Precontact vegetation and soil nutrient status in the shadow of Kohala Volcano, Hawaii

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Abstract

Humans colonized Hawaii about 1200 years ago and have progressively modified vegetation, particularly in mesic to dry tropical forests. We use $\delta^{13}C$ to evaluate the contribution of C_3 and C_4 plants to deep soil organic matter to reconstruct pre-human contact vegetation patterns along a wet to dry climate transect on Kohala Mountain, Hawaii Island. Precontact vegetation assemblages fall into three distinct zones: a wet C_3 dominated closed canopy forest where annual rainfall is >2000 mm, a dry C_4 dominated grassland with annual rainfall <500 mm, and a broad transition zone between these communities characterized by either C_3 trees with higher water-use efficiency than the rainforest trees or C_3 trees with a small amount of C_4 grasses intermixed. The likelihood of C_4 grass understory decreases with increasing rainfall. We show that the total concentration of rock-derived nutrients in the <2-mm soil fraction differs in each of these vegetation zones. Nutrient losses are driven by leaching at high rainfall and by plant cycling and wind erosion at low rainfall. By contrast, nutrients are best preserved in surface soils of the intermediate rainfall zone, where rainfall supports abundant plant growth but does not contribute large amounts of water in excess of evapotranspiration. Polynesian farmers exploited these naturally enriched soils as they intensified their upland agricultural systems during the last three centuries before European contact.
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1. Introduction

The vegetation and soils of the Hawaiian Islands have been altered substantially by human activity. Polynesian colonists arrived around AD 800, and they began to alter Hawaiian landscapes through hunting, gathering, agriculture, and introduction of animals. Land-cover change increased with the development of complex Hawaiian culture and intensive agricultural practices and accelerated further after the arrival of Europeans in the late 18th century (Allen, 1991, 1992; Athens and Ward, 1993; Athens, 1997; Burney et al., 2001). Knowledge of the distribution of vegetation and soil nutrients prior to the Polynesian discovery of Hawaii is fragmentary, except in specialized environments where pollen is preserved (Selling, 1948; Athens and Ward, 1993; Hotchkiss,

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1998; Hotchkiss and Juvik, 1999; Burney et al., 2001). Archaeological studies demonstrate that low-elevation, dry-land forests and savannas were strongly modified by Polynesian farmers, who increased fire frequency, developed extensive irrigated pondfield systems, and in some dryland environments intensively cultivated fields bounded by readily identifiable walls and trails (Kirch, 1994; Ladefoged et al., 1996). Increasing European influence over Hawaiian land-use practices during the last two centuries resulted in clearing of tracts of wet and high-elevation forests to facilitate introduction of high-yield pasture grasses for livestock production (Cuddihy and Stone, 1990).

Here, we reconstruct the distribution of vegetation community types prior to human disturbance along a dry to wet climate transect, and investigate soil organic carbon levels and the long-term depletion of rock-derived nutrients on a 150 ky lava flow on Kohala Mountain, Hawaii. Kohala Mountain rises more than 1600 m into the northeast trade winds and creates a spectacular climate gradient where median annual rainfall drops from >3000 mm at the summit to about 150 mm near the leeward coast, a distance of less than 15 km (Fig. 1). Near-complete vegetation modification reaches from the arid coastal region to about 2000 mm of rainfall on the upper slope. At present, three broad zones of vegetation are mapped on the leeward side of Kohala Mountain: *lowland dry scrubland and grassland*; *lowland dry and mesic forest, woodland and shrubland*; and *wet forest and woodland* (Pratt and Gon, 1998). The first two plant communities have been strongly modified, and present vegetation does not reflect precontact conditions. The *lowland dry scrubland and grassland* ranges from 150 to about 500 mm rainfall and supports buffel grass (*Cenchrus ciliaria*), and the tree keawe (*Prosopis pallida*) (Fig. 2, lower right, lower left); both are recent introductions to Hawaii. In rocky sites the native grasses pili (*Heteropogon contortus*) and Kawelu (*Eragrostis variabilis*), and the native shrubs and small trees wiliwili (*Erythrina sandwicensis*), 'a'ali'i (*Dodonea viscosa*), aki'a (*Wikstroemia* spp.), and 'ilima (*Sida* sp.) still survive. The *lowland dry and mesic forest, woodland and shrubland* ranges from about 500 to 2000 mm of rainfall and supports cactus (*Opuntia* spp.), buffel, lantana (*Lantana* spp.), keawe, kikuyu (*Pennisetum clandestinum*), rye grass (*Lolium multiflorum*) and orchard grass (*Dactylis* spp.) with occasional native plants represented by 'ohi'a (*Metrosideros polymorpha*), wiliwili, 'a'ali'i, lama, and pili (Fig. 2, middle left). The *wet forest and woodland* zone is composed of 'ohi'a as the dominant tree with an understory composed largely of tree fern (*Cibotium* spp.), and locally uluhe (*Dicranopteris linearis*) (Fig. 2, upper left). Although less clearing has disturbed these high elevation forests, large tracts of land have been converted to pasture (Fig. 2, upper right).

An extensive dry-land agricultural system supported an extensive population of pre-contact Hawaiians in the *lowland dry and mesic forest, woodland and shrubland* zone (Fig. 2, middle right) (Ladefoged et al., 1996; Vitousek et al., 2004). The intricate system of walls and terraces was bounded by low rainfall at low elevation and low nutrient supply at high elevation. Within the field system, the soils have greater nutrient supply compared to either drier or wetter areas, a condition that preceded human use of the land (Vitousek et al., 2004), suggesting that long-term nutrient cycling by the pre-human vegetation assemblage was responsible for its elevated nutrient status (Vitousek et al., 2004).

It is difficult to determine what plants grew on the leeward flanks of Kohala Mountain before Hawaiian agriculture, because of the poor spatial distribution of sites conducive to preserving pollen and/or plant macro-fossils. Analyses of remnant vegetation (McEldowney, 1983) and scant remains of charcoal (Murakami, 1983), seeds (Allen, 1983), pollen (McEldowney, 1983), snails (Christensen, 1983), and phytoliths (Pearsall and Trimble, 1983, 1984) in soils and archaeological excavations along an elevational gradient in leeward South Kohala suggest that pre-human vegetation consisted of closed-canopy wet forest with 'ohi'a dominant above about 1200 m elevation (> ≈1000 mm rainfall). Below 800 or 900 m (< ≈800 mm rainfall), a few relict individuals of koai'a (*Acacia koaia*), naio (*Myoporum sandwicense*), mamane (*Sophora chrysophylla*), and 'iliahi remain, suggesting that they were abundant in native communities of this area, (McEldowney, 1983), and buried phytolith assemblages reflect more open forests and shrublands with some grass cover (Pearsall and Trimble, 1983, 1984). The overall frequency and diversity of relict trees decreases substantially below about 600 m elevation (< ≈500 mm rainfall) (McEldowney, 1983), but phytoliths from several excavated soil horizons below the apparent influence of Hawaiian agriculture reflect an initial abundance of woody vegetation followed by later land clearance (Pearsall and Trimble, 1983, 1984). While the relict vegetation implies a continuous shift from C_3 to C_4 dominance with decreasing rainfall, the phytolith assemblages suggest high relative abundance of C_3 plants in the high rainfall zone, more open forests with some C_4 grasses in the intermediate zone, and increasing abundance of C_3 shrubs in the dry lowland zone near the coast.

