Kaniku
NH_4-N (μg/g)									
<100	5.8 (0.9)	–	–	–	–	–	–	–	–
300	7.3 (1.1)	–	–	–	–	10	0	33 (6)	11
750	6.7 (1.6)	29 (9)	–	47 (2)	24 (7)	35	2.7 (1.7)	30 (4)	157
1200	20.0 (2.6)	29 (7)	18 (2)	18 (3)	10 (2)	7	0.7 (0.1)	11 (1)	23 (5)
1600	4.0	1	11	33 (5)	12 (0.14)	+	0	12 (2)	14
2000	+	+	+	12 (2)	26 (8)	0	1.8	20 (3)	9 (5)
2400	0	0	+	1.5 (0.1)	15.1	–	–	–	–
NO_3-N (μg/g)									
<100	0	–	–	–	–	–	–	–	–
300	0	–	–	–	–	3.9	0	1.4 (0.3)	0.2
750	0	0	–	0	1.5 (0.5)	1.6	0.1	0.6 (0.2)	15
1200	0	0	0	0	1.3 (0.3)	0.1	0.1	0.7 (0.1)	4.8 (1.3)
1600	0	0	0	0	3.1 (0.4)	+	0	1.4 (0.4)	3.4
2000	+	+	0	0.6 (0.1)	1.0 (0.3)	0	0	2.7 (0.4)	1.3 (0.2)
2400	0	0	–	0	1	–	–	–	–
PO_4-P (μg/g)									
<100	22 (7)	–	–	–	–	–	–	–	–
300	16 (9)	–	–	–	–	3.6	0	30 (19)	650
750	21 (2)	23 (5)	–	45 (3)	26 (2)	1.2	28	17 (6)	500
1200	28 (4)	18 (5)	41 (3)	15 (4)	55 (3)	9.4	38	25 (6)	40 (13)
1600	15	6	8.5	8 (4)	1.4 (0.4)	+	0	12 (4)	17.6
2000	+	+	79	23 (3)	34 (6)	0	27	3.3 (2.1)	13.9 (6.8)
2400	0	0	–	0.6 (0.2)	3.2	–	–	–	–

Table 6. Foliar characteristics of *Metrosideros polymorpha* leaves at 1200 m elevation on 9 flows on the Mauna Loa environmental matrix. LMA is leaf mass/area (g/m²); all foliar nutrient concentrations are in %. Values are means of 5 trees/site, with standard errors in parentheses. Where no errors are reported, values are based on a composite sample. "Pub" represents pubescent varieties of *Metrosideros,* and "glab" represents glabrous varieties; these are reported independently where both occur on the same site. A "+" indicates that *Metrosideros* did not occur on that flow at that elevation

		Wet					Dry			
		Young			Old		Young		Old	
		pāhoehoe		'a'a	pāhoehoe	'a'a	pāhoehoe	'a'a	pāhoehoe	'a'a
		1881	1855	1852	Punahoa		1859	1859		Kaniku
LMA	Pub	307	286 (12)	284 (11)			253 (10)	246 (13)	+	213
	Glab	293	243 (8)	254 (4)	219 (8)	198 (10)				
N	Pub	0.58	0.60 (0.04)	0.59 (0.02)			0.70 (0.03)	0.71 (0.03)	+	0.80
	Glab	0.61	0.60 (0.01)	0.66 (0.03)	0.86 (0.04)	0.85 (0.04)				
P	Plub	0.041	0.039 (0.003)	0.039 (0.003)			0.073 (0.018)	0.062 (0.009)	+	0.048
	Glab	0.045	0.049 (0.004)	0.055 (0.004)	0.057 (0.003)	0.050 (0.005)				
Ca	Pub	0.94	0.79 (0.11)	1.52 (0.09)			2.06 (0.56)	2.31 (0.28)	+	0.85
	Glab	1.77	0.90 (0.19)	1.36 (0.11)	0.85 (0.09)	1.22 (0.2)				
Mg	Pub	0.11	0.09 (0.01)	0.20 (0.04)			0.10 (0.02)	0.18 (0.04)	+	0.29
	Glab	0.14	0.10 (0.02)	0.18 (0.02)	0.12 (0.01)	0.21 (0.04)				
K	Pub	0.34	0.31 (0.02)	0.36 (0.03)			0.40 (0.04)	0.40 (0.04)	+	0.36
	Glab	0.38	0.51 (0.03)	0.55 (0.03)	0.20 (0.03)	0.40 (0.07)				

