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Vegetation changes along gradients of long-term soil development in the Hawaiian montane rainforest zone

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Abstract

The development of the Hawaiian montane rainforest was investigated along a 4.1-million-year soil age gradient at 1200 m elevation under two levels of precipitation, the mesic (c. 2500 mm annual rainfall) vs. wet (> 4000 mm) age gradient. Earlier analyses suggested that soil fertility and foliar nutrient concentrations of common canopy species changed unimodally on the same gradients, with peak values at the 20,000–150,000 yr old sites, and that foliar concentrations were consistently lower under the wet than under the mesic conditions. Our objectives were to assay the influences of soil aging and moisture on forest development using the patterns and rates of species displacements. The canopies at all sites were dominated by *Metrosideros polymorpha.* Mean height and dbh of upper canopy *Metrosideros* trees increased from the youngest site to peak values at the 2100–9000 yr sites, and successively declined to older sites. A detrended correspondence analysis applied to mean species cover values revealed that significant variation among sites occurred only on one axis (axis 1), for both soil-age gradients. Sample scores along axis 1 were perfectly correlated with soil age on the mesic gradient, and significantly correlated on the wet gradient. Higher rainfall appeared to be responsible for the higher rates of species turnover on the wet gradient probably through faster rock weathering and greater leaching of soil elements. We concluded that the changes in species cover values and size of the canopy species was a reflection of the changing pattern of nutrient availability associated with soil aging.

Introduction

Several theoretical models describe changes in soil nutrient availability to plants during pedogenesis over millions of years. For instance, Mueller-Dombois (1986) suggested that both soil nutrient availability and forest biomass in Hawaiian montane ecosystems change in synchrony and unimodally over the course of pedogenesis ($> 1 \times 10^6$ yr on a logarithmic scale) with a peak at c. 1000–3000 yr. Fox *et al.* (1991) presented a general model of tropical soil pedogenesis that, given enough rainfall and drainage, soil fertility increases rapidly as a function of time and weathering intensity before proceeding to a nutrient depletion phase and eventually to an asymptotical decline with elevated soil toxicity. Walker & Syers (1976) emphasized phosphorus transformation in pedogenesis. They consider rock-derived primary mineral phosphorus to be the dominating form of phosphorus in a soil profile at the initiation of pedogenesis. Primary mineral phosphorus is transformed, first into non-occluded phosphorus (i.e. adsorbed to secondary minerals, and largely available), and then increasingly into phosphorus occluded by iron and aluminum hydrous oxides (i.e. biologically unavailable). Organically bound phosphorus increases early, and declines later. One outcome is that organic and inorganic phosphorus availability becomes substantially decreased. Walker *et al.* (1983) provided a vegetation dynamics model which predicts that vegetation on juvenile (fertile) soils has a high potential to

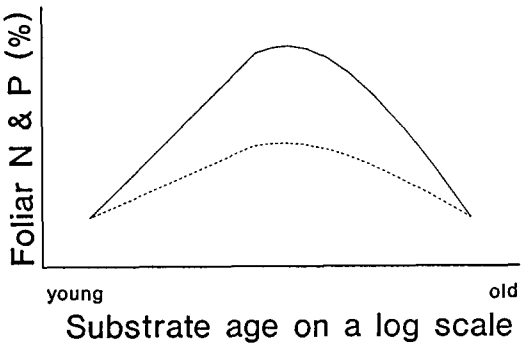

Fig. 1. Patterns in the changes of nitrogen and phosphorus concentrations in *Metrosideros polymorpha* leaves along two soil age gradients which differ from each other in precipitation (after Vitousek *et al.* 1995). Solid line for concentrations on the mesic gradient (c. 2500 mm annual rainfall), and dashed line for those on the wet gradient (> 4000 mm). Depicted patterns are highly schematic and actual data points are scattered along the curves.

recover to its pre-disturbance state after large-area disturbances. As the soils become older and less fertile, vegetation mass becomes irreversibly lower after such disturbances.

Recently, Crews *et al.* (1995) substantiated Walker & Syers' model (1976) with geochemical evidence from a soil age chronosequence in the Hawaiian montane rainforest zone (1200 m asl with 2500 mm annual rainfall). Their results, however, suggested that non-occluded phosphorus occurred indefinitely over the 4.1-m-yr chronosequence. Vitousek *et al.* (1995) studied changes in foliar nutrient concentrations of *Metrosideros polymorpha* Gaud., the dominant rainforest tree, and other common canopy species on the same chronosequence as Crews *et al.* (1995) with two parallel moisture regimes (wet vs. mesic). Vitousek *et al.*'s results, as predicted, demonstrate that concentrations of phosphorus and nitrogen in leaves of *Metrosideros* canopy trees peak at 20,000 to 150,000 yr, and then decline over the course of soil aging for both regimes (see Fig. 1). They also found that concentrations were consistently lower under the wet than under the mesic regime, and suggested that different patterns of leaching and nutrient supply exist between wet and mesic moisture regimes. Thus, the magnitude of variation in foliar concentrations, and probably in soil fertility, was greater under the mesic regime (Fig. 1).

Based on this evidence, we hypothesized: $H_0 1$) that patterns of long-term forest development would be homologous along the wet and mesic gradients, with vegetation on both gradients showing a peak of standing biomass on relatively young soils due to variations in soil nutrient availability; $H_0 2$) that the rate of successional displacement of species (hereafter termed species turnover) would be faster on the wet gradient because soil aging processes are accelerated by higher amounts of rainfall; and $H_0 3$) that species modes would show a stronger tendency toward clumping on the mesic than on the wet gradient because of the higher magnitude of variation (i.e. more heterogeneous) in soil fertility on the mesic gradient.

We studied forest development on the same two parallel long-term soil age gradients (wet vs. mesic rainfall regimes) as Vitousek *et al.* (1995) by testing the above hypotheses. Our gradients also in part overlap Crews *et al.*'s (1995) gradient.

Methods

Study areas

The Hawaiian Islands chain (Fig. 2) is ideal for investigations of long-term ecosystem dynamics because the sequence of the high islands (Hawaii to Kauai) represents a geological and soil age gradient while latitude varies little. The Hawaiian Islands are formed from basaltic lava that has been extruded from a stationary hot spot, which is southeast of the island of Hawaii (Macdonald *et al.* 1983). As the Pacific Plate moves northwestward, the islands are successively carried along and new volcanoes are formed on the deep ocean floor (Macdonald *et al.* 1983). As one proceeds from the youngest (Hawaii) to the oldest island (Kauai), the mountains decrease in height and surface area, and their slopes become more deeply incised (Carlquist 1980).

We selected two parallel, equally long soil age gradients at c. 1200 m asl, which differ from each other only in precipitation; one with c. 2500 mm (mesic) and the other with c. 4000 mm or more (wet) mean annual rainfall (determined based on Giambelluca *et al.* 1986). Hereafter, they are called the mesic and wet gradients. Each gradient consisted of eight sites. Ages, and soil types of the sites are given in Table 1. The ages were determined from the geological maps in Macdonald *et al.* (1983), Stearns (1985), Lockwood *et al.* (1988) and Lockwood (pers. comm.).

