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VEGETATION SUCCESSION (1967-89) ON FIVE RECENT MONTANE LAVA FLOWS, MAUNA LOA, HAWAII

Summary: Vegetation succession on 4 recent (1852-1942) montane lava flows on Mauna Loa, Hawaii, was remeasured 22 years after the first measurement in 1967. Colonisation patterns of vascular plant species were observed on a new lava flow (1984) which overwhelmed part of the earlier studied 1852 flow. An influx of adventive species, positively correlated with flow age, was noted at the remeasured sites; most were herbs and grasses that do not appear to interfere with the succession to *Metrosideros*-dominated forest. Some indigenous species important in older forest, e.g., *Cibotium glaucum*, had apparently colonised all four remeasured flows regardless of flow age. Densities and total basal area of *Metrosideros polymorpha* increased on all flows, but a closed-canopy forest had not yet developed. Vascular plant aggregations comprising a mixture of adventive and indigenous species were found on the 1984 flow associated with soil or logs of the overwhelmed forest. This phenomenon may allow rare individual *Metrosideros* trees to be in place on a new flow within 10 years of its formation. A closed-canopy, self-thinned *Metrosideros* forest can develop within 400 years but dieback of colonising *Metrosideros* individuals and/or invasion of adventive species capable of altering ecosystem processes can delay this process.

Keywords: vegetation; lava; primary succession; *Metrosideros polymorpha*; Hawaii**.**

Introduction

Atkinson (1969, 1970) and more recently Drake and Mueller-Dombois (1993) and Kitayama *et al.* (1995) have used the chronosequence approach to predict *Metrosideros polymorpha*[1] forest succession on recent lava flows in the montane zone (*sensu* Gagne and Cuddihy 1990) on the eastern slopes of the Hawaiian volcano Mauna Loa. Atkinson inferred that within 400 years, on both aa and pahoehoe lava, a closed-canopy forest dominated by *M. polymorpha* developed following self-thinning, with an understorey of shade-tolerant species, especially treeferns (*Cibotium* spp.). Drake and Mueller-Dombois showed for aa lava that after 3000 years a *Metrosideros-Cibotium* forest is present in which other species participate in the succession but generally contribute little to forest structure, and do not displace the *Metrosideros-Cibotium* forest on well drained, moist sites.

The chronosequence approach, often used because it allows predictions over longer time spans than are afforded by direct assessments, is, however, limited in that its validity depends on all sites having identical edaphic, climatic, and microclimatic conditions and similar histories of environment and vegetation succession (Miles 1979). This paper, which mainly uses the direct assessment approach to investigate change over 22 years on 4 montane lava flows erupted between 1852 and 1942, therefore aims to provide information complementary to the previous chronosequence studies. It is based on remeasurement of sites first described by Atkinson (1969). In particular, arrival time of key later successional species e.g., *Cibotium* and the development of a self-thinned, closed-canopy forest are examined. In the intervening years a new lava flow (1984) overwhelmed part of the earlier studied 1852 flow, and this was also sampled to determine colonisation patterns, bringing to 5 the total number of flows studied.

Study area

The sites were located between 1035 m and 1280 m above sea level on basalt lavas of the eastern slopes of Mauna Loa (Fig. 1). Rainfall at these altitudes is approximately 4000 mm/yr (Giambelluca *et al.* 1986), and mean monthly temperature ranges from 15.5°C in January to 18.3°C in August (State of Hawaii 1970). Lava ages at the time of survey (January 1989) ranged from 5 to 137 years (United States Department of the Interior Geological Survey

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[1]. Nomenclature follows Wagner, Herbst and Sohmer (1990) and Valier (1995), except that some taxa reduced to synonyms in the first-mentioned publication are retained to prevent loss of potentially useful ecological information.

