Vegetation Succession Following Clearcutting of Lowland Hawaiian Rainforest on the Island of Hawai'i[1]

Dennis H. Grossman[2,4] *and R. Flint Hughes*[3]

Abstract: This study evaluates the secondary successional pathways of Hawaiian lowland rainforest following anthropogenic disturbance. Whereas primary succession on lava flows has been well studied in Hawaii, secondary successional dynamics on disturbed habitats in the presence of nonnative species has been poorly researched and documented. Our study was based on two vegetation sampling efforts conducted on 200–400-year-old lava flows 2 and 27 years following a 400-hectare clearcutting operation in the Puna District of the southeast quadrant of Hawaii Island. Intact forest adjacent to the clearcut area provided a baseline to compare against succession dynamics in the clearcut area. The most important trees of the uncut primary forest, based on frequency, density, and dominance, were keystone Hawaiian forest species *Metrosideros polymorpha*, followed by *Psychotria hawaiiensis*, *Psidium cattleianum*, *Ciboteum glaucum*, and *Cibotium chamissoi*. Whereas early successional nonnative species dominated the initial vegetation colonizing the clearcut site, *M. polymorpha*, *P. cattleianum*, and *Cibotium* species were also present. Twenty-seven years later we found the clearcut site colonized by two distinct secondary forest types: *M. polymorpha*-dominated forest and *Falcataria moluccana*-dominated forest. Whereas *M. polymorpha* maintained a similar level of dominance in uncut primary forest and *M. polymorpha*-dominated secondary forest stands, it was nearly absent from *F. moluccana*-dominated secondary forest stands. Results demonstrated that the keystone Hawaiian native tree species can effectively reestablish across disturbed landscapes, but are unable to outcompete in areas where fast growing nonnative trees become established. This underscores the critical need to suppress early nonnative tree establishment in disturbed habitats if the objective is to reestablish Hawaiian native forests.

Keywords: deforestation, *Falcataria moluccana*, forest succession, Hawai'i, invasive species, Lowland Rain Forest, *Metrosideros polymorpha*, *Psidium cattleianum*, secondary succession, second-growth forests, regeneration

FOREST SUCCESSION, whether primary succession occurring on wholly new or newly exposed substrate (e.g., lava flows, landslides, riverbeds) or secondary succession following fires, storm events, or anthropogenic disturbance, determines the presence, patterns, and dynamics of plant communities and ecosystems through time. Primary succession by native vegetation in barren 'a'a and pahoehoe lava substrates in Hawaii typically begins with colonization by young cohorts of *M. polymorpha* that develop as monotypic forest stands during the first 100–200 years of succession (Atkinson 1970, Grossman 1992,

[1]Manuscript accepted 7 September 2023.
[2]Auburn, CA, USA.
[3]Institute of Pacific Islands Forestry, Pacific Southwest Research Station, USDA Forest Service, Hilo, HI, USA.
[4]Corresponding author (email: denny.grossman@gmail.com).

Pacific Science (2023), vol. 77, no. 2–3:327–347
doi:10.2984/77.2.12

Aplet and Vitousek 1994, Aplet et al. 1998). As succession proceeds, *M. polymorpha*-dominated stands develop into increasingly diverse and structurally complex forests as additional species establish during subsequent centuries (Kitayama et al. 1995, Zimmerman et al. 2008).

In contrast to primary succession, secondary succession following forest disturbance often provides greater opportunities for invasion of a variety of nonnative plant species that would not occur under undisturbed conditions (Crawley 1987, Hobbs and Huenneke 1992, D'Antonio 1993, Burke and Grime 1996). When nonnative species exhibit characteristics and/or functions that are novel to systems within which they have established (e.g., Vitousek and Walker 1989, Hughes and Denslow 2005), they may modify plant community successional dynamics in ways that exclude or diminish otherwise abundant and influential native species.