Table 7. Foliar characteristics of *Metrosideros polymorpha* leaves at 1600 m elevation on the Mauna Loa environmental matrix. Values are means of 5 trees, with standard errors in parentheses. Abbreviations as in Table 6

		Wet					Dry			
		Young			Old		Young		Old	
		pāhoehoe		'a'a	pāhoehoe	'a'a	pāhoehoe	'a'a	pāhoehoe	'a'a
		1881	1855	1852	Punahoa		1859	1859		Kaniku
LMA	Pub	368	320 (14)	306 (12)	298 (15)	292 (20)	289 (15)	289 (24)	250 (18)	240 (8)
	Glab	277	283		282					
N	Pub	0.60	0.64 (0.04)	0.70 (0.03)	0.65 (0.03)	0.89 (0.06)	0.76 (0.04)	0.65 (0.07)	1.00 (0.06)	0.95 (0.04)
	Glab	0.53	0.54		0.81					
P	Pub	0.038	0.045 (0.005)	0.043 (0.003)	0.036 (0.002)	0.043 (0.005)	0.076 (0.02)	0.037 (0.008)	0.056 (0.003)	0.055 (0.005)
	Glab	0.050	0.044		0.043					
Ca	Pub	1.48	0.85 (0.09)	1.09 (0.08)	0.82 (0.18)	1.03 (0.20)	2.72 (0.31)	3.0 (0.11)	1.82 (0.18)	1.36 (0.23)
	Glab	1.32	1.27		1.34					
Mg	Pub	0.14	0.09 (0.01)	0.18 (0.02)	0.08 (0.01)	0.14 (0.02)	0.14 (0.03)	0.21 (0.04)	0.36 (0.06)	0.24 (0.04)
	Glab	0.12	0.14		0.20					
K	Pub	0.28	0.27 (0.03)	0.40 (0.04)	0.17 (0.04)	0.30 (0.02)	0.46 (0.04)	0.36 (0.03)	0.31 (0.02)	0.32 (0.04)
	Glab	0.42	0.43		0.31					

reported separately. Glabrous leaves invariably had lower leaf mass per area (LMA) and higher potassium concentrations where the forms co-occurred; there was also a trend towards higher concentrations of phosphorus, calcium, and magnesium in glabrous foliage. Those differences were also observed in at least 5 of the 6 sites at other elevations where both pubescent and glabrous forms of *Metrosideros* were collected.

Results for foliar nitrogen and phosphorus concentrations (dry mass basis) from all 56 of the sites that supported *Metrosideros* are summarized in Fig. 3. Foliar nitrogen and phosphorus contents (leaf area basis) and LMA are reported in Fig. 4, and calcium, magnesium, and potassium concentrations (mass basis) are summarized in Fig. 5. Where both glabrous and pubescent forms of *Metrosideros* co-occurred in a site (most often on young, wet-side flows at low elevation), the average of the two is plotted.

Overall, foliar nitrogen concentrations were higher on the dry northwest flank of Mauna Loa than the wet east flank (Fig. 3). Leaves from old flows generally had higher concentrations than those from young flows regardless of climate, elevation, or flow texture. Foliar nitrogen concentrations decreased significantly with increasing elevation on the wet-side pāhoehoe flows and dry-side 'a'a (Vitousek et al. 1990); this pattern was either weak or absent on the other flows. The pattern for phosphorus was very similar to that for nitrogen in the wet sites, but the young dry-side flows had relatively high foliar phosphorus concentrations at lower elevations. The variability in foliar phosphorus was much greater within sites (Tables 6, 7), within flows, and among flows on the dry side compared with the wet side.