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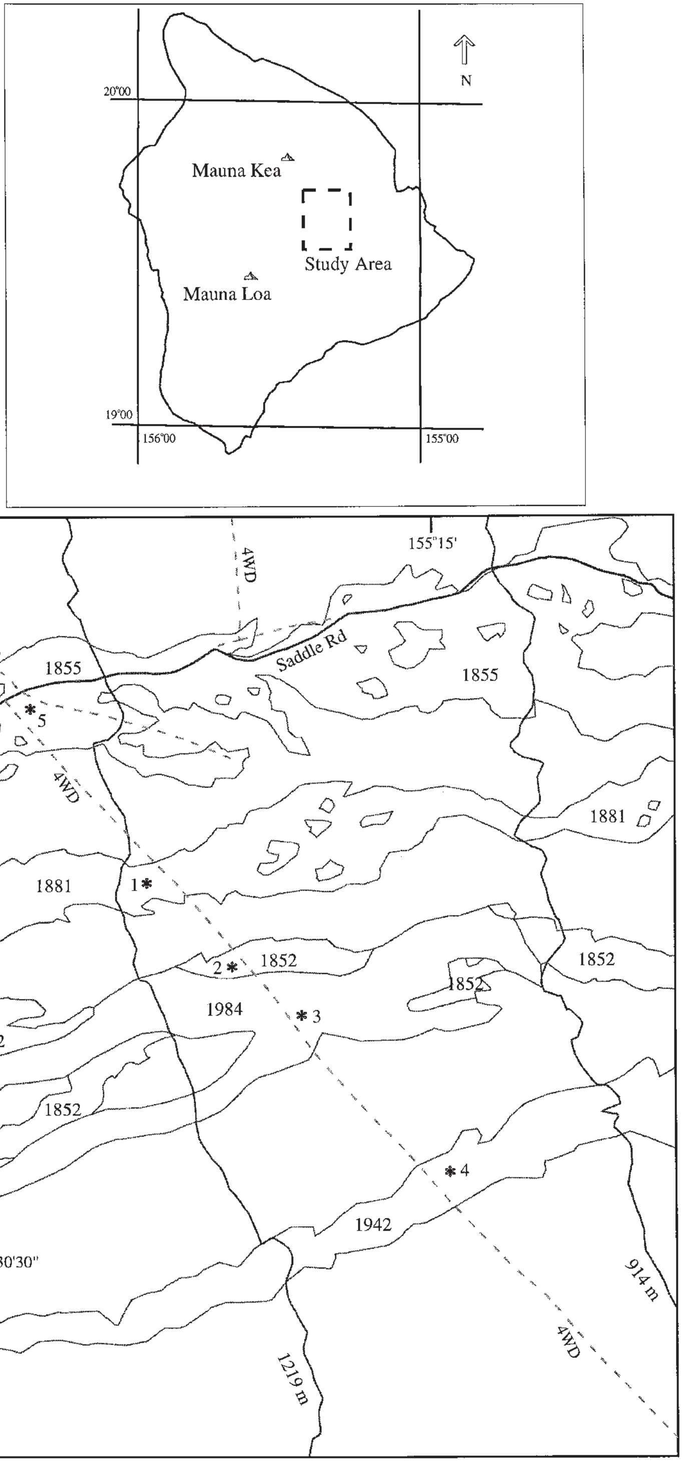

Figure 1: *Location of study sites on Mauna Loa, Hawaii.*

1986); three flows were of the aa type and two were of the pahoehoe type. Pahoehoe lava is characterised by smooth, billowy or ropy surfaces, whereas aa has a very rough spiny or rubbly surface (MacDonald *et al*. 1986). Soil development was minimal and there were no deposits of volcanic ash; plants rooted directly on lava albeit in cracks and crevices on pahoehoe and between particles or in pores of aa.

Methods

The methods used mainly followed those of Atkinson (1969, 1970) and Atkinson and Swindale (1974). An exact re-measurement of plots was not possible as they were not originally designed for this approach (I.A.E. Atkinson, pers. comm.). However, the site details provided by Atkinson and Atkinson and Swindale *loc. cit.* were carefully followed so that the measurements came from the same locality. A 50 m x 50 m plot was located at least 50 m from the edge of flows in order to avoid any edge effects. Within this all vascular plant species were recorded. Two non-vascular species, *Racomitrium lanuginosum* and *Stereocaulon vulcani*, were also recorded because they were easily identifiable and were an important component of the vegetation.