Conservation of native biodiversity is of paramount importance in Hawaii, where endemism exceeds 90%, and more endangered species are found per square kilometer than anywhere else on earth (Wagner et al. 1999). *M. polymorpha* is the foundational tree of Hawaii's forests and occurs across a wide set of environmental conditions. Because *M. polymorpha* forests were characterized in the 1900s as slow growing and intolerant of disturbance, many nonnative tree species were introduced in Hawaii to presumably improve the provision of ecosystem services by Hawaiian forests (Woodcock 2003). The introduction of these nonnative trees have strongly contributed to reduction in the extent and integrity of *M. polymorpha* forests in general and the lowland *M. polymorpha* tall-statured rainforest type in particular.

Here we report the results of 27 years of secondary succession following deforestation of intact, mature, *M. polymorpha* dominated forest on Kilauea Volcano of Hawaii Island. During 1984 and into 1985, approximately 400 ha of intact, mature *M. polymorpha* dominated forest was deforested from the gentle south-eastern slopes of Kilauea volcano on Hawaii Island. The objective of the logging operation was to cut down all *M. polymorpha* trees in the area, grind them into wood chips, and burn those chips to generate electric power at a nearby sugar mill (Holden 1985). This clearcutting activity kindled a controversy over conversion of this forest type in general and this unique stand of lowland rainforest in particular (Holden 1985). Hawaiian lowland rainforest has been lost on all other islands due to land-use conversion, and extant examples remain in only a few areas on the Island of Hawaii. Of these remaining lowland forest areas, the Kalapana region was recognized as supporting among the tallest-statured lowland rainforest stands documented in Hawaii (Holden 1985).

The main point of controversy in light of this clearcutting operation was whether the secondary forest recovering following the clearcut would retain its native character in the presence of competitive nonnative species within the highly modified landscape. The landholder, the Estate of James Campbell, and wood chipping company, Bio Power, argued that native Hawaiian rainforest was well-adapted to volcanic disturbance and thus possessed characteristics that would result in successful recovery and re-establishment of the native rainforest ecosystem on this site. A substantive argument to this claim was not available due to the lack of research findings regarding secondary forest succession in Hawaii.

After protests by local environmentalist groups were ignored by the chipping company, Dr. Dieter Mueller-Dombois became involved as the leading expert on Hawaii's forest ecosystems. The Bio Power president challenged Dr. Mueller-Dombois to prove that wood-chipping activities would cause "irreparable damage" to the forest ecosystem. Mueller-Dombois characterized forests occupying the study area as among the few remaining tall-statured, native-dominated lowland forests in Hawai'i, noting that they contained the full spectrum of native species richness and native forest successional states of this increasingly rare ecosystem type, "from nearly barren lava flow to mature and senescing rainforest" (Mueller Dombois 1985). Along with Dr. Charles Lamoureux, Mueller Dombois predicted that native-

dominated forest would unlikely regenerate if more than half was destroyed and provided recommendation for forestry practices to provide greater probability of successful native forest restoration.

The landowner and biofuel company planned to deforest the entire 1300 hectare tract. Fortunately, concerted efforts of scientists, conservation groups (e.g., Friends of Hawai'i's Forests) and opposition from the general public were successful in halting the clearcut operation after 400 hectares were clearcut. Across this disturbed area all *M. polymorpha* trees were cut to the ground, and the entire site was bulldozed, creating an extensive area of exposed, highly-disturbed lava substrate.

This unfortunate instance of clearcutting a significant portion of Hawaii's last and best examples of lowland rainforest highlighted the need for secondary succession research, as there was no documentation regarding how to respond and manage this controversy. Primarily due to the encouragement and guidance from Dr. Mueller-Dombois, this resulted in the study of secondary succession dynamics of the Kalapana lowland rainforest following clearcutting and site disturbance, and contrasts the vegetation patterns in 2nd-growth sites with those of adjacent uncut mature forests. A survey of the primary intact vegetation and the secondary post-disturbance vegetation on the 200–400-year-old lava flow was carried out 2 years after the clearcutting activity (Grossman 1992), and 27 years later (Hughes et al. 2022) on the same site.