We used the stable C isotopes of soil organic carbon (SOC) to decipher the pre-contact distribution of woody
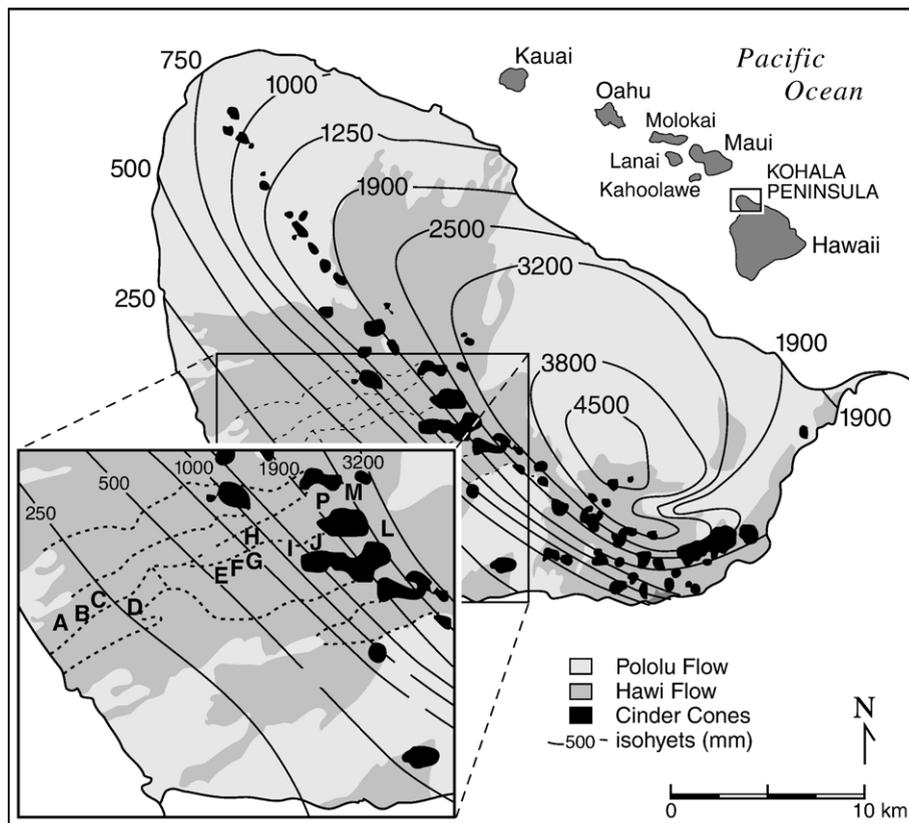
Fig. 1. Location of the soil sampling sites with respect to median annual rainfall on Kohala Mountain, Hawaii. Rainfall isohyets from Giambelluca et al. (1986) http://www.state.hi.us/dbedt/gis/index.html.

species versus native grasses along the Kohala precipitation gradient. In Hawaii as elsewhere, the ecological character and distribution of plants possessing the C_3 and C_4 photosynthetic pathways is largely controlled by the combined influences of temperature and precipitation (Rundel, 1980). The carbon isotopic composition of plant material from trees (C_3 metabolic pathway) and lowland tropical grasses (C_4 metabolic pathway) differ and this isotopic signal is passed on to SOC during decomposition (Teri and Stowe, 1976; Rundel, 1980; Emanuel et al., 1985; Pentico and Tieszen, 1991; Ehleringer et al., 1993). The biogeographical distribution of C_3 and C_4 plants can be inferred from the isotopic composition of SOC, but in Hawaii as in other human-modified areas, interpretation of this isotopic signal is complicated by the conversion of tropical forest to pasture dominated by C_4 grasses. The contribution of introduced pasture grass to SOC has altered only the top 40 cm of soil (Kelly et al., 1998); however, we use carbon isotopes preserved in SOC deep in soil profiles to reconstruct the long-term distribution of plant growth forms along a wet to dry transect on leeward Kohala. We

focus on identifying the transition between the mesic and dry forest, and on testing whether the present-day arid grassland had an analog before humans arrived. We then attempt to infer the soil nutrient status of these vegetation systems, with a focus on the long-term fate of rock derived nutrients.

2. Methods

We analyzed element concentrations and the C isotope composition of SOC for 13 soil profiles sampled along a climosequence on Hawi series lava flows which are alkalic in geochemical composition and approximately 150 ky in age (Spengler and Garcia, 1988; Wolfe and Morris, 1996; Chadwick et al., 2003) (Fig. 1). Hawi lava flows have 'a'a morphologies, creating locally rough topography and a complex suite of local landscape positions. Soil profiles were sampled in slight concavities within convex landform positions to preserve the initial cumulic (tephra mixed into and overlying lava) stratigraphy, but limit the effect of local erosion/deposition. Modern vegetation varies along the

Fig. 2. Photographs representative of zones of vegetation on leeward Kohala. Upper left: 'ohi'a-fern forest in the *wet forest* zone; upper right: kikuyu pasture in the *wet to mesic forest* zone; middle left: stunted 'ohi'a with a fountain grass understory in the *lowland dry forest woodland and shrubland* zone (on Mauna Loa Volcano); middle right: kikuyu covered terraces that make up the Hawaiian dryland agricultural system in the *lowland dry and mesic forest, woodland and shrubland* zone; lower left: buffel grass and keawe shrub in the *lowland dry shrubland and grassland* zone not long after the end of seasonal rains; lower right: buffel and keawe after drought in the *lowland dry shrubland and grassland* zone (the background cinder cones are near the top of the mountain in the *wet forest* zone).

climate gradient, with all but the wettest site being dominated by exotic pasture grasses (buffel at low rainfall, kikuyu at high rainfall) (Table 1). Pollen-based paleoclimate reconstruction, using cores extracted from

bogs in cinder cones at the top of Kohala Mountain, indicates that at the last glacial maximum annual rainfall in the higher and wetter parts of the mountain may have been as much as 50% less than today (Hotchkiss, 1998:

Hotchkiss et al., 2000). Mineral properties and element leaching patterns of the soils suggest that the high rainfall sites have equilibrated to the high rainfall that has predominated during the last 10 ky (Chadwick et al., 2003). Based on the stratigraphy, mineralogy, and mineral isotope composition of the soil, it appears that the low rainfall sites have always been influenced by aridity (Porter, 1997; Chadwick et al., 2003).

In past work, we have assigned the quantity of average annual rainfall to each sampling site using two different methods depending on whether the intent was to maximize the precision of estimation at the sites themselves (cf. Chadwick et al., 2003) or to extrapolate results from the sites to a broader area on Kohala Mountain or to Hawaii in general (cf. Vitousek et al., 2004). In the former case, we made use of nine rainfall stations arrayed along the leeward slope in close proximity to the sampling sites to develop a regression to predict rainfall as a function of elevation (Chadwick et al., 2003). In the latter case, we assigned rainfall values based on site location with respect to rainfall isohyets initially mapped by Giambelluca et al. (1986) and now embedded in a GIS layer at http://www.state.hi.us/dbedt/gis/index.html. Table 1 presents rainfall estimates from both methods, but we use the estimates determined from the isohyets because we are discussing vegetation zones broadly distributed across the volcanic slope.

$^{13}C/^{12}C$ ratios are expressed as a δ value where: $\delta^{13}C = (R_{sample}/R_{standard} - 1) \times 10^3$ and R equals the $^{13}C/^{12}C$ ratio of the sample or standard. Plants with C_3 metabolic pathways differ in $\delta^{13}C$ from C_4 plants, with mean values of −26.0‰ to −27.0‰ for C_3 and −12.0‰ to −13.0‰ for C_4, respectively (Teri and Stowe, 1976). Because SOC has a $\delta^{13}C$ value that is closely related to the relative amounts of C_3 and C_4 biomass contributing to it (Kelly et al., 1991), we measured the stable C isotope composition of SOC from deep soil horizons (>60 cm) that have not been impacted by recent change in land cover and, therefore, reflect the pre-contact geographical distribution of C_3 and C_4 plants. The percentage of C_4 vegetation can be determined by % $C_4 = ((\delta^{13}C_{sample} - \delta^{13}C_{C3})/(\delta^{13}C_{C4} - \delta^{13}C_{C3})) \times 100$, where $\delta^{13}C_{sample}$ is the $\delta^{13}C$ value of the sample, $\delta^{13}C_{C3}$ is the $\delta^{13}C$ value of the C_3 end member, and $\delta^{13}C_{C4}$ is the $\delta^{13}C$ value of the C_4 end member. Determining these end members can be tricky, because isotopic fractionation in C_3 plants differs as an inverse function of the ratio of internal to ambient CO_2 concentration (ci/ca) (Farquhar et al., 1982). This ratio tends to be wider in drought-stressed environments, shifting the C_3 end-member slightly towards C_4 values— in Hawaiian trees (Vitousek et al., 1990; Austin and

Vitousek, 1998) as elsewhere. Austin and Vitousek (1998) observed an increase in $\delta^{13}C$ from −29.9‰ in a site receiving 5000 mm/year of precipitation to −25.6‰ in a site receiving 500 mm/yr; one dryland species averaged −23.6‰. While this effect is small relative to the C_3–C_4 difference, it makes it difficult to detect a low abundance of C_4 grasses in a C_3-dominated forest with confidence.