Leaf mass per area increased with increasing elevation on both wet- and dry-side flows, but much more steeply on the wet side (Fig. 4). At most elevations, old flows supported leaves with lower LMA than young flows on both wet and dry sides. On the wet side, the net result of decreasing N and P concentrations and increasing LMA

with increasing elevation was a gradual increase in N and P contents (per unit leaf area) up to approximately 1600 m (Fig. 4), and a more rapid increase in contents above that elevation. The higher N and P concentrations (mass basis) and lower LMA on old flows tended to offset each other such that variation among flows in N and P per area was less than that in N and P per mass. No such patterns were evident on the dry side, except that N contents tend to be higher and P contents lower on old compared to young flows.

Foliar calcium concentrations were generally higher in dry-side than wet-side foliage, and higher in foliage from young than from old flows (Fig. 5). There was no consistent pattern with elevation anywhere. Magnesium concentrations were also higher on the dry side; they tended to be higher on 'a'a than pāhoehoe flows, and on old rather than young flows on the dry side. Finally, potassium concentrations were more similar to nitrogen and phosphorus than to the other cations, in that they decreased with increasing elevation on the wet-side flows. There were no clear trends with flow age or surface texture. Foliar potassium was higher on the dry than the wet side at intermediate and high elevation, and generally higher on the young than the old dry-side flows (Fig. 5).

Discussion

Variation in foliar and soil nutrients generally is associated across the Mauna Loa environmental matrix, although not in every case. For example, the dry-side sites had both higher foliar nitrogen concentrations and lower soil carbon:nitrogen ratios than wet-side sites, and nitrate was present in the soil of most dry sites and absent from most wet ones. Among the wet-side sites, foliar nitrogen increased and soil C:N ratios decreased with increasing age. However, there was no consistent change in soil C:N ratios with elevation, despite a substantial decrease in foliar N (Fig. 3).

For phosphorus, foliar concentrations and extractable P both generally decreased with increasing elevation. Foliar and soil extractable calcium and magnesium concentrations were relatively high on the dry side (Table 4, Fig. 5). These descriptive results are sufficient to conclude that plant and soil nutrients are broadly but imperfectly correlated among sites on Mauna Loa.

Effects of substrate age

We expected two major changes in ecosystem characteristics with increasing substrate age: 1) Nitrogen availability should increase with increasing age across the range of sites examined; and 2) the potential losses of carbon, nitrogen, and phosphorus should decrease in that order, resulting in a relative enrichment of phosphorus in soils of the older ecosystems. The increase in nitrogen availability was expected because fresh lava contains no nitrogen but large quantities of other nutrients, and early primary succession should therefore involve nitrogen accumulation and an increase in its relative availability (Walker and Syers 1976; Reiners 1981; Vitousek et al. 1989b). This accumulation phase could be protracted where symbiotic nitrogen fixers are absent, as is the case over most of the Mauna Loa matrix.

We were unable to determine nitrogen turnover (a better measure of nitrogen availability than soil nitrogen concentration) on the wet-side sites – attempts to measure net nitrogen mineralization using incubations yielded net immobilization of nitrogen in all pāhoehoe sites (Vitousek et al. 1988 and unpublished data). However, foliar nitrogen concentrations in Metrosideros polymorpha increase from young to old flows in all situations (Fig. 3), suggesting that nitrogen availability does increase with soil age across the matrix. Vitousek et al. (1987) used fertilization to show that nitrogen was limiting to the growth of Metrosideros polymorpha on a 28 y and a 200 y old volcanic ash site in Hawai'i, but not a several thousand y old ash site; no comparable information is available for lava flow-derived sites.