Given the opportunity afforded by the clearcut event and serial post-disturbance succession evaluations (Grossman 1992, Hughes et al. 2022), we wanted to address the following questions: What was the composition, particularly with regard to native and nonnative species, in secondary successional sites 2 years after the clearcut and how did the composition and structure develop in the course of the following 25 years? How did vegetation in the developing secondary growth forests contrast with that of adjacent uncut primary forests? How did uncut primary forest vegetation change from when it was measured in 1987 to when it as measured 25 years later? To answer these questions, we measured species composition, cover, stem density, and basal area of constituent species in plots established within the deforested areas and adjacent intact forest. These datasets allowed for analysis of secondary succession through time in the clearcut area and provided additional information regarding the vegetation succession of the adjacent intact forest during the 27-year time frame. In addition, the uncut primary *M. polymorpha* dominated forests areas immediately adjacent to the deforestation event provided baseline and end point reference conditions to compare dynamics of forest composition, structure, and function of secondary succession in the clearcut areas.

METHODS

Study Site Location and Characteristics

The study area is approximately 6 km upslope and northwest of Kalapana in the Puna District of Hawai'i Island (UTM 5Q 0288419° E; 2145932° N) (Figure 1). The area's climate is characterized as warm and wet; annual temperatures average 20.6°C (Giambelluca et al. 2014), and annual precipitation averages 3,150 mm (Giambelluca et al. 2013). The study region is a matrix of relatively young 'a'a and pahoehoe lava flows emanating from the East Rift Zone of Kilauea Volcano (Wolfe and Morris 1996). Lava flows in this area range from very young (i.e., <10–40 years old) to those 1,500–3,000 years old (Grossman 1992, Wolfe and Morris 1996). All vegetation plots for this research were located on 'a'a lava flows aged 200–400 years before present. The vegetation is supported by thin organic soils which cover the young volcanic landscape. Early classifications identified these Ola'a or 'ōhi'a soils as Rockland 'a'a lava lithosol present where rainfall averages 1,905 mm per year at elevations between 244 and 412 m (USDA 1955).

1987 and 2012 Vegetation Sampling Design

In 1987, two years after the clearcut event, a square kilometer vegetation sampling grid was