Soils were sampled by genetic horizon to a depth of 1 m or to bedrock (whichever was encountered first), and the chemical and physical properties were fully characterized and reported elsewhere (Kelly et al., 1998; Chadwick et al., 2003). Soil samples used in SOC isotope determination were passed through a 2-mm sieve, acidified with 0.1 M HCl to assure carbonate removal, rinsed with H_2O, and were oven- and then freeze-dried. Carbon concentrations and $\delta^{13}C$ values were determined by combusting the samples at 875 °C, purifying the resulting CO_2 cryogenically, and determining its quantity using a manometer and isotopic composition using a mass spectrometer (Northfeldt et al., 1981). Samples of soil organic carbon used for radiometric dating were sieved to remove fine rootlets, dispersed in hot acid to eliminate carbonate, repeatedly rinsed to neutrality, brought to dryness and subjected to multiple combustions under vacuum. The resulting CO_2 was purified and reacted with hydrogen on a cobalt catalyst to produce graphite. ^{14}C was measured by accelerator mass spectrometry (AMS) at Lawrence Livermore National Laboratories, University of California. Soil horizons were analyzed for total concentration of Al, P, Ca and Nb using X-ray fluorescence, and the fraction of these elements remaining in the sample was indexed relative to the "immobile" element Nb (Kurtz et al., 2000). The percentage of an element that remained in a soil sample (relative to basaltic parent material) was calculated as: $L_{i,j} = 100 * (C_{i,j}/Nb_j * C_{i,pm}/Nb_{,pm})$ where $L_{i,j}$ is the percentage of element i remaining in sample j, $C_{i,j}$ and Nb_j are the concentration of element i and Nb in sample j, and $C_{i,pm}$ and Nb_{pm} are the element concentrations in basaltic parent material (Vitousek et al., 2004).

3. Results and discussion

3.1. $\delta^{13}C$ values of soil profiles

The isotopic signatures of surface soil horizons range from −14‰ to −20‰, and reflect the input of modern C_4 biomass because of the presence of introduced pasture grasses (Fig. 3; Table 2). The sole exception to this pattern is Site L, which is in relatively pristine forest

Table 1
Physiography of the sampling sites and soil classification

Site	Elevation (m)	MAP[a] (mm)	MAP[b] (mm)	MAT (°C)	Soil water balance[c]		Plants	Soil classification[d]
					Summer	Winter		
A	77	160	170	23	Negative	Negative	Buffel, Keawe	Medial-skeletal, ferrihydritic, isohyperthermic Typic Haplotorrands
B	185	180	220	23	Negative	Negative	Buffel, Keawe	Clayey-skeletal, isotic, isohyperthermic Sodic Haplocambids
C	256	210	270	23	Negative	Negative	Buffel, Keawe	Clayey-skeletal, isotic, isohyperthermic Sodic Haplocambids
D	356	270	310	22	Negative	Negative	Buffel, Keawe	Medial-skeletal, mixed, isohyperthermic Typic Haplotorrands
E	674	570	670	20	Negative	Negative	Buffel, Keawe	Medial, amorphic, isohyperthermic Typic Haplocambids
F	833	790	830	19	Negative	Positive	Kikuyu, Keawe	Medial, ferrhydritic, isothermic Andic Haplustolls
G	922	930	1030	19	Negative	Positive	Kikuyu	Medial, ferrhydritic, isothermic Andic Haplustolls
H	992	1060	1120	18	Negative	Positive	Kikuyu	Medial, ferrhydritic, isothermic Humic Haplustands
I	1090	1260	1530	18	Negative	Positive	Kikuyu	Medial, amorphic isothermic Pachic Haplustands
J	1134	1380	1660	18	Negative	Positive	Kikuyu	Medial, amorphic, isomesic Hydric Fulvudands
P	1176	1800	2140	17	Positive	Positive	Kikuyu	Medial, amorphic, isomesic Hydric Fulvudands
M	1200	2500	2360	17	Positive	Positive	Kikuyu	Medial over hydrous, ferrihydritic, isomesic Typic Fulvudands
L	1254	3000	2780	17	Positive	Positive	'Ohi'a-Fern	Hydrous, amorphic, isomesic Alic Epiaquand

[a] Rainfall estimated from regression of rainfall vs elevation (see text for explanation).
[b] Rainfall estimated from GIS interpolation of isohyet map (see text for explanation)—these are the rainfall estimates used in this paper.
[c] Data from Chadwick et al. (2003): Negative (summer) refers to profiles where water balance was positive during winter months but negative during summer months.
[d] Classification by Chadwick and Gavenda (see Chadwick et al., 2003).

(Fig. 2, upper left) and has an isotopic signature consistent with the presence of C_3 vegetation (−26‰). In general, the isotopic signature of the SOC deep within the profiles becomes more depleted with increasing precipitation, suggesting increasing proportions of C_3-derived SOC. At the drier sites, the deeper horizons have isotopic signatures that range from −15‰ to −19‰, indicating substantial inputs from C_4 vegetation. The wettest sites have basal $\delta^{13}C$ values of −25‰ to −26‰ indicating that the SOC is derived exclusively from C_3 vegetation. Profiles receiving between 670 and 1660 mm rainfall have basal $\delta^{13}C$ values that range from −22‰ to −24‰; C_3 vegetation dominated these sites, but small contributions may have come from C_4 vegetation.

Much of leeward Kohala was converted into pasture between 100 and 150 years ago (Fig. 2), but carbon contribution to SOC from the introduced pasture grasses does not penetrate below 40 cm depth (Kelly et al., 1998). In addition, ^{14}C dates of 4130 and 8030 years BP taken on SOC deep within the soil profile for sites A and D, respectively, indicate that little recent carbon has been incorporated into the SOC. Hence, we believe that deep SOC predates Polynesian habitation, and that its stable C isotope signatures reflect long-term inputs of C isotopes from vegetation. At intermediate precipitation (670–1660 mm) the data suggest that vegetation was composed mostly of C_3 plants; a contribution from C_4 grasses may have occurred, but uncertainties in the C_3 end member resulting from systematic positive shifts in ^{13}C abun-

dance in drier sites makes it difficult to be sure. On the evidence of C isotopes, the intermediate rainfall zone could have supported savanna vegetation with C_3 trees and C_4 grasses, or a dryland forest in which C_3 trees had a very high water use efficiency, and so were relatively enriched in ^{13}C (Ehleringer et al., 1993). In Hawaii, modern C_3 vegetation in dry sites can have $\delta^{13}C$ near −24‰ to −25‰ (Vitousek et al., 1990), and atmospheric CO_2 was ~1‰ more negative in the past. For SOC $\delta^{13}C$ > −24‰ but < −22‰, we cannot be certain whether C_4 plants were part of the plant community.

In summary, $\delta^{13}C$ data suggest that before humans arrived, the leeward Kohala vegetation mosaic ranged from predominantly grasses (drier sites); to dryland forests, possibly with grass understory (intermediate sites); to a closed-canopy forest in the wettest precipitation zone. Based on the plots in Fig. 3, it seems likely that the boundaries of these communities were near the 500 mm and 2000 mm rainfall breaks used to delineate map units by Pratt and Gon (1998). In Fig. 3, and subsequent figures, we adopt the < 500 mm, 500–2000 mm and > 2000 mm rainfall breaks as a convenience for data visualization and to plot soil properties on three panels. These breaks correspond more or less to water balance properties along the leeward Kohala slope, with the break at 2000 mm separating sites that have positive water balance throughout the year from those that have negative balance in the summer months but positive water balance in the winter months (Table 1). By contrast, the 500 mm break is within the

arid precipitation zone where water balance is negative throughout the year.