Canopy cover was assessed using a point intercept method. The number of points varied according to the stature and total cover of the vegetation. In most plots 150 points were used on a 30 m transect located in the plot centre, i.e., one point every 20 cm. However, in some plots this was increased to as many as 300 points to obtain a more adequate sample determined by lack of significant variation (5%) between running means as recommended by Mueller-Dombois and Ellenberg (1974).

Table 1: *Species cover (%) on five recent lava flows on Mauna Loa, Hawaii, 1989.*

	Plot number				
	3	4	1	5	2
Eruption date (age of flow, yr)	1984 (5)	1942 (47)	1881 (108)	1855 (134)	1852 (137)
Altitude (m)	1127	1042	1203	1264	1191
Lava type	Aa	Aa	Pah	Pah	Aa
Cover					
Bare lava	25.0	4.0	6.7	2.0	0
Litter	0	4.7	10.7	18.0	4.7
Lichens, mosses and liverworts					
Stereocaulon vulcani	48.0	20.0	+	0	+
Other lichens	0	0	1.3	4.0	0.7
Racomitrium lanuginosum	27.0	10.7	+	0	+
Other mosses	0	2.0	0.7	+	6.0
Liverworts	0	1.3	+	+	+
Ferns and fern allies					
Lycopodium cernuum	0	16.0	7.3	7.3	1.3
Dicranopteris linearis	0	7.3	18.0	14.7	21.3
Nephrolepis exaltata	0	2.0	0	0	+
Polypodium pellucidum	0	0.7	+	+	+
Cibotium glaucum	0	1.3	+	+	1.3
Sadleria cyatheoides	0	+	+	+	10.7
Grasses, sedges and orchids					
Andropogon virginicus	0	2.7	1.3	+	1.3
Arundina graminifolia	0	4.0	1.3	+	+
Machaerina angustifolia	0	4.0	30.7	28.0	4.0
Shrubs and trees					
Dubautia scabra	0	7.3	+	+	0.7
Metrosideros polymorpha	0	8.6	19.3	26.0	37.3
Vaccinium calycinum	0	2.0	+	+	4.7
Hedyotis centranthoides	0	0.7	0	+	+
Coprosma ernodeoides	0	0	+	+	1.3
Styphelia tameiameiae	0	0	2.7	+	4.7

Metrosideros polymorpha population structure was assessed in plots of variable area. The minimum area used was 30 m x 2 m where 20 or more canopy individuals >1 m tall were encountered. If insufficient canopy individuals were encountered, the plot size was increased until 20 individuals had been measured or, in low-density populations, lack of significant variation (5%) between running mean densities from a further sub-plot suggested that the sample was adequate. The largest plot was 400 m^2. For *Metrosideros* individuals > 1.5 m tall, height was estimated and diameter at breast height (d.b.h.) was measured. For those 1.0 - 1.5 m tall, d.b.h. was measured half way up the stem. Individuals less than 1 m tall were tallied in two height classes <50 cm and 50 cm up to 1 m.

For the study of colonisation patterns of vascular species on the 1984 aa flow the species composition, size, and substrate type(s) of 15 patches of vegetation were recorded.

Results

Species cover in 1989

Atkinson (1969) did not provide individual species cover data so no temporal comparison of these is possible. However, the 1989 point cover composition of the 5 flows is useful as a coarse chronosequence and to illustrate differences between lava types (Table 1). The general pattern was for a dominance of *Stereocaulon* and *Racomitrium* on the 2 youngest flows and for an increasing cover of *Metrosideros* with increasing age of flow. *Lycopodium cernuum* and *Dicranopteris linearis* are important on the 47 year and older flows, regardless of lava type. *Machaerina angustifolia* is also important on the 47 year and older flows, but is more abundant on pahoehoe lava flows than on aa flows. Beyond these obvious differences the sampling design does not permit detailed comparison of succession on pahoehoe versus aa lava flows.