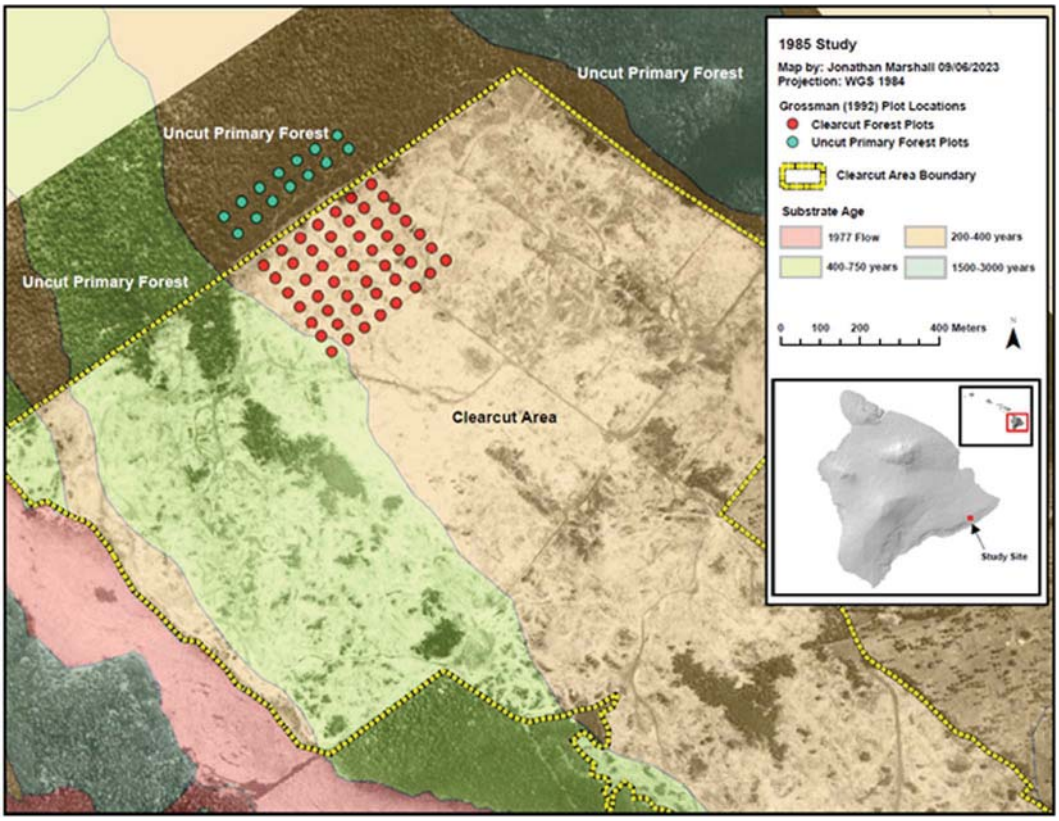

FIGURE 1. Image of clearcut landscape and adjacent uncut primary forest upslope from Kalapana in the Puna District of Hawaii Island denoting the landscape immediately following the clearcut event in 1985.

established ranging in elevation from 430 to 480 m (Figure 1). The upper third of the sample grid covered uncut, mature primary forest, and the lower two thirds of the grid occupied the clearcut area. Vegetation in the primary forest was sampled at 50 m and 100 m intervals from the forest edge along eight parallel transects spaced 50 m apart, resulting in a total of 16 quadrats that collectively sampled 1,600 m^2. Early successional vegetation of the clearcut area was sampled along the extension of these eight parallel transects from the forest edge extending 350 m into the clearcut zone (Figure 1). Seven sample points were established at 50 m intervals along each transect, and a pair of 16 m^2 quadrats were established at distances of 12 m on either side of each sample point to provide a total of 14 sample quadrats per transect. These 112 quadrats resulted a total sample of 1,792 m^2 across the clearcut area (Figure 1).

In 2012, approximately 27 years after the clearcut event and 25 years after the initial vegetation sampling effort, the vegetation was resampled in both uncut mature forests and in the 2nd-growth forests across within the clearcut area (Figure 2). The study area was stratified into sub-regions distinguished by primary or secondary forest type and dominant secondary forest canopy tree type (Hughes et al. 2022). The two secondary forest types, *M. polymorpha*-dominated stands and *F. moluccana*-dominated stands, were identified based on interpretation of remotely sensed imagery (Google Earth 2012). Vegetation sampling plots were established at 7 to 11 locations in each forest status and dominant