We expected element loss to vary in the order $C > N > P$; as a putative limiting nutrient, nitrogen should be retained actively by plants and microbes in young sites (Vitousek et al. 1989), while phosphorus is retained by reactions with aluminum, iron, manganese, and calcium in addition to biological processes (Walker and Syers 1976, Cole and Heil 1981). In fact, $C:N$, $C:P$, and $N:P$ ratios all narrowed with increasing age on the wet side. If inputs of these elements were more or less constant, then mobility does vary in the order anticipated. The very high soil $N:P$ ratio observed in young sites was unexpected; it hints that phosphorus could be more limiting to primary production than is nitrogen on young lava flows – in contrast to the situation on volcanic ash (Vitousek et al. 1987). Parton et al. (1989) reached the same conclusion in a modelling analysis of the limited set of results from Vitousek et al. (1988).

The pattern on dry-side flows is not so clear. $C:N$, $C:P$, and $N:P$ ratios are all much lower on dry than on wet sites, and if anything tend to increase with soil age (towards but not to values on the old wet sites). This difference may reflect in part the greater fraction of mineral material in dry-side soils, which in turn could reflect a greater input of wind-borne soil from the exposed mineral soils prevalent there.

Effects of elevation

Elevation was used as a surrogate for mean annual temperature on the Mauna Loa environmental matrix; temperature is closely and inversely correlated with elevation on both wet and dry slopes of the Hawaiian Islands, and the rate of change is close to the environmental lapse rate (Atlas of Hawaii 1983). We expected that lower temperatures at high elevation would decrease both primary production and decomposition, but that decomposition would be more strongly affected than production (Jordan 1971). Accordingly, accumulations of organic carbon and nitrogen eventually should be greatest at high elevation (Post et al. 1982, 1985). However, this represents the pattern expected at steady state. Developmental stages could differ systematically, and indeed Vitousek et al. (1988) demonstrated that while an old lava flow had its largest carbon and nutrient pools at intermediate and high elevations, carbon and nutrient pools on a young flow were largest at low elevation.

Results from the larger number of flows studied here demonstrate that carbon and nutrient pools accumulate most rapidly at the elevation with the most "favorable" environmental conditions. On the wet side, moisture is at least adequate through most of the elevational gradient, and the warm temperature at low elevation accelerates ecosystem development (Table 3, Fig. 2). On the dry side, carbon and nutrient accumulation is most rapid at intermediate elevation where precipitation is maximum and temperature moderate. On both sides, the old flows support their maximum carbon and nutrient pools at higher elevations than the comparable young flows (this pattern was not determinable for wet-side 'a'a, where the young flow doesn't extend to a sufficiently low elevation).