Change in species presence over 22 years

Species lists compiled for the flows in 1967 and 1989 are shown in Table 2. For all flows an increase in the total number of species was recorded, ranging from 6 (40%) on the two youngest to 18 (128%) on the oldest. Of the 18 new records on the 1852 flow, 12 (66%) were adventive (introduced) herbs or grasses and 6 (33%) were indigenous. Three species were new records for all four flows: the adventive grass *Andropogon virginicus*, the adventive orchid *Arundina graminifolia* and the indigenous tree fern *Cibotium glaucum*. *Cheirodendron trigynum* was recorded for the first time on the two oldest flows but had apparently been lost from the 1881 flow. The general trend for an increase in species, especially an influx of adventives, over two decades is unlikely to reflect sampling differences. In particular, the adventive grass *Andropogon virginicus*, not recorded at these sites by Atkinson (1969), was found with percentage point cover values ranging from <1% to 2.7%, and it is unlikely that it would have been overlooked if present then.

Changes in *Metrosideros polymorpha* populations over 22 years

Densities of live canopy *Metrosideros* >1 m tall increased on all flows ranging from 170% on the 1881 flow to slightly more than 300% on the 1942

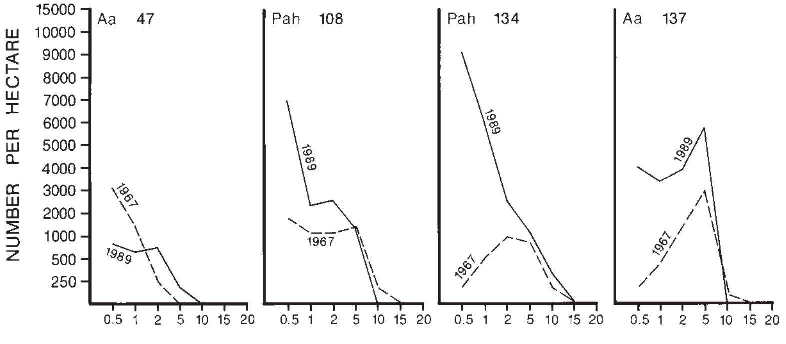

Figure 2: *Height class structure of* Metrosideros polymorpha *(1967 versus 1989) on four lava flows (1852-1942) on Mauna Loa, Hawaii.*

Table 2: *Species presence in 1967 vs. 1989 on four lava flows on Mauna Loa, Hawaii. Data for 1967 are from Atkinson (1969). * = adventive species*