All sites are located on windward slopes of the islands facing to moisture-laden trade winds, which occur approximately 65–80% of the time during a normal year (Blumenstock 1961). The mesic gradient is slightly more sheltered than the wet gradient. The mean

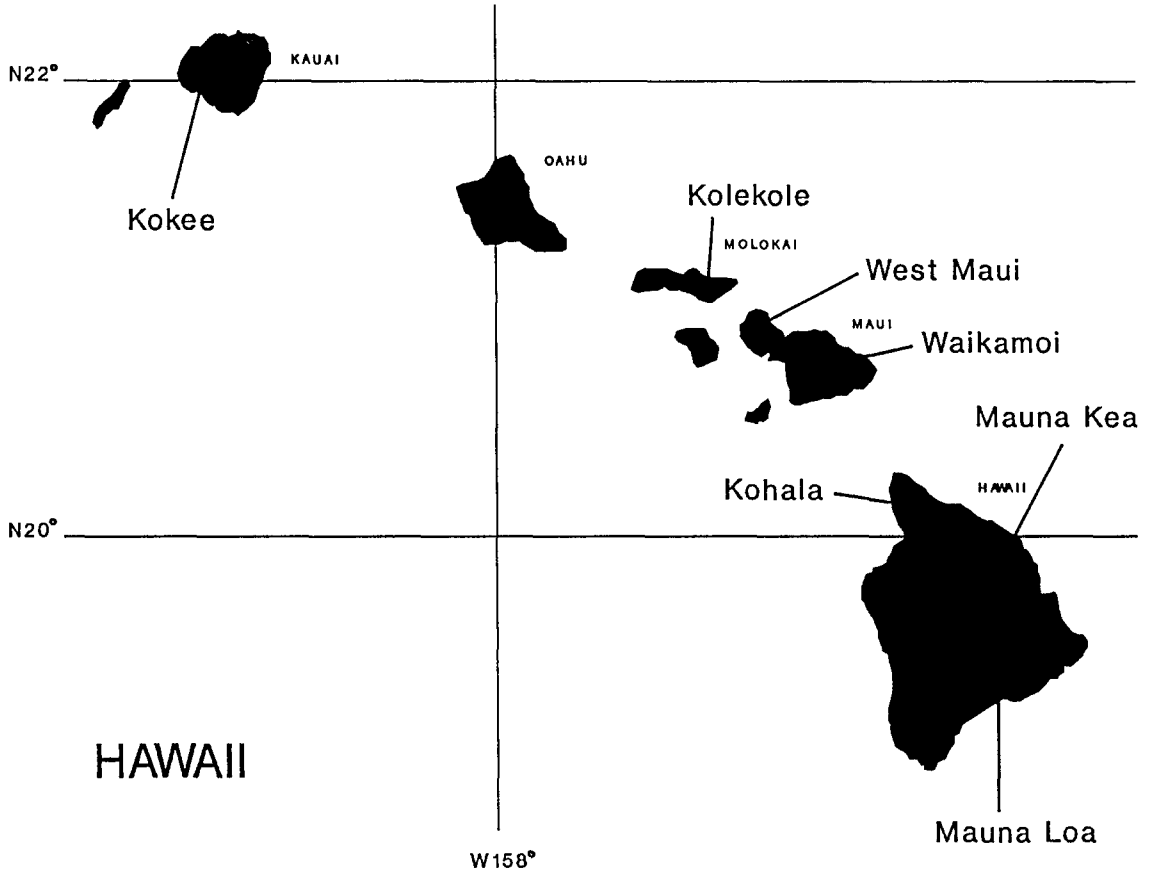

Fig. 2. Locations of study sites.

annual air temperature predicted from the mean temperature lapse rate (0.55 °C per 100 m, Blumenstock 1961) is c. 16 °C at all sites.

All sites are underlain by tephra deposited over lava. The chemical make-up of the substrates is comparable across the gradients, although those ≥ 150,000 yr old (post shield building volcanoes) contain slightly higher mineral phosphorus than the younger substrates (shield building volcanoes) (Macdonald *et al.* 1983; Crews *et al.* 1995). The topography of the sites < 150,000 yr represents gentle slopes of shield volcanoes without dissections. As soil age increases, macro-scale topography is more dissected. We selected the older sites on the meso-scale topography of broad interfluves or gentle slopes, assuming that these represent oldest surfaces.

The floras on both gradients are similar. The major difference which could potentially affect ecosystem processes is the presence of nitrogen fixing *Acacia koa* A. Gray on the mesic gradient. *Acacia koa* is, however, very sparse and we avoided its influences through site selection. As pointed out by Vitousek *et al.* (1995) and Crews *et al.* (1995), oscillations in paleoclimate have obviously changed the rates of pedogenesis and related biological processes in the past. The basis of our comparative analysis is the assumption that the age gradient (Table 1) represents a relative sequence of soil development primarily as a function of the predominating time factor with more-or-less constant weathering intensity (climate) in the past.

Sampling and analyses

We chose stands with closed canopies and no evidence of recent human disturbances. We placed five 20 × 20 m quadrats at each site nearly contiguously along a transect which started from a randomly selected point. In each quadrat, the forest vegetation was stratified into structural layers and all vascular taxa (species, subspecies and varieties) in each layer were inventoried with the Braun–Blanquet cover-abundance scale (Mueller-Dombois & Ellenberg 1974). We measured

Table 1. Description of the study sites on the mesic and wet gradients. Each gradient represents a soil age gradient with controlled climatic conditions. Mean annual rainfall is c. 2500 mm for the mesic gradient, and at least 4000 mm for the wet gradient. All sites are at c. 1200 m asl except for the wet 9000 yr site which is at 1120 m asl. Soil types follow United States Department of Agriculture Soil Conservation Service (1972), where soil subgroups and great groups are indicated. All sites are underlain by tephra over lava.

Site	Age (yr)	Region & island	Soil type
Mesic			
Thurston	300	Mauna Loa, Hawaii	Hydric Dystrandept
Olaa	2100	Mauna Loa, Hawaii	Typic Hydrandept
Laupahoehoe Flow	5000	Mauna Kea, Hawaii	Typic Hydrandept
Laupahoehoe Ash	20,000	Mauna Kea, Hawaii	Typic Hydrandept
Kohala-Hawaii	150,000	Kohala, Hawaii	Typic Placandept
Waikamoi[a]	410,000	Haleakala, Maui	Typic Hydrandept
Kolekole	1,400,000	Kamakou, Molokai	Histic Placaquept
Kokee	4,100,000	Kokee, Kauai	Plinthic Acrudox
Wet			
400 yr	400	Mauna Loa, Hawaii	unknown, histic
1400 yr	1400	Mauna Loa, Hawaii	unknown, histic
5000 yr[b]	5000	Mauna Loa, Hawaii	unknown, histic
9000 yr	9000	Mauna Loa, Hawaii	unknown, histic
Waikamoi	410,000	Haleakala, Maui	Histic Placaquept
West Maui	1,300,000	West Maui, Maui	Histic Placaquept
Kolekole	1,400,000	Kamakou, Molokai	Histic Placaquept
Kokee	4,100,000	Kokee, Kauai	Terric Troposaprist

[a]Not included in Vitousek *et al.* (1995).
[b]Location different from that of Vitousek *et al.* (1995), but with the same age. Their site has deeper ash.

the height and dbh of the five tallest trees of *Metrosideros polymorpha*, the dominant species, in each quadrat. Height and dbh were used as an index of biomass for a first approximation to test $H_0 1$. One-way Analysis of Variance was used to test significant variations in mean height and dbh along the gradients. Actual values of above-ground biomass will be reported elsewhere.