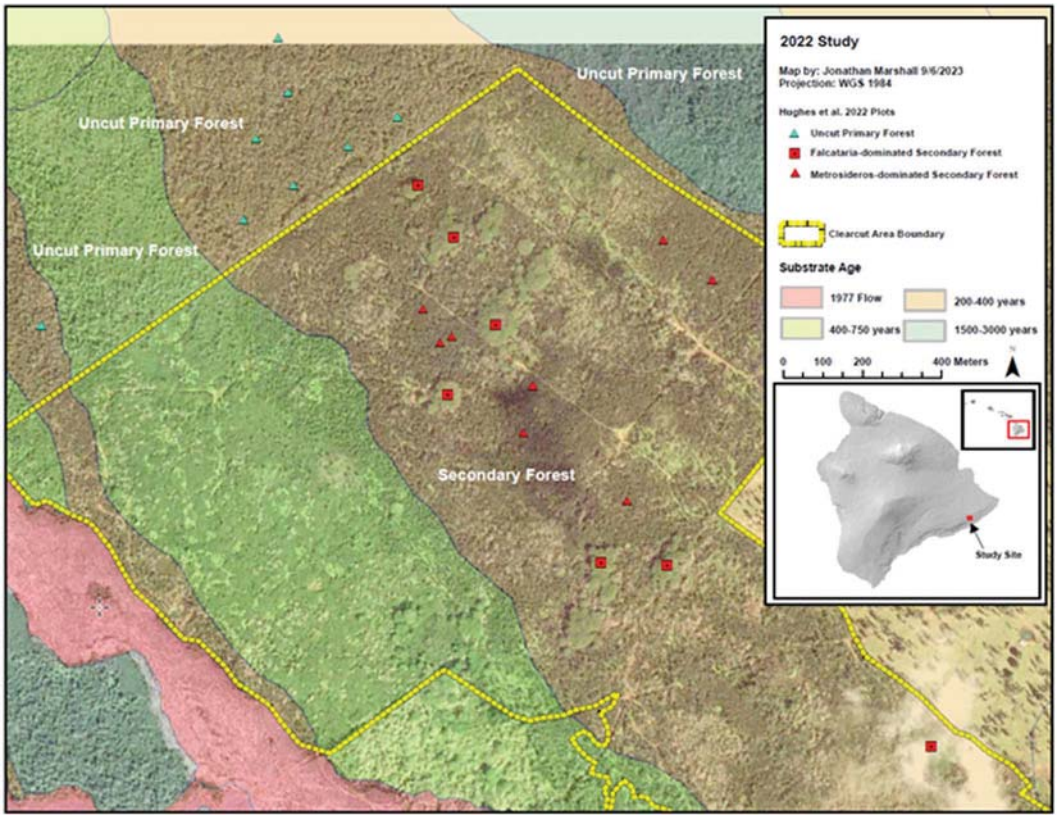

FIGURE 2. Image of clearcut landscape and adjacent uncut primary forest upslope from Kalapana in the Puna District of Hawaii Island denoting the landscape and vegetation approximately 27 after the 1985 clearcut event.

canopy tree type on the 200–400-year-old lava substrate type. A center point was established for 8 plots in intact mature primary forest, 11 plots in 2nd-growth forests dominated by *M. polymorpha*, 7 plots in 2nd-growth forests dominated by *F. moluccana* (Figure 2). These 26 circular inventory plots were 36 m in diameter, encompassing an area of ca. 0.10 ha (i.e., 1,000 m^2).

Understory Vegetation Sampling in 1987 and 2012

During 1987 vegetation sampling, we applied a modified Braun-Blanquet cover abundance scale (Mueller-Dombois and Ellenberg 1974) to determine the cover values for all understory species within each of the 112 16 m^2 quadrats established in the clearcut region. Canopy cover for each species within each quadrat was quantified using the following four classes; 1 = 0–25%, 2 = 25–50%, 3 = 50–75% and 4 = 75–100%. A midpoint percentage value was assigned for each class (e.g., 12.5% for class 1, and 62.5% for class 3) to derive a single species cover value for each quadrat. These values were applied to calculate species-specific Importance Values based on relative cover and relative frequency for each species across the clearcut area in 1987.

During 2012 sampling, understory species cover was characterized within a subset of 22 of the total 26 forest plots (i.e., 8 uncut forest plots, 8 *M. polymorpha*-dominated 2nd-growth forest plots, and 6 *F. moluccana*-dominated 2nd-growth forest plots). A modified point intercept method was employed to estimate species cover within each 0.1 ha sampling plot

and expressed as a percentage of total cover (Mueller-Dombois and Ellenberg 1974). Understory cover was measured in each plot at 1 m intervals along each of four 18 m transects emanating from plot center in each cardinal direction. This resulted in 17 sample points per line and 68 sample points per forest plot. At each sample point, a 2 m tall and 1 cm diameter metal pole was lowered through the understory cover to the forest floor. All species intersecting the pole were recorded. The pole frequently intersected multiple species at a given sample point which resulted in total cover values that were greater than 100% in most of the forest plots. In these cases, the number of "hits" for a given species was divided by the total number of "hits" from the combined 68 sample points of the four transects in each plot. This provided the relative cover values used to generate Importance Values based on the relative cover and relative frequency for each species encountered in the clearcut area in 2012.

Woody Vegetation Sampling in 1987 and 2012

During 1987 sampling efforts in the uncut primary forest, the diameter at breast height (dbh) was recorded for all woody species with a dbh greater than 3.18 cm in each of the established sixteen 100 m^2 quadrats. Plot-scale measures of species-specific stem density and basal area were expanded to a hectare basis using appropriate multipliers for overall plot and nested subplot dimensions.