Year of eruption		1942		1881		1855		1852	
Flow age (yrs to 1989)		47		108		134		137	
Year of census		1967	1989	1967	1989	1967	1989	1967	1989
Psilotum nudum	fern	+	+	-	-	-	-	-	-
Racomitrium lanuginosum	moss	+	+	+	+	-	-	-	+
Metrosideros polymorpha	tree	+	+	+	+	+	+	+	+
Machaerina angustifolia	sedge	+	+	+	+	+	+	+	+
Sadleria cyatheoides	fern	+	+	+	+	+	+	+	+
Lycopodium cernuum	fern ally	+	+	+	+	+	+	+	+
Stereocaulon vulcani	lichen	+	+	+	+	+	-	+	+
Vaccinium calycinum	shrub	+	+	+	+	+	+	-	+
Vaccinium reticulatum	shrub	+	+	-	+	+	+	+	+
Dicranopteris linearis	fern	-	+	+	+	+	+	+	+
Coprosma menziesii	shrub	-	-	-	-	+	+	+	+
Hedyotis centranthoides	shrub	+	+	-	+	+	-	+	+
Nephrolepis exaltata	fern	+	+	+	-	+	-	+	+
Styphelia tameiameiae	shrub	-	-	+	+	-	+	+	+
Coprosma ernodeoides	shrub	-	-	+	+	-	+	+	+
Polypodium pellucidum	fern	-	+	-	+	+	+	-	+
Dubautia scabra	shrub	+	+	-	+	-	+	-	+
*Andropogon virginicus**	grass	-	+	-	+	-	+	-	+
*Arundina graminifolia**	orchid	-	+	-	+	-	+	-	+
Cibotium glaucum	fern	-	+	-	+	-	+	-	+
Cheirodendron trigynum	shrub	-	-	+	-	-	+	-	+
Asplenium sp.	fern	+	-	-	-	-	-	-	-
Epilobium cinereum	herb	+	-	-	-	-	-	-	+
Pityrogramma calomelanus	fern	-	+	-	-	-	-	-	+
*Spathoglottis plicata**	orchid	-	+	-	-	-	-	-	+
Sphenomeris chinensis	fern	+	-	-	+	-	-	-	+
Vaccinium pahalae	shrub	-	+	-	-	-	-	-	-
Castillea arvensis	herb	-	+	-	-	-	-	-	-
Coprosma sp.	shrub	-	-	+	-	-	-	-	-
Ardisia sp.*	shrub	-	-	+	-	-	-	-	-
*Juncus planifolius**	rush	-	-	-	+	-	-	-	-
*Juncus tenuis**	rush	-	-	-	+	-	+	-	-
*Axonopus affinis**	grass	-	-	-	-	-	+	-	-
*Centella asiatica**	herb	-	-	-	-	-	+	-	-
*Macrothelypteris torresiana**	fern	-	-	-	-	-	+	-	-
*Setaria geniculata**	grass	-	-	-	-	-	+	-	-
*Sacciolepis indica**	grass	-	-	-	-	-	+	-	+
Pipturus albidus	shrub	-	-	-	-	-	-	+	+
Adenophorus sp.	fern	-	-	-	-	-	-	-	+
*Gnaphalium japonicum**	herb	-	-	-	-	-	-	-	+
Grammitis tenella	fern	-	-	-	-	-	-	-	+
*Buddleja asiatica**	shrub	-	-	-	-	-	-	-	+
Melicope clusiifolia	shrub	-	-	-	-	-	-	-	+
Luzula hawaiiensis	herb	-	-	-	-	-	-	-	+
Uncinia uncinata	sedge	-	-	-	-	-	-	+	-
Species totals	44	15	21	14	20	12	22	14	32
Species turnover			+6		+6		+10		+18

Table 3: *Changes in density, mean diameter at breast height, mean height, and total basal area of* Metrosideros polymorpha *trees > 1 m tall between 1967 (I. A. E. Atkinson, pers. comm.) and 1989 on four lava flows on Mauna Loa, Hawaii.*

Year of eruption	No. of live trees ha^{-1} 1967	No. of live trees ha^{-1} 1989	No. of dead trees ha^{-1} 1967	No. of dead trees ha^{-1} 1989	Mean d.b.h (cm) 1967	Mean d.b.h (cm) 1989	Mean tree height (m) 1967	Mean tree height (m) 1989	Total basal area of live trees (m^2 ha^{-1}) 1967	Total basal area of live trees (m^2 ha^{-1}) 1989
1942	250	833	0	0	0.5	3.2	1.4	1.7	0.004	0.67
1881	2450	4165	167	0	0.6	2.8	2.5	2.0	0.069	1.31
1855	1917	4000	167	667	0.6	2.5	2.5	1.9	0.054	1.96
1852	4333	9496	250	0	2.0	2.6	2.6	2.3	1.36	5.04

flow (Table 3). The rank order of densities remained the same with density obviously positively correlated with flow age (Table 3). The 1855 pahoehoe flow had densities of live trees in both 1967 and 1989 that were low relative to the numbers recorded on the other two older flows. Dead individuals were present in both sampling years; almost 15% of the individuals measured in 1989 were dead. Dead individuals were also found on two other flows in 1967 but were not recorded in the 1989 plots on any of the other flows. Population height structures for each flow also show a continuing influx of individuals, but suggest for two flows – the 1881 pahoehoe flow and the 1852 aa flow – that some loss of taller individuals may have occurred over the 22-year interval (Fig. 2).