Foliar concentrations of nitrogen and phosphorus (mass basis) generally declined with increasing elevation on most flows, as did potassium concentrations on the wet-side flows. These results suggest nutrients are less available in the high elevation, low-temperature sites. Moreover, the low foliar nutrient concentrations observed there could further slow mineralization of nutrients, establishing a positive feedback to nutrient limitation in high-elevation sites (Vitousek 1982; Pastor and Post 1986; Vitousek and Matson 1988). This result differs from that suggested by Körner (1989), who reported increased nutrient availability at high elevation based on greater foliar nutrient concentrations there. The difference may reflect in part Körner's emphasis on herbaceous species, which generally decompose and recycle nutrients more rapidly than trees (Grubb 1989). However, the trees that Körner did sample followed the same
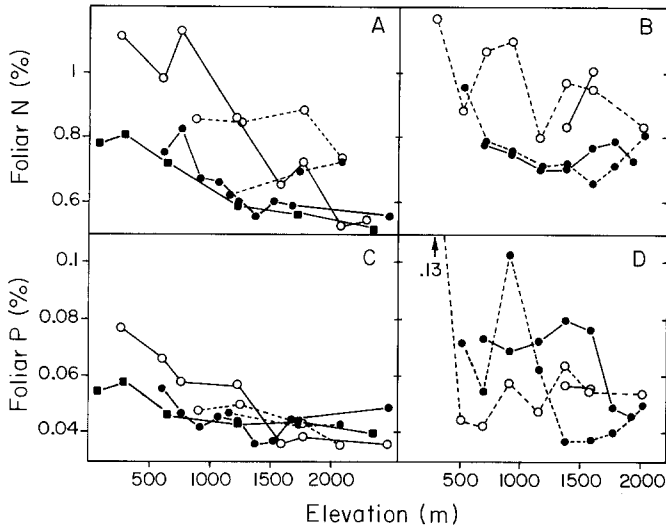
Fig. 3A–D. Foliar nitrogen and phosphorus concentrations (in %, on a dry mass basis) in *Metrosideros polymorpha* as a function of elevation on Mauna Loa lava flows. Symbols and lines as in Fig. 2. **A.** Nitrogen on the wet east flank. **B.** Nitrogen on the dry northwest flank. **C.** Phosphorus on the east flank. **D.** Phosphorus on the northwest flank
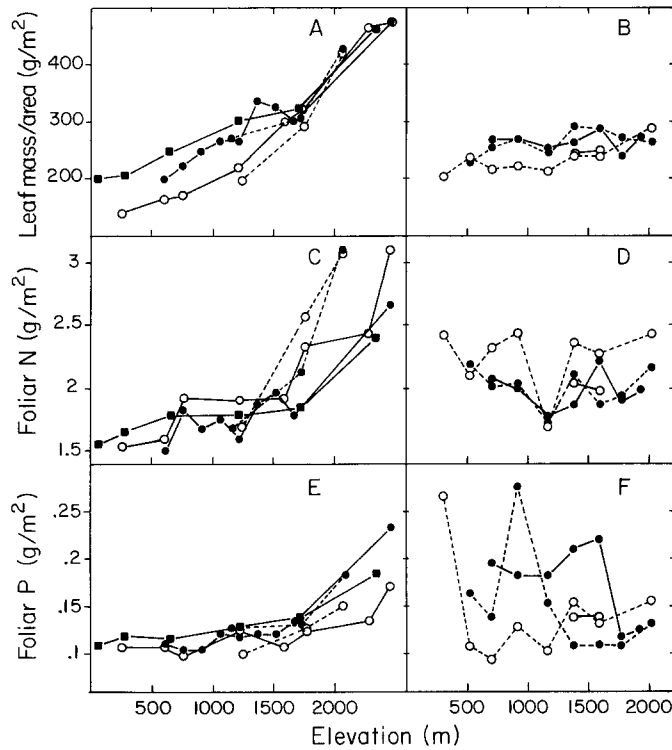

Fig. 4A–F. Leaf mass per area (LMA, in g/m²) and foliar nitrogen and phosphorus contents (in g/m², on a leaf area basis) in *Metrosideros polymorpha* as a function of elevation on Mauna Loa lava flows. Symbols and lines as in Fig. 2. **A.** LMA on the wet east flank. **B.** LMA on the dry northwest flank. **C.** Nitrogen on the east flank. **D.** Nitrogen on the northwest flank. **E.** Phosphorus on the east flank. **F.** Phosphorus on the northwest flank
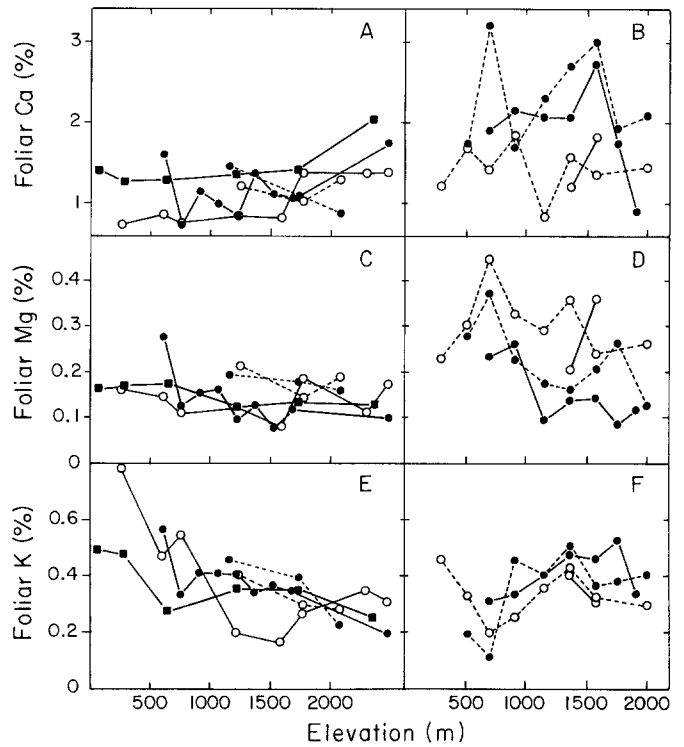