3.2. Soil nutrient properties

In this section, we evaluate the impact of climate and associated vegetation assemblages on carbon concentration and soil nutrients. Specifically, we evaluate the loss or accumulation of the rock-derived nutrients, Ca and P, by developing two comparisons: first, present concentrations to those in the parent basalt as a way of indexing change; second, the behavior of Ca and P to Al, which is sparingly mobile in soil and not strongly cycled by biota.
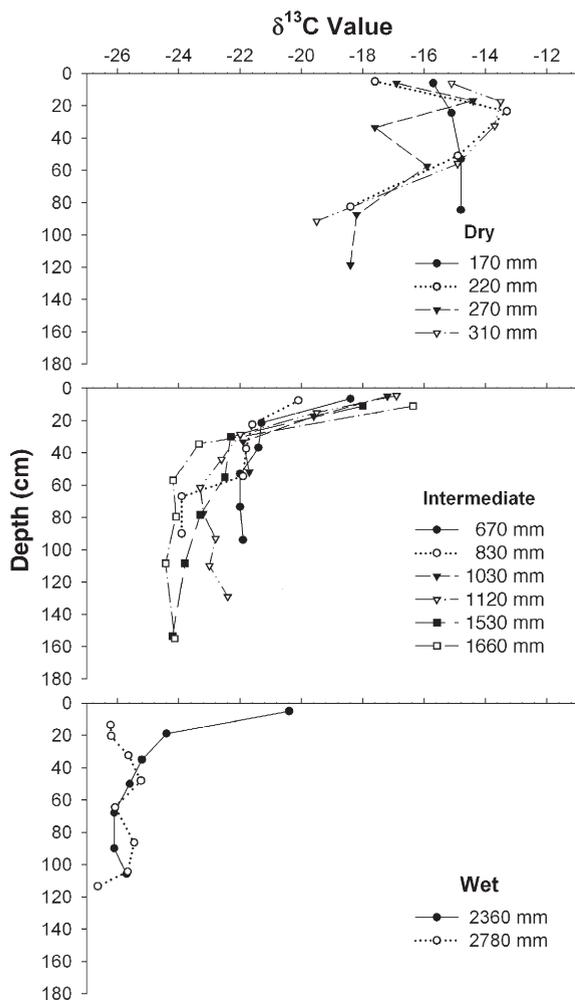

Fig. 3. Depth plots of δ^{13}C of soil organic matter shown as a function of rainfall in millimeters (see Table 1 for the correspondence between rainfall and site letter designations) and broken into three rainfall zones: dry (<500 mm); intermediate (500–2000 mm), wet (>2000 mm).

Concentrations of soil organic carbon are highest in the surface horizons and decrease gradually with increasing depth (Fig. 4). Compared with soils globally, the concentrations of carbon are much higher than usual for mineral soils because these volcanic soils have large concentrations of non-crystalline clays that stabilize the SOC (Torn et al., 1997; Chadwick et al., 2003; Chorover et al., 2004). In general, SOC increases with increased annual rainfall. Aluminum remaining in the profile relative to the parent material varies from about 75% to 140% within the dry and intermediate soil profiles (Fig. 5). The dry profiles have maximum values near the surface suggesting that accumulation of exogenous dust is augmenting Al concentrations (Kurtz et al., 2001). The intermediate profiles also show high levels of Al remaining at the surface, but several of the profiles show a maximum or secondary maximum in subsurface horizons, suggesting that Al has been translocated and concentrated within the profiles. By contrast, at the wet sites, Al remaining in the profiles is only 20–40% in the surface horizons and increases to 80–100% in deeper horizons. In these profiles an overall loss of Al occurs, and it is particularly acute in the surface horizons. This pattern is true even though the high rainfall sites receive more dust (Stewart et al., 2001). The losses from the wet soils probably result from a combination of increased Al solubility at low pH (Table 2) and increased chelation by low-molecular-weight organic acids (Kurtz et al., 2000; Chadwick et al., 2003; Chorover et al., 2004). In either case, the positive water balance at these sites ensures that water and solutes move out the bottom of the soils.

Phosphorus is a plant nutrient that has minimal solubility in volcanic soils because it participates in a number of secondary reactions after release from primary minerals (McLaughlin et al., 1981; Parfitt, 1989). Interestingly, P has been depleted at the dry sites; in most cases less than 50% P remains in the dry profiles (Fig. 6). A similar depletion occurs in the wet sites, but here the profiles show a subsurface maximum in P remaining, suggesting maximum losses from the surface horizons with some redistribution to deeper horizons. Some of those putative accumulation horizons reach nearly 100% remaining. By contrast, the intermediate zone has very different patterns of P remaining. Many of the surface horizons show large augmentations of P, ranging from 80% to 350% P relative to parent material. The subsurface horizons show losses of P, and the two driest sites in the intermediate group have depth profile patterns that are more similar to the dry sites than to the wetter intermediate profiles.

The relationship between Al and P losses from the soil profiles is instructive. In a chronosequence of wet

Table 2
Selected properties of pedons along bioclimatic gradient, Kohala Peninsula, Hawaii

Site/depth (cm)	Horizon	pH	Nb (ppm)	P_2O_5 (%)	CaO (%)	Al_2O_3 (%)	Organic C (%)	$\delta^{13}C$ of organic C (‰)
A								
0–12	A	7.4	70	0.83	1.64	20.27	3.4	−15.7
12–37	Bw1	7.6	98	0.61	0.80	26.93	1.8	−15.1
37–69	Bw2	7.7	127	1.07	1.37	28.68	1.5	−14.8
69–100+	Bw3	7.7	122	1.21	1.36	28.65	1.5	−14.8
B								
0–10	A	7.2	96	0.66	0.58	25.86	1.7	−17.6
10–37	Bw1	6.7	118	0.45	0.33	28.92	1.6	−13.3
37–65	Bw2	7.3	143	0.42	0.43	31.55	1.0	−14.9
65–100	2Cr	8.0	131	0.68	0.99	28.01	0.3	−18.4
C								
0–12	A	7.2	74	1.02	1.10	20.65	4.3	−16.9
12–22	Bw1	7.3	76	0.62	0.34	25.42	1.2	−14.4
22–45	Bw2	7.2	89	0.38	0.34	26.49	1.2	−17.6
45–70	Bw3	7.3	90	1.22	1.76	25.28	1.0	−15.9
70–105	Bw4	7.6	93	1.06	1.93	24.49	1.1	−18.2
105–132	Bw5	8.2	65	1.21	4.87	19.34	0.1	−18.4
D								
0–12	A	7.2	99	0.69	0.94	23.60	4.7	−15.1
12–23	Bw1	6.6	114	0.61	0.49	27.01	2.9	−13.5
23–42	Bw2	6.5	120	0.60	0.43	28.98	2.6	−13.7
42–70	Bw3	6.8	120	0.63	0.51	29.70	1.9	−14.9
70–113	Cr	7.7	131	0.59	0.62	30.26	0.4	−19.5
E								
0–13	A	6.9	77	1.28	1.44	21.73	4.6	−18.4
13–30	Bt1	7.2	82	0.83	1.13	23.06	2.4	−21.3
30–44	Bt2	7.4	90	0.55	0.84	24.84	1.5	−21.4
44–62	Bt3	7.6	82	0.43	0.88	26.18	1.6	−22.0
62–85	BC1	7.7	96	0.48	0.87	26.24	1.0	−22.0
85–103	BC2	7.9	103	0.41	0.78	27.20	0.8	−21.9
F								
0–15	A	6.7	57	1.21	2.04	19.32	5.4	−20.1
15–30	Bw1	7.2	58	0.75	1.76	21.07	4.1	−21.6
30–45	Bw2	7.4	88	0.52	1.49	22.81	2.7	−21.8
45–64	Bw3	7.6	99	0.74	1.97	23.07	5.3	−21.9
64–70	BC	7.8	85	1.07	2.48	22.59	5.1	−23.9
70–110	Cr	7.7	93	0.98	2.26	23.08	5.2	−23.9
G								
0–10	Ap1	6.1	54	2.43	1.81	17.49	9.4	−17.2
10–25	Ap2	6.6	60	1.93	1.66	20.26	5.0	−19.6
25–41	Bw1	7.0	89	0.75	1.18	24.09	2.6	−21.9
41–63	Bw2	7.0	91	0.87	1.64	24.42	2.9	−21.7
63–100	2Cr	7.0		–	–	–	–	−22.2
H								
0–9	Ap1	6.0	51	2.91	1.79	17.19	12.5	−16.9
9–21	Ap2	6.6	54	2.43	1.89	18.97	10.3	−19.5
21–36	Bw1	7.1	97	1.11	1.36	22.71	6.4	−22.0
36–52	Bw2	7.3	127	0.82	1.10	23.65	3.5	−22.6
52–71	Bw3	7.5	134	0.61	0.88	24.57	2.2	−23.3
71–84	2Btb	7.6	112	0.71	1.01	24.41	2.1	−23.2