The cover-abundance scales of species were converted into mid-point values and these were used for computing mean species values for each site. This procedure resulted in two data tables consisting of species and sites. A detrended correspondence analysis was applied to the data tables to ordinate sites with DECORANA (Hill 1979). The sequence of sample (site) scores along the axis with the highest eigenvalue was statistically compared with the sequence of substrate ages using Spearman's rank correlation. Sørensen's community coefficients were computed reciprocally among the sites to examine differences in floristic composition. An unweighted pair-group cluster analysis was applied to the resulting similarity matrixes with MVSP Plus 2.0 (Kovach 1990).

Species turnover rates, R(X), at position x on each of the gradients were determined over log-transformed ages based on the following equation (Wilson & Mohler 1986) to test $H_0 2$:

$$R(X) = (1/dX)\sum_i |dY_i| \qquad (1)$$

where Y_i is the abundance of the i-th species at position X. The computation of R(X) was derived from the use of GRADBETA (Wilson & Mohler 1986).

Distribution patterns of species modes were statistically analyzed for randomness to test $H_0 3$. Species modes were determined based on species scores along the ordination axis with the highest eigenvalue for each gradient. The ordination axis was divided into even segments of 10 scores and the number of species modes

in each segment was counted. Frequencies of segments having the number of species modes= 0, 1, 2, ..., r were compared with the expected frequencies by the Poisson distribution using the chi-square goodness-of-fit test. When randomness was rejected, the observed frequencies were compared for clumping patterns with the frequencies expected from the negative binomial model using the chi-square goodness-of-fit test. An ordination by correspondence analysis was used in this analysis to avoid rescaling of axes and randomization of species modes; the extracted axes were tested again for correlation with the age sequence. Species occurring less than 3 times were excluded from this analysis to reduce bias toward clumping.

In addition, species diversity was computed using Simpson's index (D):

$$D = 1/\sum p_i^2 \qquad (2)$$

where p_i=relativized species dominance value of the i-th species. The nomenclature followed Wagner *et al.* (1990) for flowering plants except for *Vaccinium*, and the 1987 version of the unpublished checklist by Wagner & Wagner (unpubl.) for pteridophytes. Species of the genus *Vaccinium* appeared to have distinct morphological variants specific to certain island(s); we classified these variants and used for analyses (see Appendices 1 and 2). Leaf pubescence was the character to key out *Metrosideros* varieties; apparent intermediate forms with caducous hairs were identified as a glabrous variety. However, these forms were identified as a pubescent variety by Vitousek *et al.* (1995), and care should be taken when comparing our results with theirs.

Results

A total of 177 and 168 taxa were sampled from the mesic and wet gradients, respectively. While most canopy and subcanopy species are common to all sites on each gradient, there are a number of herbaceous and low shrub species which are specific to one site (Appendices 1 and 2).

Although the canopies were dominated by *Metrosideros polymorpha* at all sites, there were apparent infra-specific shifts in leaf morphology in this species along each gradient (Appendices 1 and 2). On both gradients, leaf-morphological varieties shifted from predominantly pubescent (*polymorpha*) on the substrates $\leq$ 2100 yr to predominantly glabrous (*glaberrima*). The glabrous variety remained dominant on substrates $\geq$ 5000 yr. Another pubescent variety (*incana*) appeared with low cover values after 1,400,000 yr on the mesic and after 410,000 yr on the wet gradient. Pubescent varieties were, however, not found in the oldest sites (4,100,000 yr) on either gradient.

Table 2. Eigenvalues, and sample scores along the first and second axes defined by DECORANA. DECORANA generated four axes, but the eigenvalues of the third and fourth axes were trivial (< 0.04) for both gradients.

	Ax 1	Ax 2
Mesic gradient		
Thurston	368	40
Olaa	225	40
Laupahoehoe Flow	152	95
Laupahoehoe Ash	126	146
Kohala-Hawi	101	119
Waikamoi	97	0
Kolekole	91	178
Kokee	0	91
Eigenvalue	0.679	0.267
Wet gradient		
400 yr	0	53
1400 yr	4	66
5000 yr	84	93
9000 yr	81	92
Waikamoi	299	61
West Maui	237	0
Kolekole	258	67
Kokee	245	196
Eigenvalue	0.609	0.250

Site clusters produced by the unweighted pair-group cluster analysis were generally correlated with age on both gradients (Fig. 3). Clustering patterns were more distinct on the wet than on the mesic gradient; there were fewer clusters at higher similarities on the wet gradient. Overall cohesiveness was greater on the wet than on the mesic gradient (42.6% similarity at the top rank on the wet vs. 36.5% on the mesic gradient).

Results of the detrended correspondence analysis are shown in Table 2. Only the first axis had a high eigenvalue for both gradients (mesic 0.679, and wet 0.609). The other axes had trivial eigenvalues, suggesting that most species variation among sites occurred only along the first axis for both gradients.

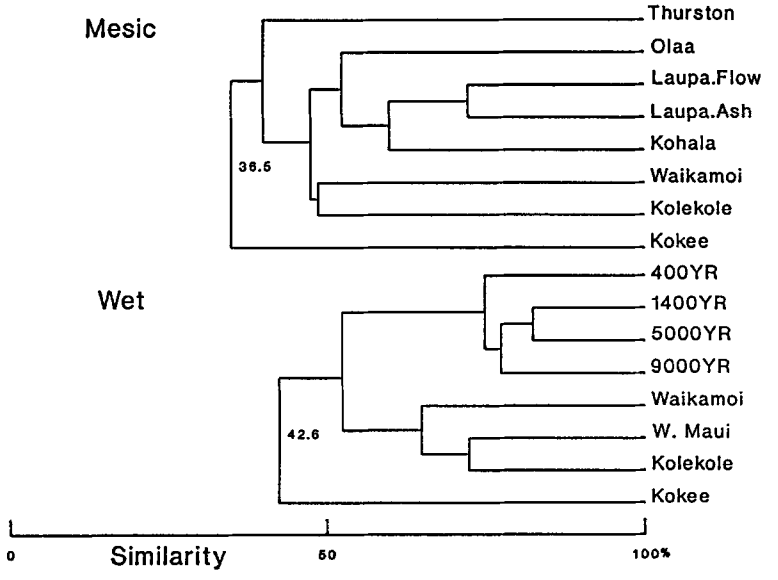

Fig. 3. Site clusters by an unweighted pair-group cluster analysis based on Sørensen's community coefficients.