Fig. 5. Foliar calcium, magnesium, and potassium concentrations (in %, on a mass basis) in *Metrosideros polymorpha* on Mauna Loa lava flows. Symbols and lines as in Fig. 2. **A.** Calcium on the wet east flank. **B.** Calcium on the dry northwest flank. **C.** Magnesium on the east flank. **D.** Magnesium on the northwest flank. **E.** Potassium on the east flank. **F.** Potassium on the northwest flank

nutrient release by mineralization therefore is relatively slow.

Effects of precipitation

We expected and observed much slower carbon and nutrient accumulation on young flows and lower pool sizes on old flows on the dry than the wet side, presumably due to water limitation (Table 3, Fig. 2). To the extent precipitation is a dominant source of nutrients, a greater input of nutrients (particularly nitrogen) on the wet side could also contribute to this pattern. In addition, we expected that nutrient availability (particularly nitrogen availability) would be less on the dry than on comparable wet-side sites due to water limitation of decomposition and hence nutrient cycling. That pattern was not observed; foliar nutrient concentrations were higher (Figs. 3, 4, 5), carbon:nutrient ratios in soil lower (Table 3), and exchangeable cation concentrations higher (Table 5) in the dry-side sites. The pattern for cations can be explained by the reduced leaching of dry-side soils; for the nitrogen and phosphorus, we conclude that decomposition and nutrient cycling in these sites are less affected by drought than are primary production and carbon accumulation, so that nutrient supply from soils is closer to matching nutrient demand by plants on the dry than the wet sites. There is no evidence of an interaction between water and nutrient limitation (cf Pastor and Post

pattern as did his herbaceous species. Another possibility is that even the older lava flows we sampled have relatively low nutrient availability because they remain successional at high elevation – in the sense that soil organic matter and nutrient pools are still accumulating and

1988); rather it appears that water is limiting and nutrients are less so on the dry side.

Effects of parent material texture

We expected that the more finely divided 'a'a lava would support higher rates of rock weathering and a greater abundance of favorable sites for colonization than would pāhoehoe – so that 'a'a flows would accumulate carbon and nutrients more rapidly and ultimately to higher levels than pāhoehoe flows. We also expected foliar nutrient levels to be higher on 'a'a, at least for nutrients other than nitrogen.

The expected pattern for soils was observed on the wet-side flows, at least below 2000 m elevation (Table 3, Fig. 2); 'a'a sites accumulated carbon and nutrients more rapidly and to higher levels than pāhoehoe sites. However, the reverse was observed on the dry side, and at the highest elevation (which is also relatively dry) on the wet side. Perhaps the fact that some soil material was lost into the 'a'a matrix contributed to this apparent pattern in dry sites. However, a similar pattern has been observed for initial rates of plant colonization (J. Juvik, personal communication; Aplet, unpublished); colonization is most rapid on 'a'a lava in wet areas and on pāhoehoe lava in dry areas. In dry sites, initial colonization generally occurs in cracks in the smooth pāhoehoe lava surfaces; the surrounding lava surface may act as a microwatershed, increasing effective water availability on pāhoehoe flows.