Table 2 (*continued*)

Site/depth (cm)	Horizon	pH	Nb (ppm)	P$_2$O$_5$ (%)	CaO (%)	Al$_2$O$_3$ (%)	Organic C (%)	δ^{13}C of organic C (‰)
84–102	2Bw1	7.7	104	0.73	1.09	24.78	2.5	−22.8
102–118	2Bw2	7.8	99	0.90	1.17	24.99	2.6	−23.0
118–140	3Bw	7.8	89	0.70	1.01	25.73	1.8	−22.4
I								
0–22	Ap	6.0	41	3.69	2.49	16.82	7.4	−18.0
22–38	Bw1	6.6	70	2.45	1.49	21.45	3.4	−22.3
38–72	Bw2	6.8	86	1.11	1.01	24.09	2.5	−22.5
72–85	Bw3	6.9	70	0.99	1.17	23.33	3.7	−23.3
85–132	Bwb	7.1	111	1.42	1.11	23.86	5.2	−23.8
132–175	2Bwb	7.0	109	1.66	1.19	24.86	5.2	−24.2
J								
0–22	A	5.9	63	2.69	1.26	14.67	7.8	−16.4
22–47	Bw	6.2	85	1.54	0.88	19.11	4.5	−23.3
47–67	Bw2	6.3	92	1.33	0.73	21.63	4.1	−24.2
67–92	Bw3	6.4	60	1.52	1.11	22.60	3.7	−24.1
92–125	Bt	6.4	90	1.62	1.02	24.57	2.0	−24.4
125–185			85	1.52	0.82	23.99	1.5	−24.1
P								
0–8	Oi	4.2	124	1.55	0.26	13.45	18.7	
8–26	A	4.2	163	1.18	0.20	11.44	13.0	
26–37	Bw1	4.6	121	1.09	0.15	16.31	8.8	
37–59	Bw2	4.5	105	1.94	0.68	20.89	8.46	
59–70	Bw3	5.1	94	2.52	1.04	23.85	2.79	
M								
0–10	Ag	4.4	101	0.76	0.17	10.91	10.5	−20.4
10–28	Bw1	4.5	112	0.75	0.14	11.58	4.5	−24.4
28–42	Bw2	4.8	116	0.76	0.22	16.13	3.8	−25.2
42–58	Bw3	5.1	109	0.89	0.16	18.48	3.4	−25.6
58–79	Bw4	5.1	136	1.16	0.14	19.33	2.8	−26.1
79–101	2Cr	5.2	114	2.34	0.42	24.06	3.3	−26.1
101–110	2Ab	5.0	194	1.26	0.1	20.26	2.9	−25.7
110–120	3Bwb1	5.1	260	1.46	0.12	15.89	5.0	−25.4
120–132+	3Bwb2	5.3					6.3	−25.7
L								
0–5	Oe	3.6	180	1.21	0.18	6.36	44.9	−25.8
5–11	Oa	4.0	204	2.15	0.14	9.53	22.9	−26.6
11–16	A	3.9	215	2.49	0.09	15.47	19.3	−26.2
16–25	AB	4.0	136	2.70	0.14	29.91	14.1	−26.2
25–40	Bw1	4.7	109	3.28	0.33	30.98	11.7	−25.6
40–56	Bw2	4.8	113	3.17	0.09	31.87	4.2	−25.2
56–73	Cr1	5.5	138	2.67	0.06	31.89	3.1	−26.1
73–100	Cr2	5.6	124	1.88	0.06	32.7	4.2	−25.5
100–109	Cr3	5.5	300	1.43	0.06	30.14	4.3	−25.7
109–118	Cr4	5.3		−	−	−		−26.6

soils, P is lost at about the same rate as Al (Vitousek, 2004), and the correspondence of Al and P losses is borne out in the wet profiles shown here (Figs. 5 and 6); 50–75% of the Al and P have been leached from the upper 40 cm profiles and deeper in the profiles these elements trend back toward parent material values although the mineral form has changed (Chadwick et al., 2003). In the intermediate rainfall zone, a contrast develops between the patterns for Al and P. Phosphorus shows large accumulations in the surface horizons of the higher rainfall intermediate zone soils, and the accumulation is accompanied by losses at depth; a pattern that is suggestive of plant uptake and subsequent deposition at the surface. The depth plots for Al are variable but do
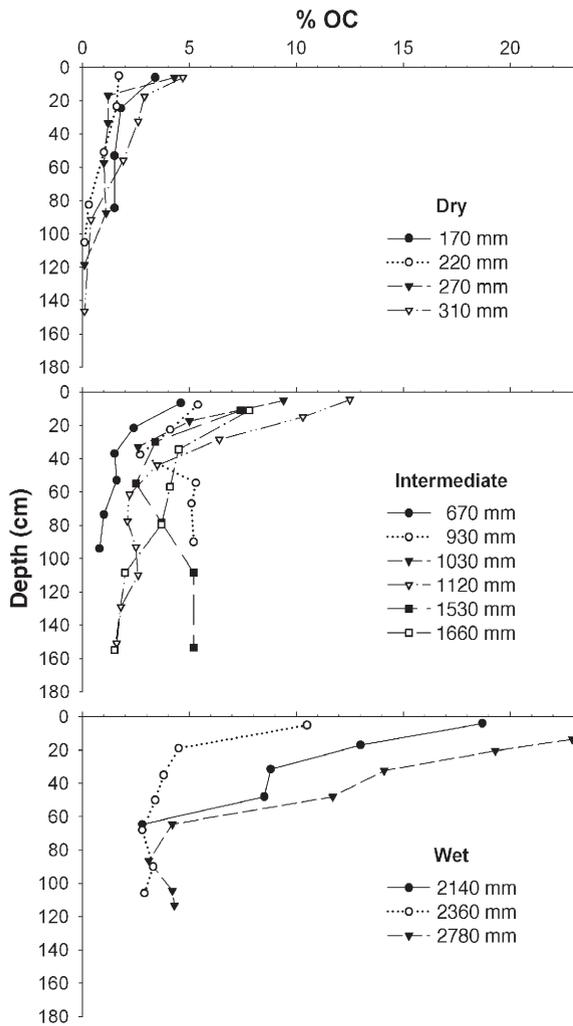
Fig. 4. Depth plots of soil organic carbon shown as a function of rainfall in millimeters (see Table 1 for the correspondence between rainfall and site letter designations) and broken into three rainfall zones: dry (<500 mm); intermediate (500–2000 mm), wet (>2000 mm).

dry sites is protected from erosion by a rock pavement caused by soil profile inflation similar to that described for Cima volcanic field in the Mojave Desert in California (Wells et al., 1985; Dohrenwend et al., 1986; McFadden et al., 1987).

In desert ecosystems, nutrients contained in senescent plant material are redistributed among bare patches, shrubs and/or bunch grasses (Schlesinger et al., 1997; Schlesinger and Pilmanis, 1998). Erosion of organic and mineral soil from the bare patches produces islands of fertility at the base of plants accompanied by overall ecosystem nutrient depletion (Schlesinger et al., 1990; Coppinger et al., 1991). Leeward Kohala is buffeted by strong downslope winds with average annual windspeeds ranging from 5.6 to 6.4 m s^{-1} (Sanderson, 1993) that can
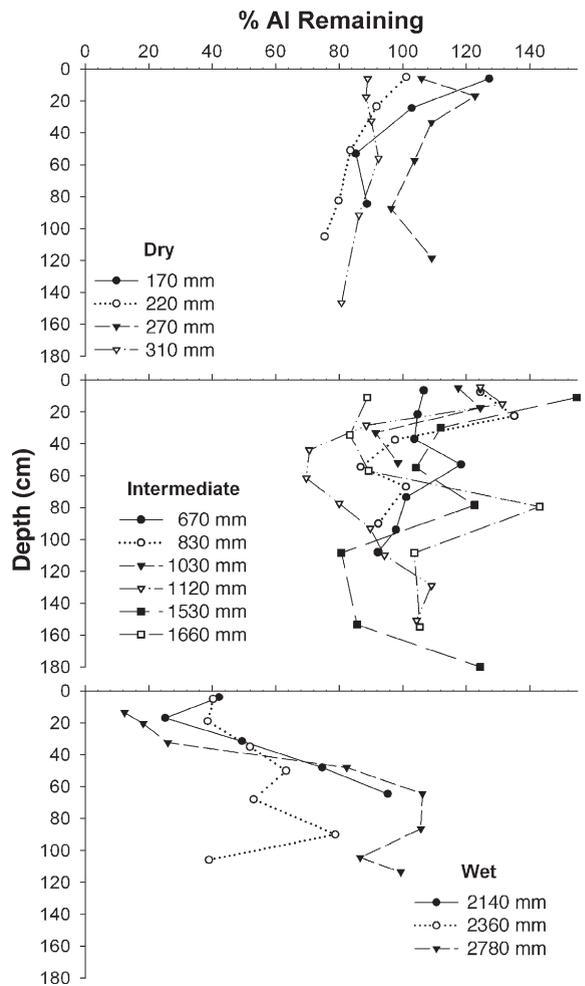