During 2012 sampling efforts, the dbh of all stems greater than 5 cm were recorded for all species rooted within the boundary of each 36 m diameter forest inventory plot. In addition, all species with stems >1 and <5 cm dbh rooted within a 12 m diameter subplot were identified and recorded. These measurements were collected in 26 forest plots of which 8 plots in intact mature primary forest, 11 plots in 2nd-growth stands dominated by *M. polymorpha*, and 7 plots in 2nd-growth stands dominated by *F. moluccana* (Figure 1). Plot-scale measures of species-specific stem density and basal area were expanded to a hectare basis using appropriate multipliers for overall plot and nested subplot dimensions.

Forest Seed Bank Analysis

The forest soil seed bank was analyzed to assess the potential contribution of this seed source for regeneration success following clearcutting. Soil seed-bank samples were gathered at 50 m and 100 m points from the forest edge on the eight sampling transects. The samples were collected just beneath the litter layer and down to 16 cm in crevices of the clinker substrate, and samples were taken to the UH Botany Department greenhouse at Manoa where each sample was separated into sun and shade treatments and transferred into germination trays with 36 sections per tray. The shade treatment was designed to simulate a forest gap environment, and the sun treatment simulated an extensive loss of forest canopy as in a large clearcut. Each section of the germination tray was filled with 20 ml of vermiculite and capped with 5 g (approx. 2 cm) of the forest soil samples. Trays were watered at least twice a week, depending on the drying conditions.

The germination process was initiated on November 20, 1986. Data were recorded on November 30, December 7, December 24, January 11, and February 13. Analysis of full sunlight germination trays ended on March 11, 1987, when the greenhouse experienced a power failure which killed most of the sunlight treatment plants. The shade trays were continuously monitored until June 17, 1987.

The initial recordings tabulated the numbers of germinants per plot per treatment. Average number of plants per sample and total number of plants per plot were monitored over a four month (sun treatment) to seven month (shade treatment) period. Each germination plot in sunlight and shade treatments was analyzed and each species was given an importance value by the average of its relative frequency and relative density values. Species values were compared in relation to the different light treatments, and in relation to the species in both forest and clearcut associations.

Statistical Analyses

Importance values (IV) were used to evaluate vegetation between the intact primary forest, newly colonizing clearcut area, and secondary forest types established across the clearcut area after 27 years. The IVs were calculated for each species encountered during 1987 and 2012 sampling of quadrats located in uncut primary forest, as well as vegetation across the clearcut area 2 years and 27 years after the deforestation event. Understory species IVs were calculated using the sum of relative frequency and relative cover. Frequency was calculated as the number of plots where a given species was encountered divided by the total number of plots. Relative frequency was calculated by dividing the frequency by the sum of the frequencies of all species, multiplied by 100 to obtain a percentage. Cover was calculated as the total cover percentage of a given species recorded within all plots of a given forest type. Relative cover was calculated by dividing the cover value of a given species by the sum of the cover values of all species, multiplied by 100 to obtain a percentage. The sum of relative frequency and relative cover values was then divided by 2 to maintain a constant final IV score in the scale of 0–100.

IVs for woody vegetation encountered in forest quadrats (1987 sampling) and plots (2012 sampling) were calculated as the sum of relative frequency, relative density and relative dominance of each species. Frequency of each woody species encountered was calculated as described above for understory vegetation. Relative frequency was calculated by dividing the frequency by the sum of the frequencies of all species, multiplied by 100 to obtain a percentage. Density was calculated as the total number of individuals of a given species within a forest type. Relative density was calculated by dividing each species-specific density by the sum of the densities of all species, multiplied by 100 to obtain a percentage. Dominance was calculated as the total basal area of a given species within a given forest type. Basal area values of each stem were derived from measured dbh values of each stem encountered on each plot. Relative dominance was calculated by dividing the species-specific dominance value by the sum of the dominance of all species, multiplied by 100 to obtain a percentage (Curtis and McIntosh 1951, Kent 2011). The sum of relative frequency, relative cover and relative dominance values was then divided by 3 to maintain a constant final IV score in the scale of 0–100.