The sequence of the sample scores along the first axis was correlated with the sequence of the substrate ages for both gradients, and statistical significance was greater on the mesic than on the wet gradient (Spearman's rank correlation; $p < 0.01$ on mesic vs. $p < 0.05$ on wet). Thus, axis 1 was associated with soil age for both gradients.

The differences in both mean height and dbh of *Metrosideros polymorpha* top-canopy trees across soil ages were highly significant ($p < 0.0001$) for both moisture regimes. The mean height and dbh peaked on the younger substrates of both gradients within a few thousand years (between 2100 and 9000 yr) before they successively declined (Fig. 4). The peak mean dbh appeared at an earlier substrate age than that of mean height on both gradients. Mean dbh values were almost consistently higher on the mesic than on the wet gradient for comparable ages. Interestingly, trends in mean height values were reversed in that mean height values were almost consistently lower on the mesic gradient.

Species turnover rates varied between wet and mesic gradients (Fig. 5). The turnover rates on the mesic gradient were nearly constant across all sites, and consistently lower than those of the wet gradient. Because the rates were reported on a logarithmic scale, constant rates actually indicate ever decreasing rates of species turnover on an absolute time scale. The rates on the wet gradient fluctuated with a low peak at the 5000-yr site, and a protruded peak from West Maui (1,300,000 yr) to Kokee (4,100,000 yr).

The distribution pattern of species modes along the age gradient was quite different between the two moisture regimes (Fig. 6). It was significantly random for the wet gradient (for the Poisson model $\chi^2=1.2$, $p > 0.05$, df=3), and significantly clumped for the mesic gradient (for the negative binomial model $\chi^2=1.41$, $p > 0.05$, df=3). The tested ordination axes were significantly correlated with the age sequence in both cases ($p < 0.05$ for wet, $p < 0.01$ for mesic).

The number of taxa per site (0.2 ha) ranged from 34 to 93 on the mesic gradient, and from 57 to 74 on the wet gradient (Table 3). The greatest richness occurred on the island of Maui for both gradients; 93 taxa at Waikamoi (mesic), and 74 at West Maui (wet). There were no recognizable linear trends in richness and species diversity indexes along the gradients.

Discussion

Mean dbh and height of *Metrosideros polymorpha* canopy trees changed somewhat unimodally on the soil age gradients (Fig. 4). These patters are in accordance with the variation of nitrogen and phosphorus concentrations in *Metrosideros* leaves (Vitousek *et al.* 1995) (see Fig. 1). Although we do not have direct evidence, this similarity appears to justify that the size of upper canopy species reflects the availability of soil

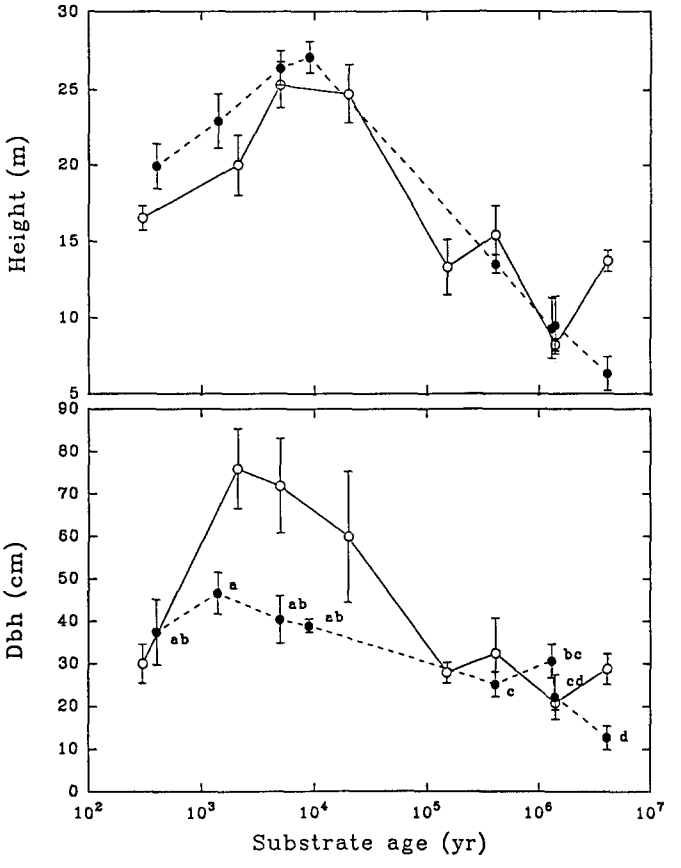

Fig. 4. Changes in mean (± standard deviation) height and dbh of top canopy *Metrosideros* trees (N=5 per plot, 5 plots per site) along each gradient. Hollow circles with solid lines for mesic, and solid circles with dashed lines for wet. Mean dbh values on the wet gradient (where the variation is relatively low) are indicated with results of the Tukey's HSD multiple range test at p=0.05; values which share common letters do not differ significantly.

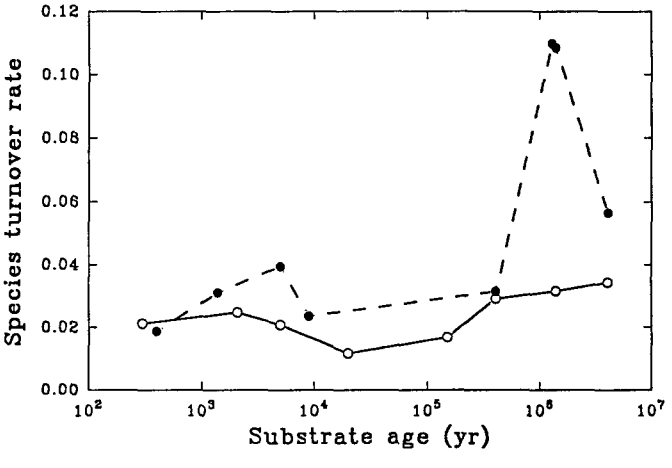

Fig. 5. Species turnover rates along each of the wet and mesic gradients. Hollow circles with a solid line for mesic, and solid circles with a dashed line for wet.

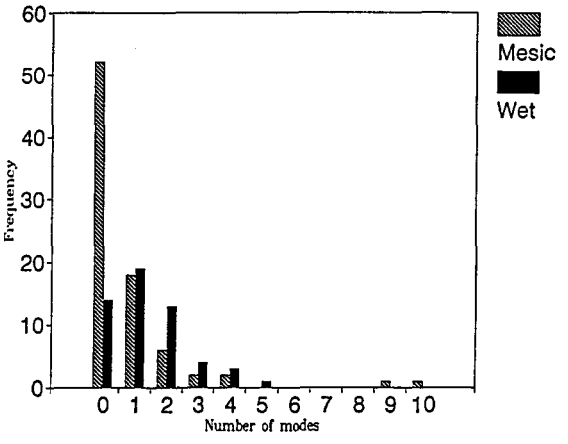

Fig. 6. Frequency distributions of soil-age gradient segments having species mode(s) = 0, 1, 2, 3 – 10. Each gradient was partitioned into 10-score segments. Species occurring less than 3 times were omitted from the computation.

nitrogen and phosphorus. Crews *et al.* (1995) showed that short- and medium-term cycling of nitrogen and phosphorus on the same mesic gradient was low early in ecosystem development; later nitrogen availability increased with age, but it was offset by low phosphorus availability on old soils.