Overall

The Mauna Loa environmental matrix allows descriptive analyses of controls on ecosystem pools and processes that would be extremely difficult to duplicate in any continental situation. At present, we believe that the coarse-scale description of ecosystems on the wet side of Mauna Loa is reasonable; we can associate patterns of variation in ecosystem pools and processes with putative controlling factors in a plausible way. Not many flows have been described, and of those only the 1855 and 1881 pāhoehoe flows can be considered near-replicates – but their overall similarity is encouraging. Moreover, the research potential of this area is far from exhausted; many more flows with intermediate characteristics are available for descriptive studies, and the well-defined background should make process-level measurements and ecosystem-level experiments rewarding.

In contrast, while the overall differences between wet- and dry-side sites are explicable, our understanding of variations among dry-side sites is relatively poor. Often ecosystem characteristics varied among wet-side sites more or less as expected, while the dry-side sites had an entirely different pattern – or no consistent pattern at all. Our relative inability to explain these patterns in terms of controlling processes may simply reflect the relative inadequacy of our understanding of the functioning of dry compared with wet tropical forests (Murphy and

Lugo 1986). We believe that the climatic contrast between the otherwise extraordinarily similar sites on the wet east and dry northwest flanks of Mauna Loa can provide a useful system for developing and testing our understanding of dry tropical forest ecosystems.

References

Atlas of Hawaii, Second Edition (1983) Department of Geography, University of Hawaii, University of Hawaii Press, Honolulu
Carlquist SC (1980) Hawaii, A Natural History. Pacific Tropical Botanical Garden, Lawai, Kauai, Hawaii
Cole CV, Heil RD (1981) Phosphorus effects on terrestrial nitrogen cycling. In: Clark FE, Rosswall TH (eds), Terrestrial Nitrogen Cycles. Ecol Bull (Stockholm) 33:363–374
Dawson JW, Stemmermann L (1990) Metrosideros (Myrtaceae). In: Wagner WL, Herbst DR, Sohmer SH (eds), Manual of the Flowering Plants of Hawai'i. Bernice Pauahi Bishop Museum and University of Hawaii Press, Honolulu
Eggler W (1971) Quantitative studies of vegetation on sixteen young lava flows on the island of Hawaii. Trop Ecol 12:66–100
Giambelluca TW, Nullet MA, Schroeder TA (1986) Rainfall atlas of Hawai'i. Dept. Land Natural Resources, State of Hawaii. 267 p
Grubb PJ (1977) Control of forest growth and distribution on wet tropical mountains with specific reference to mineral nutrition. Ann Rev Ecol Syst 8:83–107
Grubb PJ (1989) The role of mineral nutrients in the tropics: a plant ecologist's view. In: Proctor J (ed), Mineral nutrients in tropical forest and savanna ecosystems. Blackwell Scientific, Oxford, pp 417–439
Jacobi JD, Gerrish G, Mueller-Dombois D (1983) 'Ōhi' a dieback in Hawai'i: vegetation changes in permanent plots. Pac Sci 37:327–337
Jenny H (1941) Factors of Soil Formation. McGraw-Hill, New York, 281 p
Jenny H (1980) Soil Genesis with Ecological Perspectives. Springer-Verlag, New York, 560 p
Jordan CF (1971) A world pattern in plant energetics. Am Scient 59:425–433
Juvik JO, Singleton DC, Clarke GG (1978) Climate and water balance on the island of Hawaii. Mauna Loa Observatory 20th Anniversary report. pp 129–139
Körner CH (1989) The nutritional status of plants from high elevation: a worldwide comparison. Oecologia 81:379–391
Lockwood JP, Lipman PW, Peterson LD, Warshauer FR (1988) Generalized ages of surface lava flows of Mauna Loa Volcano, Hawaii. U.S. Geological Survey Miscellaneous Publications Map I–1908, U.S. Government Printing Office, Washington, D.C.
Mueller-Dombois D (1987) Forest dynamics in Hawaii. Trend Ecol Evol 2:216–220
Murphy PG, Lugo AE (1986) Ecology of tropical dry forest. Ann Rev Ecol Syst 17:67–88
Olsen SR, Sommers LE (1982) Phosphorus. In: Page AC, Miller RH, and Keeney DR (eds), Methods of Soil Analysis, Part II. Chemical and Microbiological Properties. American Society of Agronomy, Madison, Wisconsin, pp 403–430
Parton WJ, Sanford RL, Sanchez PA, Stewart JB (1989) Modeling soil organic matter dynamics in tropical soils. In: Coleman DC, Oades JM, and Uehara G (eds), Dynamics of Soil Organic Matter in Tropical Ecosystems. NifTAL Project, Univ. of Hawaii Press, Honolulu, pp 153–171
Pastor J, Post WM (1986) Influence of climate, soil moisture, and succession on forest carbon and nitrogen cycles. Biogeochemistry 2:3–27
Pastor J, Post WM (1988) Response of northern forests to CO_2-induced climate change. Nature 334:55–58