Fig. 5. Depth plots of the change in aluminum, relative to parent material and indexed to niobium, shown as a function of rainfall in millimeters (see Table 1 for the correspondence between rainfall and site letter designations) and broken into three rainfall zones: dry (<500 mm); intermediate (500–2000 mm), wet (>2000 mm).

not show the strong differentiation between surface and subsurface horizons that exists for P. The contrast between P and Al is particularly striking at the dry sites where up to 75% of the P has been lost but Al hovers between 20% loss and 20% gain. Leaching of P is unlikely because water balance at these sites is strongly negative most of the time. It seems likely that the loss of P, but not Al, from the dry sites (and the dry intermediate sites) results from uptake of P by plants followed by removal of the surface material. The losses could be mediated by either water or wind erosion of biomass or of surface soil, but we think wind removal of dead and partly decomposed organic material or residual ash after fire is the most likely mechanism. The surface soil at the
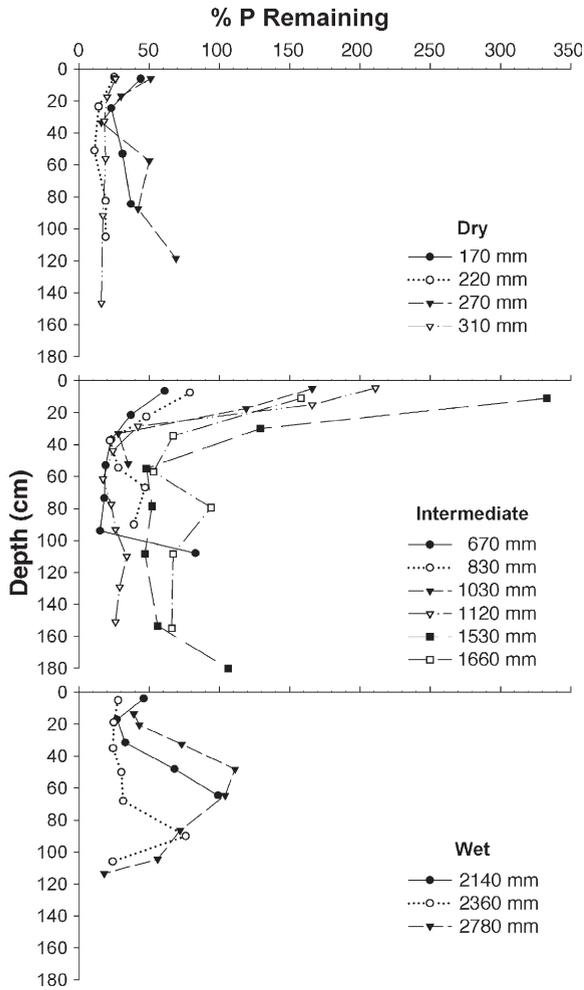
Fig. 6. Depth plots of the change in phosphorus, relative to parent material and indexed to niobium, shown as a function of rainfall in millimeters (see Table 1 for the correspondence between rainfall and site letter designations) and broken into three rainfall zones: dry (<500 mm); intermediate (500–2000 mm), wet (>2000 mm).

easily redistribute dead biomass. By contrast with continental deserts, the nearby ocean acts as a sink from which no P returns. Assuming linear losses of P over 150,000 years, about 7% of the present-day biomass would have to be removed from low rainfall ecosystems to explain the cumulative loss of P. If instead, we assume an exponential increase in P loss (to recognize the recent impact of human-set fires), the present-day losses need to be 20% of present-day biomass. (These calculations are generalized based on the following measured but abstracted parameters: parent material density and P_2O_5 concentration of 1.25 g cm^{-3} and 1.25%, respectively; P loss of 75% for the top meter (see Fig. 6); 40% rock fragment that has not lost any P; above-ground grass biomass of 1500 kg ha^{-1}; and biomass P concentration of

0.2%.) At the intermediate sites, the vegetation does not dry out for as long, and historically fewer fires have occurred. Greater plant cover would have protected dead organic litter from surface wind. Overall, these patterns suggest that different pedogenic processes are intensified within the different bioclimatic regions.

Calcium is more mobile than Al or P, and all sites regardless of precipitation have a net loss of Ca relative to the parent material (Fig. 7). At the wet sites, only 5–10% of the original Ca remains in the profiles; the rest has been leached. At the intermediate sites, Ca remaining ranges from 10% to 40% with maxima near the surface and near the bottom of the profiles, suggesting that leaching may not be removing all the Ca from the bottom of the profiles
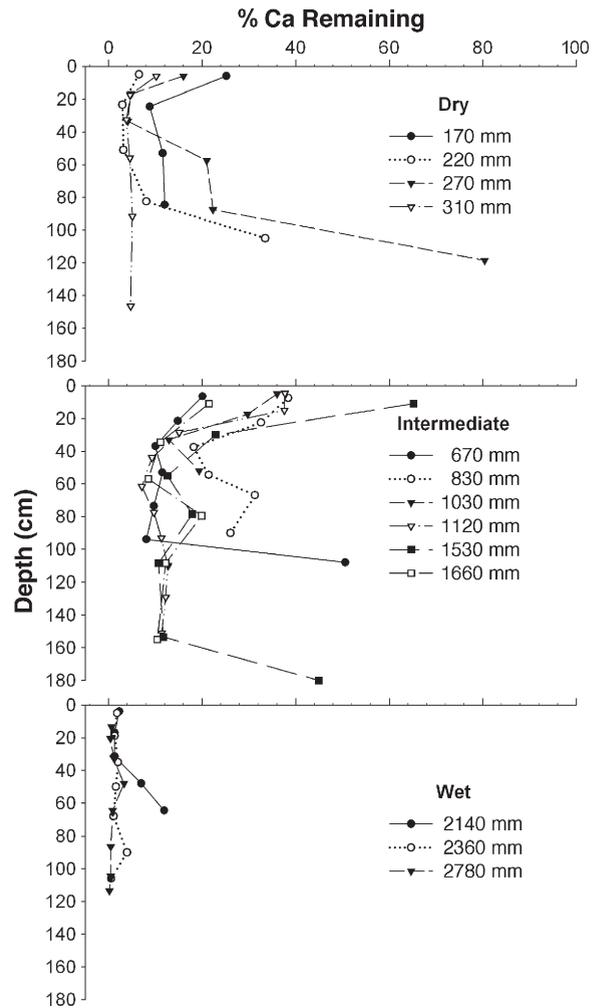

Fig. 7. Depth plots of the change in calcium, relative to parent material and indexed to niobium, shown as a function of rainfall in millimeters (see Table 1 for the correspondence between rainfall and site letter designations) and broken into three rainfall zones: dry (<500 mm); intermediate (500–2000 mm), wet (>2000 mm).
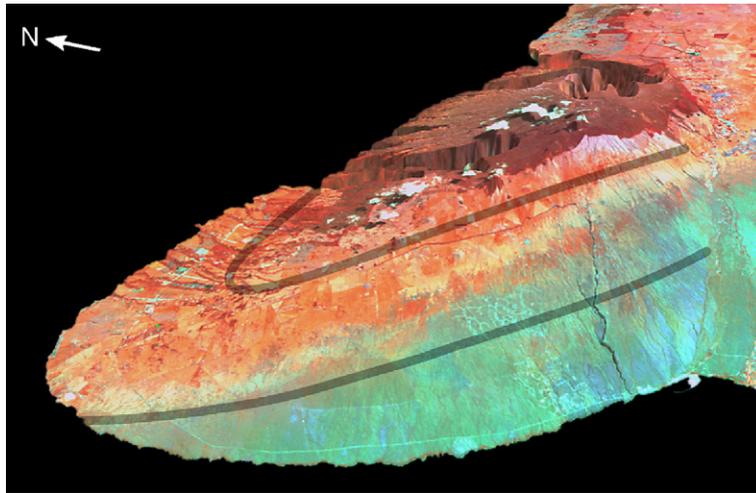
Fig. 8. Kohala Volcano viewed from the southwest. The image provides a view of the north-northeast side where high rainfall and old Pololu lava flows yield an eroded landscape. In contrast, the south-southwest slopes lie in a rain shadow with rainfall decreasing toward the coast. The lines show the approximate position of the 500-mm and 2000-mm rainfall isohyets. The image was developed by draping a SPOT Image mosaic over a US Geological Survey 30' Digital Elevation Model.

and that plant cycling may be augmenting Ca in the surface horizons. The dry sites range from 5% to 25% Ca remaining in the surface horizons and from about 5% to 85% remaining in the subsurface horizons. As in many arid soils, Ca accumulates as carbonate minerals deep in the profiles. At the dry sites, Ca may be lost through occasional deep leaching as well as by the plant uptake and biomass erosion mechanism invoked previously for P removal.