While the peaks of foliar nitrogen and phosphorus in Vitousek *et al.*'s analyses coincided with the peaks of mean dbh and height on the wet gradient, those on the mesic gradient appeared at much older ages than mean dbh and height. Although we assumed that *Metrosideros* trees were fully grown to their maximum stature at all sites, the possibility of human or natural disturbances cannot be ruled out (Vitousek *et al.* 1995).

In comparison to tree sizes, it is more difficult to assay such long-term pedogenesis by species assemblages because evolution (speciation and extinction) becomes another source of variation. As shown by the cluster analysis using species presence/absence in Fig. 3, the mean reciprocal similarity among all sites on the mesic gradient (36.5% at the top rank) was lower than that of the wet gradient (42.6%). This difference suggests that a higher proportion of the mesic flora is site-specific than the wet flora.

In this sense, the results of the detrended correspondence analysis (Table 2) seem more robust in assaying effects of soil aging on vegetation because the analysis is based on quantitative species values. Soil fertility would influence the size and probably biomass of dominating species more strongly than species presence/absence as shown in Fig. 4. Thus, the near perfect correlations between the sample scores and ages seem to support that quantitative species changes and the direction of the changes are determined by soil fertility. Furthermore, it should be noted again that the mesic gradient had higher statistical significance in the correlation between sample scores and age than the wet gradient; these results suggest that quantitative species changes are more strongly regulated by soil aging on the mesic than on the wet gradient.

The high intensity of element leaching on the wet gradient (Vitousek *et al.* 1995) probably rapidly leads to 'a near steady asymptotic state' in top-soil nutrient concentrations on older islands (i.e. Maui to Kauai). Under this condition, other noise factors (e.g. island flora, microclimate, and stochastic events) could have significant effects on species quantity. That species turnover rates are consistently higher on the wet gradient (Fig. 5) may support this suggestion that ecosystem development proceeds faster with increased mean annual rainfall. The sharp peak in turnover rate at the late stage of the wet gradient (Fig. 5) is probably caused by noise factors (e.g. the appearance of another variety of *Metrosideros, incana*).

Another factor that could decrease the correlation between sample scores and age on the wet gradient (Table 2) is a high water table. Where high amounts of rainfall favor the formation of an iron hardpan in subsurface horizons (Kitayama & Mueller-Dombois 1994), water infiltration is retarded and desilication rates are reduced, leading to even severer waterlogging. Consequently, roots are restricted to surface organic horizons away from potentially nutrient richer mineral horizons. Our sites on the mesic gradient are probably more intensively influenced by desilication,

Table 3. Species diversity and evenness expressed with Simpson's index, and species richness (number of taxa per 0.2 ha) across the age gradients. Equation for species diversity is given in the text; evenness is defined as the species diversity divided by the log of the species richness (Kovach 1990).

Mesic	Thurst	Olaa	Laup F	Laup A	Kohala	Waikam	Koleko	Kokee
Diversity	0.728	0.610	0.760	0.813	0.757	0.816	0.628	0.720
Evenness	0.475	0.363	0.426	0.486	0.439	0.414	0.387	0.396
Richness	34	48	61	47	53	93	42	66

Wet	400 yr	1400 yr	5000 yr	9000 yr	Waikam	W.Maui	Koleko	Kokee
Diversity	0.733	0.761	0.752	0.795	0.837	0.898	0.826	0.716
Evenness	0.407	0.425	0.429	0.447	0.458	0.481	0.461	0.392
Richness	63	62	57	60	67	74	62	67

resulting in the formation of abundant iron and aluminum oxide clays (Sherman & Ikawa 1968) with high water-infiltration rates. Plants with restricted roots in older sites of the wet gradient cannot effectively reach to mineral horizons and would have to increasingly depend on nutrients cycled through litterfall.

While species turnover rates were constant across ages on a logarithmic scale, species modes were clumped to certain segments of the mesic gradient, as opposed to the random pattern on the wet gradient (Fig. 6). This implies that the magnitude of variation in soil fertility is greater on the mesic gradient. This higher variability is realized as 'heterogeneous' by species, leading to clumped species modes. In fact, foliar nitrogen and phosphorus concentrations of *Metrosideros* also demonstrated a higher magnitude of variation on the mesic gradient (Vitousek *et al.* 1995) (see Fig. 1).

Species richness is apparently not determined by soil fertility alone. The occurrence of maximum richness on Maui suggests that species richness on a small plot basis (i.e. alpha diversity, *sensu* Whittaker 1972) is determined by regional floristic richness (i.e. richness of each island; gamma diversity, *sensu* Whittaker 1972) in combination with the structure of forest. A taller forest will provide a greater substratum to house obligate epiphytes, and other small shrub and herbaceous species. The sites on Maui have smaller sizes of canopy trees than those on the island of Hawaii, which is a function of soil fertility (Fig. 4). However, Maui's regional floristic richness is highest among the Hawaiian Islands (Merhoff pers. comm.). Kauai's richness and endemism are also very high (Merhoff pers. comm.), but many endemic species are restricted in occurrence and the forests are substantially reduced in size (the 4,100,000 yr site in Fig. 4). Some workers (e.g. Grime 1979; Wilson & Tilman 1991a,b) predicted high species richness under low levels of productivity. Our results are not directly comparable with their hypotheses because regional floristic richness differs among islands.

Conclusions

The results of our vegetation analyses are in accordance with the changing pattern of nutrient availability established by Crews *et al.* (1995) and Vitousek *et al.* (1995) for the long-term soil age gradient. Since the size of canopy trees and the turnover of associated plant species vary as predicted from the established pattern of nutrient availability, we suggest that the underlying resource gradient is a principal cause for the observed vegetation patterns. As the magnitude of variation in resource availability is greater on the mesic gradient, species are more preferentially adapted to certain soil fertility regimes, and result in clumped modes. Rates of forest ecosystem development are faster across all sites on the wet than on the mesic gradient, despite that a higher number of species are site-specific and clumped on the mesic gradient. Intensive rock weathering coupled with greater element leaching promoted by high rainfall is probably responsible for the faster rates of forest development on the wet gradient.

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Appendix 1. Species composition at the sites on the mesic gradient. Means of mid-point cover values.