Hierarchical Cluster Analysis was used to elucidate the similarities and differences for both understory and woody components of each vegetation types and sample date. Analyses employed Centroid linkage and Euclidian distance parameters in each case. Importance Values provided the numerical basis to make comparisons of understory vegetation for all vegetation types and woody vegetation for all forest types. Statistical analyses were conducted using Systat version 13.

RESULTS

Understory Vegetation Patterns and Dynamics

Multivariate cluster analysis of species Importance Values (IVs) for understory vegetation within uncut primary forest, 2-year post-clearcut vegetation, and 27-year secondary forest stands revealed clear delineations related to disturbance, successional stage, and stand type (Figure 3). Uncut primary forest differed distinctly from the three secondary succession stand types recovering from the 1985 clearcut event, and the 2-year post-clearcut vegetation was distinctly different from both *M. polymorpha*-dominated secondary forest and *F. moluccana*-dominated secondary forest stands. Greatest understory vegetation similarity occurred between *M. polymorpha*-dominated and *F. moluccana*-dominated secondary forest stands (Figure 3).

Understory species exhibiting high IVs in the uncut forest were *C. hirta* (30%), *P. cattleianum* (21%), *Ciboteum* spp. (7%), *Vaccinium* spp. (6%), *P. hawaiiensis* (5%), *Microlepia strigosa* (4%), *Melastoma* spp. (4%), *Dicranopteris linearis* (4%), *Freycinetia arborea* (4%), *Nephrolepis multiflora* (4%) and *Zingiber zerumbet* (2%). The individual species'

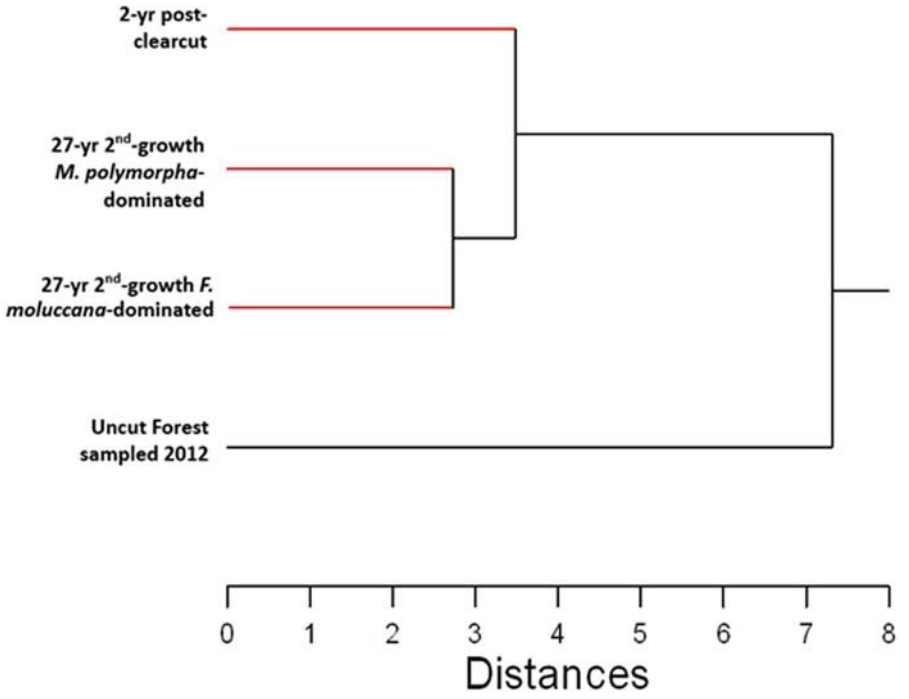

FIGURE 3. Cluster analysis of IV values of understory cover in *Metrosideros*-dominated and *Falcataria*-dominated secondary forests, the 2-year post-clearcut site, and uncut primary forest in the Ki Ula forest of Kalapana, Puna District, Hawaii Island.