4. Conclusions

Human modification of land cover, particularly in the drier low-elevation parts of the Hawaiian Islands, has made it difficult to determine the distribution of pre-human contact vegetation. For instance, it has been hypothesized that C_4 grasses existed in the warm, dry areas, and pili grass (a C_4 plant) has been suggested as a probable component of that precontact ecosystem (Cuddihy and Stone, 1990). We document that C_4 plants grew in dry leeward Kohala although we cannot definitively say that pili was one of them.

Mapping of the probable vegetation zones in Hawaii by Pratt and Gon (1998) has identified three distinct vegetation zones on leeward Kohala. The distribution of C_3 and C_4 carbon isotope signatures we observe in soils are similar to the biogeographical ranges reported by Rundel (1980) and provide another view of the same zonation identified by Pratt and Gon (1998). The low elevation C_4 dominated zone and high elevation C_3 dominated zone are unambiguous, whereas the impor-

tance of C_4 plants in the intermediate zone is uncertain. The observed isotopic signatures are consistent with either dryland forest plants with high water use efficiency, or a small contribution of C_4 plants. Pearsall and Trimble (1983, 1984) used phytoliths from soil and archeological sites to infer closed-canopy forest at high rainfall, open forest and shrub land with some C_4 grasses at intermediate rainfall, and in contrast with our results, they found an abundance of C_3 shrubs in the dry lowland zone. It may be that the introduced C_3 shrub Keawe has contributed to the signal that they document.

The climatic gradient on leeward Kohala is one of the most spectacular on Earth (Figs. 1 and 8). The northeast trade wind is forced up the windward side of the mountain and over the top (Sanderson, 1993). As it cascades down the leeward side it becomes progressively hotter and drier and finally shoots offshore (afternoon is a treacherous time for kayakers along the leeward coast of Kohala). The ecosystems arrayed along the leeward slope are impacted by very different evaporation and leaching regimes (Hsieh et al., 1998; Chadwick et al., 2003), and they retain rock-derived nutrients with varying success. In all zones, biocycling of P and Ca would have been important—but over the long-term, different types and intensities of loss mechanisms have produced differences in present-day nutrient status. In the wet sites, nutrients are lost as water carries them below the rooting depth of plants. By contrast, the dry sites, minimally affected by leaching, have lost considerable amounts of nutrient elements but not Al. The losses are severe and likely result from the strong downslope winds that can carry dead plant

material, litter and/or ash into the adjacent ocean (Fig. 8). We have previously shown the importance of ocean to land transfers of Ca (Kennedy et al., 1998; Chadwick et al., 1999); here we suggest a land to water transference of P and probably other nutrients.

The intermediate zone is particularly nutrient rich and benefits from rainfall amounts that are adequate to keep vegetation non-senescent for long periods, but not so great that leaching is a major loss mechanism. It is in this zone where nutrients that have been taken up by roots and deposited on the surface are recycled with a minimum of below ground or above ground losses. The dryland forests and savannas are the most nutrient-rich and productive areas on leeward Kohala because they preserve nutrient capital most effectively.

The Hawaiians recognized this trove of accumulated nutrients in the intermediate zone and intensified their agricultural efforts in this region (Vitousek et al., 2004)—as is observed elsewhere in the tropics (Murphy and Lugo, 1986; Ewel, 1999). Dryland forests are the most productive tropical regions because they combine seasonal rains with nutrient rich soils. On leeward Kohala, as everywhere on Earth, water and land interact in complex ways to determine plant distribution and the productivity of ecosystems.

Acknowledgments

References

Allen, M.S., 1983. Analysis of archaeobotanical materials. Archaeological Investigations of the Mudlane–Waimea–Kawaihae Road Corridor, Island of Hawai'i. Honolulu, Hawaii, Department of Anthropology, Bernice Pauahi Bishop Museum, pp. 384–400.

Allen, J., 1991. The role of agriculture in the evolution of the pre-contact Hawaiian state. Asian Perspect. 30, 117–132.

Allen, J., 1992. Farming in Hawaii from colonization to contact. Radiocarbon chronology and implications for cultural change. N. Z. J. Archaeol. 14, 45–66.

Athens, J.S., 1997. Hawaiian native lowland vegetation in prehistory. In: Kirch, P.V., Hunt, T.L. (Eds.), Historical Ecology in the Pacific Islands: Prehistoric Environmental and Landscape Change. Yale University Press, New Haven, pp. 248–270.

Athens, J.S., Ward, J.V., 1993. Environmental change and prehistoric Polynesian settlement in Hawaii. Asian Perspect. 32, 205–223.

Austin, A.T., Vitousek, P.M., 1998. Nutrient dynamics on a precipitation gradient in Hawai'i. Oecologia 113, 519–529.

Burney, D.A., James, H.F., Burney, L.P., Olson, S.L., Kikuchi, W., Wagner, W.L., Burney, M., McCloskey, D., Kikuchi, D., Grady, F.V., Gage II, R., Nishek, R., 2001. Fossil evidence for a diverse biota from Kaua'i and its transformation since human arrival. Ecol. Monogr. 71, 615–641.

Chadwick, O.A., Derry, L.A., Vitousek, P.M., Huebert, B.J., Hedin, L.O., 1999. Changing sources of nutrients during four million years of ecosystem development. Nature 397, 491–497.

Chadwick, O.A., Gavenda, R.T., Kelly, E.F., Ziegler, K., Olson, C.G., Elliott, W.C., Hendricks, D.M., 2003. The impact of climate on the biogeochemical functioning of volcanic soils. Chem. Geol. 202, 195–223.

Chorover, J., Amistadi, M.K., Chadwick, O.A., 2004. Surface charge evolution of mineral-organic complexes during pedogenesis in Hawaiian basalt. Geochim. Cosmochim. Acta 68, 4859–4876.

Christensen, C.C., 1983. Analysis of land snails. Archaeological Investigations of the Mudlane–Waimea–Kawaihae Road Corridor, Island of Hawai'i. Honolulu, Hawaii, Department of Anthropology, Bernice Pauahi Bishop Museum, pp. 449–471.

Coppinger, K.D., Reiners, W.A., Burke, I.C., Olson, R.K., 1991. Net erosion on a sagebrush steppe landscape as determined by cesium-137 distribution. Soil Sci. Soc. Am. J. 55, 254–258.

Cuddihy, L.W., Stone, C.P., 1990. Alteration of Native Hawaiian Vegetation: Effects of Humans, their Activities and Introductions. University of Hawaii Cooperative National Park Resources Studies Unit, Honolulu.

Dohrenwend, J.D., Wells, S.G., Turrin, B.D., 1986. Degradation of Quaternary cinder cones in the Cima volcanic field, Mojave Desert, California. Geol. Soc. Amer. Bull. 97, 421–427.

Ehleringer, J.R., Hall, A.E., Farquhar, G.D., 1993. Stable Isotopes and Plant Carbon/Water Relations. Academic Press, San Diego, CA.

Emanuel, W.R., Hugart, H.A., Stevenson, M.P., 1985. Climate change and the broad scale distribution of terrestrial ecosystem complexes. Clim. Change 7, 29–43.