Species	Thus	Olaa	LauP	LauA	Koha	Waik	Kole	Koke
TREE SPECIES								
Acacia koa				0.54		29		
Cheirodendron platyphyllum kauaiense								0.02
Cheirodendron trigynum	0.02	7.02	19.5	24	17	12.5	19.5	1.54
Ilex anomala	2.02	1.06	0.58	9.04	0.02	0.04		0.06
Metrosideros poly. glaberrima	4.04	16.5	72.5	87.5	77.5	57.5	87.5	47.5
Metrosideros poly. incana							3.52	
Metrosideros poly. polymorpha	87.5	7						
Myrsine lessertiana	0.58	0.58	0.04	0.06	0.04	0.58	0.08	0.02
Myrsine sandwicensis					3.08	0.52		
Psychotria hawaiiensis		0.02	0.02			0.56		
Syzygium sandwicensis								2.02
SHRUB AND TREE-FERN SPECIES								
Broussaisia arguta		0.1		0.02		1.54	0.02	0.06
Cibotium chamissoi		0.02	0.58	24	5	1.54	0.56	0.02
Cibotium glaucum	62.5	87.5	72.5	45.5	19.5	28.5	12.5	
Cibotium hawaiiense				0.02				
Clermontia arborescens waihiae						1.54		
Clermontia parviflora	0.02	0.1	0.08	0.08				
Clermontia sp.					0.02			
Coprosma foliosa						0.02	2.5	
Coprosma kauensis								0.58
Coprosma ochracea	10.6	0.5					0.08	
Coprosma pubens	0.04	1.06			4.52	0.08		
Coprosma rhynchocarpa			1.06	0.08				
Cryptocarya mannii								0.02
Cyrtandra giffardii			0.02					
Dubautia raillardioides								0.5
Elaeocarpus bifidus								1.06
Eurya sandwicensis								0.02
Hedyotis centranthoides	0.06							
Hedyotis hillebrandii			0.04			0.1		
Hedyotis terminalis		0.02				0.58	0.02	0.56
Labordia hirtella			0.02			0.04		
Labordia waialealae								0.02

Appendix 1. Continued.

Species	Thus	Olaa	LauP	LauA	Koha	Waik	Kole	Koke
Myrsine alyxifolia								0.04
Pelea anisata								0.1
Pelea clusiifolia		0.08		4.04	1.06	0.04		0.1
Pelea feddei								0.5
Pelea haleakalae						1.06		
Pelea molokaiensis						0.02		
Pelea puberula								0.02
Pelea volcanica						0.06		
Perrottetia sandwicensis		1.06	0.02					
Pipturus albidus			0.02					
Pittosporum gayanum								0.08
Psychotria mariniana								1.54
Rubus hawaiensis			0.58	0.06	0.04	0.04		
Styphelia tameiameiae						0.08	0.02	0.08
Tetraplasandra oahuensis								0.06
Vaccinium calycinum A	0.08	0.1	0.1	1.54	1.54			
Vaccinium calycinum B						0.04	0.02	
Vaccinium calycinum C						1.06	2.5	0.58
Vaccinium dentatum							0.06	
Wikstroemia oahuensis								0.1
PTERIDOPHYTIC SPECIES								
Adenophorus abietinus								0.02
Adenophorus hymenophylloides						0.02		0.02
Adenophorus pinnatifidus				0.02	1.06	0.1	0.56	
Adenophorus tamariscinus	0.04		0.04	0.04	0.04	0.1	0.58	0.1
Adenophorus tripinnatifidus					0.02	0.08		
Asplenium acuminatum							0.06	
Asplenium contiguum			1.54	5	1.54			
Asplenium insiticium						0.08		
Asplenium lobulatum		0.02	0.1	0.08	0.08	0.1	0.02	
Asplenium macraei			0.02					
Asplenium normale				4.52		0.04		0.08
Asplenium polyodon		0.06	1.06	10	0.06	0.06	0.1	0.08
Asplenium schizophyllum								0.02
Asplenium sphenotomum			0.08	0.08				0.02
Asplenium unilaterale						0.02		
Athyrium microphyllum		0.58	0.06	0.08	0.08	7.5	5	0.06
Athyrium sandwichianum		12	9.02	0.08	19	77.5	0.06	0.56

Appendix 1. Continued.

Species	Thus	Olaa	LauP	LauA	Koha	Waik	Kole	Koke
Callistopteris baldwinii						0.56		
Coniogramme pilosa			0.04			0.08		
Ctenitis rubiginosa			0.08	0.08	0.04	0.1		0.02
Dicranopteris linearis	6.02				0.54	1.02	3.06	0.5
Diplopterygium pinnatum						0.52		
Dryopteris acutidens						3.56		
Dryopteris fusco-atra			0.08	0.04		0.06		
Dryopteris glabra			0.56	4.04	2.02	0.58	1.54	0.08
Dryopteris hawaiiensis					0.02			
Dryopteris insularis						0.04		
Dryopteris nuda			0.02					
Dryopteris sandwicensis						0.5		
Dryopteris unidentata		0.02						
Dryopteris wallichiana	0.02		21	13.5	1.04	0.08	0.08	0.04
Elaphoglossum alatum					0.1	0.08		43
Elaphoglossum crassifolium	0.02				0.02	0.08		0.1
Elaphoglossum hirtum	0.02	0.06	0.1	0.02	0.1	0.1	1.06	0.58
Elaphoglossum wawrae		0.02				0.06		0.58
Grammitis hookeri	0.02	0.08	0.1	0.04		0.04	0.04	
Grammitis tenella	0.06	0.08	0.02		1.54	0.1	0.08	0.1
Huperzia phyllanthum					0.02			
Huperzia serratum			0.02					
Hypolepis punctata						0.02	0.5	
Lycopodium cernuum	0.54							0.5
Marattia douglasii						0.06		
Mecodium recurvum	0.02	0.08	0.58	0.04	1.54	1.54		0.08
Microlepia strigosa			0.08	0.08	0.06			0.02
Nephrolepis cordifolia					0.04		0.06	0.04
Nephrolepis exaltata								10.5
Odontosoria chinensis					0.02			
Ophioglossum pendulum					0.02			
Pleopeltis thunbergiana			0.1	0.06	0.1	0.04	0.1	0.1
Polypodium pellucidum		0.04	0.02		0.06	0.08	0.02	
Psilotum complanatum		0.06	0.06	0.02	0.06	0.04	0.1	
Psilotum nudum		0.02	0.04					0.06
Pteris excelsa			0.04			0.04		
Pteris irregularis						0.02		

Appendix 1. Continued.