Mean d.b.h. also increased on all flows, ranging from a mean increase of 0.6 cm on the 1852 flow to 2.7 cm on the 1942 flow. These increases are equivalent to annual diameter increments of 0.27 mm yr^{-1} and 1.23 mm yr^{-1}. The mean height values show decreases for three flows and an increase of 0.3 m for the 1942 flow. However, neither the mean d.b.h. nor the mean height values are useful indicators of individual tree growth rates, as they have been severely affected by the large recruitment of individuals into the >1 m height classes (Fig. 2). This causes a decline in the mean height values and gives comparatively low annual diameter increments. A more accurate estimate of annual diameter increment is obtained by taking the mean diameter of the five largest individuals (assuming these are the earliest established) and dividing by the age of the flow. This gives mean annual diameter increments ranging from 0.41 mm yr^{-1} to 1.57 mm yr^{-1}. All these values will be underestimates, as there would be some delay – approximately 10 years, as evidenced by the 1984 flow – before *Metrosideros* actually colonised a new flow. Thus, the highest average annual increment calculated is likely to be the best estimate.

Total basal area is also positively correlated with flow age (Table 3) but again the 1855 pahoehoe flow stands out as having a lower-than-

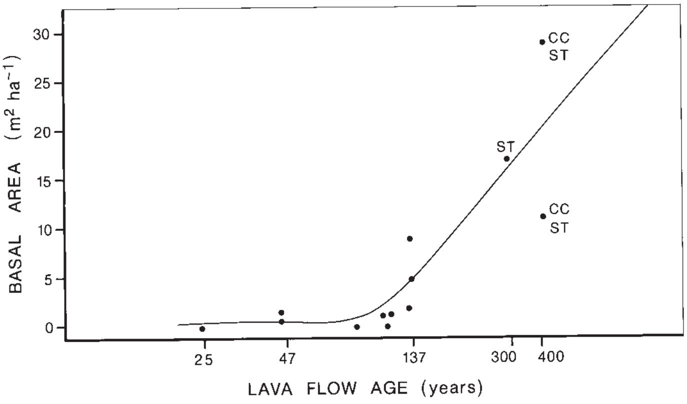

Figure 3: *Non-parametric regression of* Metrosideros polymorpha *basal area versus lava flow age (CC = closed canopy stand; ST = self-thinned stand) on five lava flows on Mauna Loa, Hawaii.*

expected total basal area because of the presence of dead stems already discussed. A non-parametric regression (GAM: Hastie and Tibshirani 1990) relating total basal area to flow age (Fig. 3), calculated using data from the present study and from Atkinson (1969) and Drake and Mueller-Dombois (1993), indicates that basal area remains at very low levels for the first 100 years, then increases almost linearly, although with increasing variation between sites of similar age.

Species colonisation patterns on the 1984 aa flow

The aa substrate of the 1984 flow was colonised exclusively by the moss *Racomitrium lanuginosum* and the lichen *Stereocaulon vulcani*. However, aggregations or patches of vegetation were associated with dead *Metrosideros* and *Cibotium* logs and soils from the former forest which had been rafted along on the surface of the flow as it was emplaced. Fifteen such aggregations were assessed

Table 4: *Species composition by presence/absence of vegetation patches on 1984 aa at 1158 m a.s.l. Substrate types: S = soil; C =* Cibotium *log; M=* Metrosideros *log); * = adventive species; D = dead*