382

Post WM, Emanuel WR, Zinke PJ, Stangenberger AG (1982) Soil carbon pools and world life zones. Nature 298:156–159

Post WM, Pastor J, Zinke PJ, Stangenberger AG (1985) Global patterns of soil nitrogen storage. Nature 317:613–616

Reiners WA (1981) Nitrogen cycling in relation to ecosystem succession: a review. Ecol Bull (Stockholm) 33:507–528

Sherman GD, Ikawa H (1968) Soil sequences in the Hawaiian Islands. Pac Sci 22:458–464

Skottsberg C (1941) Plant succession on recent lava flows in the island of Hawaii. Götenborgs Kungl. Vetenskaps-och Vitterhets-sämhalles Handlingar Sjätte följden, ser. B., Band 1, no. 8.

Stemmermann L (1983) Ecological studies of Hawaiian Metrosideros in a successional context. Pac Scien 37:361–373

Technicon Instrument Systems. 1976. Technicon Methods Guide. Tarrytown, New York

Vitousek PM (1982) Nutrient cycling and nutrient use efficiency. Am Natural 119:553–572

Vitousek PM, Matson PA (1988) Nitrogen transformations in tropical forest soils. Soil Biol Biochem 20:361–367

Vitousek PM, Van Cleve K, Balakrishnan N, Mueller-Dombois D (1983) Soil development and nitrogen turnover on recent volcanic substrates in Hawaii. Biotropica 15:268–274

Vitousek PM, Walker LR, Whiteaker LD, Mueller-Dombois D, Matson PA (1987) Biological invasion by Myrica faya alters ecosystem development in Hawaii. Science 238:802–804

Vitousek PM, Matson PA, Turner DR (1988) Elevational and age gradients in Hawaiian montane rainforest: foliar and soil nutrients. Oecologia 77:565–570

Vitousek PM, Shearer G, Kohl DH (1989a) Foliar ^{15}N natural abundance in Hawaiian rainforest: patterns and possible mechanisms. Oecologia 78:383–388

Vitousek PM, Matson PA, Van Cleve K (1989b) Nitrogen availability and nitrification during succession: primary, secondary, and old-field seres. Plant Soil 115:229–239

Vitousek PM, Field CB, Matson PA (1990) Variation in foliar δ^{13}C in Hawaiian Metrosideros polymorpha: a case of internal resistance? Oecologia 84:362–370

Walker TW, Syers JK (1976) The fate of phosphorus during pedogenesis. Geoderma 14:1–19

Wright TL (1971) Chemistry of Kilauea and Mauna Loa lava in space and time. USGS Professional Paper 735, Washington, D.C.

Wright TL, Helz RT (1987) Recent advances in Hawaiian petrology and geochemistry. In: Decker RW, Wright TL, Stauffer PH (eds), Volcanism in Hawaii. USGS Professional Paper 1350, pp 625–640

Yost RS, Uehara G, Fox RL (1982) Geostatistical analysis of soil chemical properties of large land ares. Soil Sci Soc Am J 46:1028–1037