Species	Thus	Olaa	LauP	LauA	Koha	Waik	Kole	Koke
Sadleria cyatheoides							0.02	
Sadleria pallida	0.02	0.58		0.02		4.04		
Sadleria souleyetiana	0.04							
Sphaerocionium lanceolatum	0.1	0.06	0.04	0.08	1.06	0.56		0.58
Sphaerocionium obtusum	0.02							
Sticherus owhyhensis							3.06	1
Thelypteris cyatheoides							0.02	
Thelypteris globulifera							0.56	
Thelypteris keraudreniana			0.02					
Thelypteris sandwicensis	5	0.06			0.04			
Vandenboschia davallioides		0.02	2.02	0.08	0.52	1.06		
Xiphopteris saffordii					0.04	0.1	0.02	0.04
LOW SHRUB SPECIES								
Cyanea mceldowneyi						0.02		
Cyanea pilosa longipedunculata		0.02						
Cyrtandra lydgatei						0.04		
Cyrtandra lysiosepala		0.02						
Cyrtandra platyphylla		1.54				0.1		
LIANA SPECIES								
Alyxia oliviformis			0.02	1.06		0.06		2.02
Embelia pacifica						0.02		
Freycinetia arborea		0.04	0.02	0.04		0.1		
Phyllostegia ambigua						0.02		
Smilax melastomifolia						0.04		0.1
Stenogyne calaminthoides		0.02						
Stenogyne kamehamehae						0.02		
Stenogyne macrantha			0.04					
Stenogyne purpurea								0.56
HERBACEOUS SPECIES								
Astelia argyrocoma								0.08
Astelia menziesiana	0.54	0.58	0.1	0.1	0.02	0.1	0.08	
Carex alligata					0.02	0.54		0.08
Dianella sandwicensis								0.1
Gahnia vitiensis kauaiensis								0.04
Isachne distichophylla	0.08							
Luzula hawaiiensis								0.02
Machaerina angustifolia	0.06							
Nertera granadensis						0.58	2.5	

Appendix 1. Continued.

Species	Thus	Olaa	LauP	LauA	Koha	Waik	Kole	Koke
Peperomia cookiana			0.08	0.56	0.04	0.04	0.02	
Peperomia eekana						0.04		
Peperomia expallescens						0.06		
Peperomia hesperomannii								2.02
Peperomia hirtipetiola						0.56		
Peperomia hypoleuca		0.1	0.04	1.5	0.58			
Peperomia macraeana		0.04				0.08		
Peperomia membranacea			0.06					
Uncinia uncinata	0.04	0.1	0.06			0.52		
PARASITIC SPECIES								
Korthalsella complanata						0.06		
Korthalsella cylindrica								0.04
Korthalsella latissima								0.02
ALIEN SPECIES								
Ageratina adenophora						0.04		
Anthoxanthum odoratum							0.04	
Brassicaceae sp.			0.04					
Commelina diffusa						0.02		
Deparia petersenii			0.08	0.54	0.04			
Digitaria sp.					0.08		0.56	
Ehrharta stipoides	0.02		9.52	1.04				
Erechtites valerianifolia				0.02				
Hedychium gardnerianum	57.5	0.1			0.06			1.54
Juncus effusus			2.02					
Lapsana communis		0.02						
Ligustrum vulgare		0.02						
Myrica faya	0.02							
Paspalum conjugatum					1			
Passiflora mollissima			1.54	3.52				
Phaius tankarvilleae	0.06	0.04						
Polygonum glabrum		0.02	1.06	1.02	3.56			
Prunella vulgaris						0.02		
Psidium cattleianum	1.06	0.04	0.02		0.58		0.04	
Rubus argutus	0.06					0.02		0.1
Rubus ellipticus		0.04						
Rubus rosifolius			0.06	0.06	3.52	0.02	0.04	
Veronica serpyllifolia					0.02			

Appendix 2. Species composition at the sites on the wet gradient. Means of mid-point cover values.

Species	400	1400	5000	9000	Waik	M.Ma	Kole	Koke
TREE SPECIES								
Cheirodendron platyphyllum kauaiense								4.52
Cheirodendron trigynum	2.5	5	12.5	7.5	12.5	24	14.5	0.1
Ilex anomala	1.06	4.04	1.04	4.52	0.06	0.08	0.08	0.06
Metrosideros poly. glaberrima	9.52	14.5	87.5	72.5	35.5	53	67.5	77.5
Metrosideros poly. incana					9.5	25.5	10.5	
Metrosideros poly. polymorpha	33	42.5						
Myrsine lessertiana	0.58	1.06	0.1	0.58	1.06	1.06	0.1	0.06
Myrsine sandwicensis	0.1	0.06		0.08	4.52	9.04		
Psychotria hawaiiensis	0.08	1.54	2.5	2.5	0.02	0.52	0.06	
Syzygium sandwicensis								0.08
Xylosma hawaiiense				0.02				
SHRUB AND TREE-FERN SPECIES								
Broussaisia arguta	2.02	1.54	7.5	10	1.54	9.52	1.54	2.02
Cibotium chamissoi	0.1	1.06	0.58	0.58	9.52	0.08	15	7.5
Cibotium glaucum	87.5	82.5	87.5	72.5	4.04	0.08	0.1	0.54
Cibotium hawaiiense			0.08					
Clermontia arborescens waihiae					0.1	0.04	0.02	
Clermontia fauriei								3.56
Clermontia grandiflora munroi						0.06		
Clermontia micrantha						0.02		
Clermontia montis-loa	0.1	0.1		0.08				
Clermontia parviflora	0.04		0.06					
Coprosma elliptica								0.58
Coprosma kauensis								0.06
Coprosma ochracea	4.04	0.54				0.08	0.58	
Coprosma pubens	0.58	1.06	1.06	0.58	0.04			
Cyanea macrostegia						0.58		
Cyrtandra grayana						0.08	0.02	
Cyrtandra procera							3.06	
Cyrtandra giffardii			0.06					
Cyrtandra longifolia								0.06
Dubautia laxa hirsuta								0.08
Dubautia laxa laxa						4.04		
Dubautia paleata								1.06
Dubautia raillardioides								0.02
Elaeocarpus bifidus								0.02
Eurya sandwicensis	0.02							

Appendix 2. Continued.

Species	400	1400	5000	9000	Waik	M.Ma	Kole	Koke
Hedyotis centranthoides	0.02							
Hedyotis terminalis	2.5	1.54	1.54	0.1	0.58	0.08	2.02	0.1
Labordia waialealae								0.1
Labordia waiolani							0.1	
Myrsine wawraea								0.1
Nothocestrum longifolium		0.02	0.08	0.02				
Pelea clusiifolia	0.1	0.1	0.02	0.1		12.5	0.08	2.02
Pelea feddei								0.08
Pelea haleakalae					4.04			
Pelea orbicularis					0.54	1.02		
Pelea parvifolia							0.06	
Pelea pseudoanisata	0.06	0.06		0.1				
Pelea volcanica					0.02			
Perrottetia sandwicensis			0.08	0.04				
Pipturus albidus		0.02		0.04				
Pittosporum gayanum								0.06
Pittosporum glabrum						0.52	0.5	
Rubus hawaiensis	0.02		0.02		0.02			
Scaevola glabra								6.52
Styphelia tameiameiae	0.06				0.1	0.04	0.04	0.1
Tetraplasandra oahuensis	3			0.5	0.02	0.02		
Trematolobelia macrostachys						0.02		
Vaccinium calycinum A	0.1	0.1	0.1	0.1				
Vaccinium calycinum B					0.56	1.06	0.06	
Vaccinium calycinum C					5	1.54	0.58	1.06
Vaccinium dentatum								0.02
Wikstroemia oahuensis oahuensis					0.54	0.04	0.02	0.02
Wikstroemia sandwicensis		0.02						
PTERIDOPHYTIC SPECIES								
Adenophorus abietinus								0.04
Adenophorus hymenophylloides	0.04	0.02	0.02	0.02	0.02	0.02		0.08
Adenophorus montanus					0.08	1		
Adenophorus pinnatifidus	0.02			0.06	0.06	0.06	0.04	
Adenophorus tamariscinus	0.1	0.1	0.1	1.54	0.1	0.1	0.08	0.08
Adenophorus tripinnatifidus	0.02	0.04			0.54		4.04	0.04
Asplenium acuminatum						0.06	0.52	
Asplenium contiguum		0.04						
Asplenium lobulatum		0.06	0.08	0.1	0.02	0.02		

Appendix 2. Continued.