Patch diameter (m)		0.6	0.8	0.8	0.9	1.2	1.6	1.8	2.3	2.6	4.5	6.0	8.5	6.6	7.5	6.0
Plot number		4	1	2	3	5	6	7	8	9	10	11	12	13	14	15
Substrate type(s)		MC	SC	SMC	SMC	SMC	C	C	SMC	SMC	SMC	SC	SMC	SMC	SMC	SMC
Pityrogramma calomelanus	fern	+	-	-	+	-	-	+	+	+	+	+	+	+	+	+
Dryopteris glabra	fern	+	-	-	-	+	+	-	-	+	-	-	+	+	-	-
Polypodium pellucidum	fern	+	-	-	-	-	-	-	-	+	-	+	-	+	+	-
Metrosideros polymorpha	tree	+	+	-	-	-	-	-	-	-	+	-	-	+	-	-
*Nephrolepis multiflora**	fern	-	+	-	+	+	+	-	+	-	+	+	+	+	+	+
*Cuphea cartilaginea**	herb	-	+	+	-	-	-	-	-	+	-	-	+	+	+	+
*Juncus tenuis**	rush	-	-	+	-	-	-	-	-	-	-	-	-	+		
*Hypericum mutilum**	herb	-	-	+	-	-	-	-	-	-	-	-	-	-	+	+
*Erechtites valerianifolia**	herb	-	-	-	+	D	-	-	+	-	D	-	D	D	-	+
*Rubus rosifolius**	shrub	-	-	-	-	+	-	-	-	+	-	-	+	+	+	+
Cibotium glaucum	fern	-	-	-	-	+	+	-	+	-	-	-		+	+	+
Vaccinium calycinum	shrub	-	-	-	-	+	-	+	-	-	+	+	+	+	+	-
Rubus hawaiiensis	shrub	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-
*Andropogon virginicus**	grass	-	-	-	-	-	+	-	+	+	-	-	+	-	+	+
*Arundina graminifolia**	orchid	-	-	-	-	-	-	-	-	-	+	+	+	+	-	-
Pleopeltis thunbergiana	fern	-	-	-	-	-	-	-	+	+	+	-	-	-	+	-
Nephrolepis exaltata	fern	-	-	-	-	-	-	-	-	+	-	-	-	-	-	+
*Epidendren X obrienianum**	orchid	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-
*Spathoglottis plicata**	orchid	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-
*Pteris vittata**	fern	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-
*Juncus planifolius**	rush	-	-	-	-	-	-	-	-	-	+	-	-	-	-	+
Pellaea ternifolia	fern	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-
*Buddleja asiatica**	shrub	-	-	-	-	-	-	-	-	-	+	-	+	-	-	+
Christella dentata	fern	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-
Styphelia tameiameiae	shrub	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-
Dryopteris wallachiana	fern	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-
Nephrolepis cordifolia	fern	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-
Luzula hawaiiensis	herb	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-
Sphenomeris chinensis	fern	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-
Macrothelypteris torresiana	fern	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+
Dicranopteris linearis	fern	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
*Pluchea symphytifolia**	shrub	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
Dubautia scabra	shrub	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
Carex alligata	sedge	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
Sadleria cyatheoides	fern	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
*Drymaria cordata**	herb	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
Cheirodendron trigynum	shrub	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
Pipturus albidus	shrub	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
*Castillea arvensis**	herb	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
Gouldia terminalis	shrub	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
Total species:	40	4	3	3	3	6	5	2	6	8	13	5	11	15	16	22

and the results are shown on Table 4. In general, the larger the 'island' of log and/or soil the greater the number of species represented. However, there is a tendency for a reduced number of species where the substrate comprises only one or two of the three recorded rooting mediums i.e., soil, or trunk of *Metrosideros* or *Cibotium*. Most species were more commonly associated with one substrate or another; for example, *Nephrolepis multiflora* was usually on *Cibotium* logs, *Pityrogramma calomelanus* and *Cuphea cartilaginea* grew on soil, and *Metrosideros* and *Vaccinium calycinum* were perched on dead *Metrosideros* logs. However, for species recorded in four or more aggregations there was no exclusive relationship with a particular substrate. The composite herb *Erechtites valerianifolia*, behaved as an emphemeral having established in 7 aggregations, flowered, and then died back in 4 of them. Of the 40 species recorded in total, 16 (40%) were adventive (introduced) and 24 (60%) were indigenous. Of the 16 adventive species, 14 were small herbs (including orchids and sedges) and two were shrubs, *Pluchea symphytifolia* and *Buddleja asiatica*.