Ewel, J.J., 1999. Natural systems as models for the design of sustainable systems of land use. Agrofor. Syst. 45, 1–21.

Farquhar, G.D., O'Leary, M.H., Berry, J.A., 1982. On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. Aust. J. Plant Physiol. 9, 121–137.

Giambelluca, T.W., Nullet, M.A. Schroeder, T.A., 1986. Rainfall Atlas of Hawaii. Hawaii Department of Land and Natural Resources, No. R76, Honolulu Hawaii.

Hotchkiss, S.C., 1998. Quaternary Vegetation and Climate of Hawaii. PhD Thesis, University of Minnesota, Saint Paul.

Hotchkiss, S., Juvik, J.O., 1999. A late-quaternary pollen record from Ka'au Crater, O'ahu, Hawai'i. Quat. Res. 52, 115–128.

Hotchkiss, S.C., Vitousek, P.M., Chadwick, O.A., Price, J., 2000. Climate cycles, geomorphological change and the interpretation of soil and ecosystem development. Ecosystems 3, 522–533.

Hsieh, J.C.C., Chadwick, O.A., Kelly, E.F., Savin, S.M., 1998. Oxygen isotopic composition of soil water: quantifying evaporation and transpiration. Geoderma 82, 269–293.

Kelly, E.F., Amundson, R.G., Marino, B.D., DeNiro, M.J., 1991. Stable carbon isotopic composition of carbonate in Holocene grassland soils. Soil Sci. Soc. Am. J. 55, 1651–1658.

Kelly, E.F., Chadwick, O.A., Hilinski, T.E., 1998. The effect of plants on mineral weathering. Biogeochemistry 42, 21–53.

Kennedy, M.J., Chadwick, O.A., Vitousek, P.M., Derry, L.A., Hendricks, D.M., 1998. Changing sources of base cations during ecosystem development, Hawaiian Islands. Geology 26, 1015–1018.

Kirch, P.V., 1994. The Wet and the Dry: Irrigation and Agricultural Intensification in Polynesia. University of Chicago Press, Chicago.

Kurtz, A.C., Derry, L.A., Chadwick, O.A., Alfano, M.J., 2000. Refractory element mobility in volcanic soils. Geology 28, 683–686.

Kurtz, A.C., Derry, L.A., Chadwick, O.A., 2001. Accretion of Asian dust to Hawaiian soils: isotopic, elemental and mineral mass balances. Geochim. Cosmochim. Acta 65, 1971–1983.

Ladefoged, T.N., Graves, M.W., Jennings, R.P., 1996. Dryland agricultural expansion and intensification in Kohala, Hawaii Island. Antiquity 70, 861–880.

McEldowney, H., 1983. A description of major vegetation patterns in the Waimea–Kawaihae region during the early historic period. In: Archaeological Investigations of the Mudlane–Waimea–Kawaihae Road Corridor, Island of Hawai'i. Honolulu, Hawaii, Department of Anthropology, Bernice Pauahi Bishop Museum, pp. 407–448.

McFadden, L.D., Wells, S.G., Gercinovich, M.J., 1987. Influences of eolian and pedogenic processes on the origin and evolution of desert pavements. Geology 15, 504–508.

McLaughlin, J.R., Ryden, J.C., Syers, J.K., 1981. Sorption of inorganic phosphate by iron- and aluminum-containing components. J. Soil Sci. 32, 365–377.

Murakami, G.M., 1983. Analysis of charcoal from archaeological contexts. Archaeological Investigations of the Mudlane–Waimea–Kawaihae Road Corridor, Island of Hawai'i. Honolulu, Hawaii, Department of Anthropology, Bernice Pauahi Bishop Museum, pp. 514–526.

Murphy, P.G., Lugo, A.E., 1986. Ecology of tropical dry forest. Ann. Rev. Ecolog. Syst. 17, 67–88.

Northfeldt, D.W., DeNiro, M.J., Epstein, S., 1981. Hydrogen and carbon isotopic ratios of cellulose nitrate and saponifiable lipid fractions prepared from annual growth rings of California Redwood. Geochim. Cosmochim. Acta 42, 1895–1898.

Parfitt, R.L., 1989. Phosphate reactions with natural allophane, ferrihydrite and goethite. J. Soil Sci. 40, 359–369.

Pearsall, D.M., Trimble, M.K., 1983. Phytolith analysis of soil samples. Archaeological Investigations of the Mudlane–Waimea–Kawaihae Road Corridor, Island of Hawai'i. Honolulu, Hawaii, Department of Anthropology, Bernice Pauahi Bishop Museum, pp. 472–497.

Pearsall, D.M., Trimble, M.K., 1984. Identifying past agricultural activity through soil phytolith analysis: a case study from the Hawaiian Islands. J. of Archaeol. Sci. 11, 119–133.

Pentico, E.D., Tieszen, L.L., 1991. Community and soil organic matter stable carbon isotope ratios: forest–grassland transitions at Wind Cave National Park. Proc. S. Dak. Acad. Sci. 70, 69–83.

Porter, S.C., 1997. Late Pleistocene eolian sediments related to pyroclastic eruptions of Mauna Kea volcano, Hawaii. Quat. Res. 47, 261–276.

Pratt, L.W., Gon, S.M., 1998. Terrestrial Ecosystems, In: Juvik, S.P., Juvik, J.O. (Eds.), Atlas of Hawaii, 3rd edition. University of Hawaii Press, Honolulu.

Rundel, P.W., 1980. The ecological distribution of C-4 and C-3 grasses in the Hawaiian Islands. Oecologia 3, 354–359.

Sanderson, M., 1993. Prevailing Trade Winds: Weather and Climate in Hawaii. University of Hawaii Press, Honolulu.

Schlesinger, W.H., Pilmanis, A.M., 1998. Plant–soil interactions in deserts. Biogeochemistry 42, 169–187.

Schlesinger, W.H., Reynolds, J.F., Cunningham, G.L., Huenneke, L.F., Jarrell, W.M., Virginia, R.A., Whitford, W.G., 1990. Biological feedbacks in global desertification. Science 247, 1043–1048.

Schlesinger, W.H., Raikes, J.A., Harley, A.E., Cross, A.F., 1997. On the spatial pattern of soil nutrients in desert ecosystems. Ecology 77, 364–374.

Selling, O.H., 1948. Studies in Hawaiian Pollen Statistics. Part III. On the Late Quaternary History of the Hawaiian Vegetation. Bernice P. Bishop Museum Special Publication, vol. 39.

Spengler, S.R., Garcia, M.O., 1988. Geochemistry of the Hawi lavas, Kohala Volcano, Hawaii. Contrib. Mineral. Petrol. 99, 90–104.

Stewart, B.W., Capo, R.C., Chadwick, O.A., 2001. Effects of precipitation on weathering rate, base cation provenance and Sr isotope composition in a volcanic soil climosequence, Hawaii. Geochim. Cosmochim. Acta 65, 1087–1099.

Teri, J.A., Stowe, L.G., 1976. Climatic patterns and the distribution of C_4 grasses. Oecologia 23, 1–12.

Torn, M.S., Trumbore, S.E., Chadwick, O.A., Vitousek, P.M., Hendricks, D.M., 1997. Mineral control of soil carbon turnover and storage. Nature 389, 170–173.

Vitousek, P.M., 2004. Nutrient Cycling and Limitation: Hawaii as a Model System. Princeton University Press, Princeton, N.J.

Vitousek, P.M., Field, C.B, Matson, P.A., 1990. Variation in foliar $\delta^{13}C$ in Hawaiian *Metrosideros polymorpha*: a case of internal resistance? Oecologia 84, 362–370.

Vitousek, P.M., Ladefoged, T.N., Kirch, P.V., Hartshorn, A.S., Graves, M.W., Hotchkiss, S.C., Tuljapurkar, S., Chadwick, O.A., 2004. Soils, agriculture and society in precontact Hawaii. Science 304, 1665–1669.

Wells, S.G., Dohorenwend, J.D., McFadden, L.D., Turrin, B.D., 1985. Late Cenozoic landscape evolution on lava flow surfaces of Cima volcanic field, Mojave Desert, California. Geol. Soc. Amer. Bull. 96, 1518–1529.

Wolfe, E.W., Morris, J., 1996. Geologic map of the Island of Hawaii. USGS Map I-2524-A.