Species	400	1400	5000	9000	Waik	M.Ma	Kole	Koke
Asplenium polyodon			0.04		0.04	0.56	0.06	0.02
Asplenium sphenotomum								0.02
Athyrium microphyllum	0.1	1.54	0.1	0.1	1.54	7.5	33	4.04
Athyrium sandwichianum	0.04	4.52	28.5	33	3.02	3.04	0.5	0.02
Callistopteris baldwinii	0.04	0.1	0.1	0.1		0.04	0.04	
Cibotium glau x *chami*								3
Coniogramme pilosa	0.04	0.58	0.58	0.1				
Ctenitis rubiginosa						3.5	0.06	
Dicranopteris linearis	3.02				1.02	0.04		
Diplopterygium pinnatum					0.5	6.02		
Dryopteris acutidens			6.54			0.58	0.56	
Dryopteris fusco-atra						0.04		
Dryopteris glabra		0.02		0.02	0.54	0.58	4.52	2.5
Dryopteris nuda					3.52			
Dryopteris sandwicensis						0.02		
Dryopteris wallichiana	0.02				0.1	0.04	0.04	
Elaphoglossum alatum	0.06	0.04	0.1	0.1	0.56	7.02	19.5	7.58
Elaphoglossum crassifolium							0.04	0.04
Elaphoglossum hirtum	0.06	0.04	0.02	0.02	0.08	0.1	1.54	0.06
Elaphoglossum wawrae					0.58	0.1	0.58	0.04
Grammitis baldwinii								0.04
Grammitis hookeri	0.1	0.1	0.04	0.08	0.04	0.06	0.1	
Grammitis tenella	0.02	0.02	0.1	0.06	0.1	0.04	0.1	0.04
Huperzia serrata				0.02				
Hypolepis punctata					0.02		0.02	
Lycopodium cernuum					0.04			
Lycopodium venustulum						6.5	0.02	
Marattia douglasii	0.02	0.06	0.02	0.08		0.04	0.02	
Mecodium recurvum	0.1	0.58	0.1	2.02	3.56	0.08	5	1
Microlepia strigosa		0.02	0.08	0.08				
Nephrolepis cordifolia		0.02	0.04			0.02	0.02	0.06
Ophioglossum pendulum			0.02	0.06				
Pleopeltis thunbergiana				0.02		0.06	0.06	0.02
Polypodium pellucidum	0.02	0.02	0.04		0.08	0.08	0.08	
Psilotum complanatum	0.08	0.1	0.1	0.08				
Psilotum nudum	0.02							
Pteris excelsa		0.02	0.02	0.02				
Pteris irregularis			0.02					
Sadleria cyatheoides								0.02

Appendix 2. Continued.

Species	400	1400	5000	9000	Waik	M.Ma	Kole	Koke
Sadleria pallida	19.5	7.5	0.06	0.56	0.56	19	0.04	0.02
Sadleria pall. x *soul.*		0.02						
Schizaea robusta								0.08
Sphaerocionium lanceolatum	0.1	0.1	0.1	2.5	3.56	1.54	0.08	2.02
Sphaerocionium obtusum							0.02	
Sticherus owhyhensis	0.02				0.04	0.06		
Thelypteris cyatheoides		0.02	0.02					
Thelypteris globulifera		0.02						
Thelypteris keraudreniana		0.06						
Thelypteris sandwicensis	7.5	15	12.5	19.5		0.06		
Vandenboschia davallioides			0.58	0.06				
Xiphopteris saffordii	0.04	0.08		0.04	0.1		0.02	0.08
LOW SHRUB SPECIES								
Cyanea degeneriana	0.1	0.08	0.06	0.1				
Cyanea kunthiana						0.04		
Cyanea pilosa longipedunculata	0.1	0.08	0.02	0.1				
Cyrtandra lysiosepala	0.08	0.02	0.58	1.06				
Cyrtandra paludosa	0.06	0.1		0.58				
Cyrtandra platyphylla	1.54	0.58	0.58	0.1	0.06	0.02		
Labordia hedyosmifolia	1.54	0.58	0.04	0.08		1.54	0.54	
Labordia venosa					0.56			
Viola chamissoniana robusta							0.58	
Viola wailenalenae								0.1
LIANA SPECIES								
Alyxia oliviformis	0.1	0.08	0.1	0.58	0.54	0.02		0.02
Embelia pacifica						0.04		
Freycinetia arborea	0.06	0.58	2.02	2.02	0.06	0.06	0.1	
Smilax melastomifolia	0.04		0.06	0.06	0.06		0.04	0.1
Stenogyne calaminthoides	0.06	0.08	0.1	0.58				
Stenogyne kamehamehae						0.06		
Stenogyne purpurea								0.06
Stenogyne spA					0.02			
HERBACEOUS SPECIES								
Astelia argyrocoma								1.52
Astelia menziesiana	0.58	0.1	0.58	1.06	1.06	1.06	2.02	0.02
Carex alligata					60.5	3.06	0.04	0.1

Appendix 2. Continued.

Species	400	1400	5000	9000	Waik	M.Ma	Kole	Koke
Deschampsia nubigena							0.02	
Dianella sandwicensis								0.58
Gahnia vitiensis kauaiensis								0.06
Isachne distichophylla	0.02							
Liparis hawaiensis					0.06	0.02		
Machaerina angustifolia							0.02	0.02
Nertera granadensis					0.58	4.52	0.56	2.5
Peperomia eekana						4.52		
Peperomia expallescens					1.54		2.02	
Peperomia hesperomannii								14.5
Peperomia hirtipetiola					0.04			
Peperomia hypoleuca	1.54	2.5	0.58	2.5				
Peperomia macraeana					0.1	0.58	0.1	
Rhynchospora rugosa lavarum								1.06
Uncinia uncinata	1.54	1.54	0.04	0.04		0.08		
Viola kauaensis								0.08
PARASITIC SPECIES								
Korthalsella complanata					0.04			
Korthalsella latissima								0.04
ALIEN SPECIES								
Erechtites valerianifolia					0.54			
Juncus planifolius					3.54			
Phaius tankarvilleae	0.06							
Rubus argutus					0.02			
Rubus rosifolius	0.02	0.02		0.02	0.04			