Discussion

Remeasurement of Atkinson's sites showed a moderate influx of adventive (introduced) species, but the majority were herbs and grasses that do not appear to interfere with the succession to *Metrosideros*-dominated forests. The same trend was noted by Smathers and Mueller-Dombois (1974) in their study of plant invasion and recovery over a 9-year period at Kilauea Iki. As they explained, the adventive species have complementary life forms to the native species. However, one of the grass species, *Andropogon virginicus*, which had established in the last 22 years was now a significant component of the vegetation on several flows studied here. This fire-adapted species has the potential to alter ecosystem properties. The stalks of *Andropogon virginicus* do not disintegrate rapidly after it dies, providing excellent fuel for fires, and burning stimulates resprouting (Smith 1989). The natural fire regime of areas with such grasses may be altered to the detriment of native vegetation (Tunison and Leialoha 1988), and the threat of man-induced wild fires is also increased.

The colonisation by the treefern *Cibotium glaucum* of all the remeasured flows (47-137 yrs) and of the small tree *Cheirodendron trigynum* of the two oldest flows (134 yrs and 137 yrs) is notable given their importance in older forest. It is unlikely that Atkinson would have failed to detect these species on this number of sites. Drake and Mueller-Dombois (1993) also record the presence of these species on the 1885 (137 year) flow, but show that they become most abundant on flows older than 137 years. The successful establishment of species such as *Cibotium glaucum* and *Cheirodendron trigynum* may not directly relate to flow age but rather to other factors such as variation in rainfall. For example, permanent plots at 1523 m on Saddle Road (1855 aa) have revealed the invasion and loss of *Cibotium glaucum* from one plot over a 4-year period (1991-95) possibly a result of variation in rainfall (B.D. Clarkson and J.O. Juvik, unpublished data).

Densities and total basal area of *Metrosideros polymorpha* increased on all the flows, but a closed-canopy forest was still not evident on any of them. Given the level of influx of canopy individuals recorded from 1967 to 1989, especially on flows more than 100 years old, it is doubtful that the actual invasion in the sites studied is synchronised to the degree (~ 20 -30 years) envisaged by Mueller-Dombois (1987). It is too soon to expect self-thinning resulting from canopy closure suggested by Atkinson (1969) (i.e., between 115 and 400 years) and Drake and Mueller-Dombois (1993) (i.e., between 137 and 300 years), but a significant number of individuals had died on the 1855 pahoehoe flow. Field observations suggested that intraspecific root competition of individuals concentrated in the cracks or crevices of this lava type might be a factor in this mortality, which could be considered a special instance of self-thinning. Drake and Mueller-Dombois (1993) report that a 300-year-old aa flow in the vicinity still did not support the closed-canopy forest that self-thinning would produce because of windthrow of unstable trees and subsequent recruitment. The non-parametric regression calculated supports the suggestion of Drake and Mueller-Dombois (1993) that a closed-canopy forest could be expected to develop sometime between 137 and 300 years.

Vascular plant aggregations on the 1984 aa flow were associated with soil or logs of the overwhelmed former forest, and indicate the importance of these residual microhabitats for early succession. As most of the species present in these aggregations are typical of non-closed forest habitats, and many have light wind-dispersed seeds, they probably arrived in the seed rain and established because of the suitable substrate and open habitat. However, it is possible that some of the species were already on site in the seed bank of the forest soil or survived as seedlings attached to the *Metrosideros* or *Cibotium* logs. Most notable was the presence of *Metrosideros polymorpha* in four aggregations; one individual was 2.1 m tall. Drake and Mueller-Dombois (1993) note that dense seedling populations establish on new lava in < 20 years, and should support trees approximately 27 years after formation. Although the example noted by the present study may be exceptional, it does indicate that in special circumstances rare individual trees could be in place within 10 years.

In conclusion, this study does not contradict the findings of Atkinson (1969) that a closed-canopy, self-thinned *Metrosideros* forest can develop on these flows within 400 years. However, it does indicate several factors - e.g., dieback of colonising individuals and/or invasion of introduced species capable of altering ecosystem processes - which may delay this. Only by direct monitoring of developing forest stands will the precise timing of canopy closure and self-thinning be determined.

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