understory vegetation IVs that distinguished uncut primary forest from other stand types included the native species *Freycinetia arborea*, *Broussaisia arguta*, *Coprosma menziesii*, *Peperomia* spp. and *Vaccinium* spp. (Table 1) In addition, the IV of *P. hawaiiensis* in uncut forest stands was nearly double that of any other stand. The IV for the invasive nonnative tree, *P. cattleianum*, in the uncut primary forest was more than double than in any other stand type. The nonnative ginger, *Zingiber zerumbet*, was present in uncut forest stands but absent from all other stands (Table 1). Native species accounted for 60% understory species in the uncut primary forest, and 40% were nonnative (Table 1).

Understory species colonizing the 2-year post clearcut site that exhibited high IVs included *Pipturus albidus* (7%), *Nephrolepis multiflora* (6%), *Rubus rosifolius* (7%), *Pluchea symphytifolia* (7%), *C. hirta* (6%), *Buddleia asiatica* (5%), *Andropogon virginicus* (5%), *P. cattleianum* (4%), *Christella dentata* (4%), and *Crassocephalum crepidioides* (3%). A total of 103 species contributed to the overall understory plant community of the early successional site compared to only 14 to 16 species encountered in understories of later successional forest stand types, and the majority were early successional, light-loving nonnative species. The most common species in this area that were absent from the other forest stand types included nonnative shrubs *Rubus rosifolius*, *Pluchia symphytifolia*, and *Buddleia asiatica*, and nonnative grasses *Andropogon virginicus*, *Paspalum conjugatum*, *Schizachyrium condensatum*, and *Arundina graminifolia* (Table 1). *Pipturus albidus* exhibited the highest IV in the 2-year-post clearcut site; this is a native pioneer shrub that was virtually absent from the other three forest stands. The native tree *M. polymorpha* ranked in the top dozen highest IVs due to the significant number of seedlings in the 2-year post-clearcut site. Native tree ferns, *Ciboteum*

TABLE 1

Importance Values (IVs) of Understory Cover for Species Encountered in 2-Year Post Clearcut Sites, 27-Year-Old Secondary Forests, and Uncut Primary Forests in the Ki Ula Forest Above Kalapana in the Puna District of Hawaii Island

Species	2-Year Post-Clearcut (%)	*Metrosideros*-Dominated Secondary Forest (%)	*Falcataria*-Dominated Secondary Forest (%)	Uncut Primary Forest Sampled in 2012 (%)
Pipturus albidus	7.05	0.00	0.00	0.00
Nephrolepis multiflora	6.99	9.01	4.97	3.76
Rubus rosifolius	6.76	0.00	0.00	0.00
Pluchia symphytifolia	6.66	0.00	0.00	0.00
Clidemia hirta	6.17	32.53	52.76	30.43
Buddleia asiatica	5.45	0.00	0.00	0.00
Andropogon virginicus	5.35	0.00	0.00	0.00
Psidium cattleianum	3.92	8.19	10.51	21.15
Christella dentata	3.60	0.00	0.00	0.00
Crassocephalum crepidioides	3.10	0.00	0.00	0.00
Cibotium spp.	2.86	3.85	5.32	7.04
Metrosideros polymorpha	2.59	2.94	3.41	1.00
Castilleja arvensis	2.51	0.00	0.00	0.00
Paspalum conjugatum	2.44	0.00	0.00	0.00
Schizachyrium condensatum	2.25	0.00	0.00	0.00
Arundina graminifolia	2.15	0.00	0.00	0.00
Spathoglottis plicata	2.14	0.00	0.00	0.00
Cyperus halpan	1.89	0.00	0.00	0.00
Machaerina angustifolia	1.87	0.00	0.00	0.00
Sacciolepis indica	1.58	0.00	0.00	0.00
Youngia japonica	1.47	0.00	0.00	0.00
Pityrogramma calomelanos	1.35	0.00	0.00	0.00
Oplismenus hirtellus	1.13	0.00	0.00	0.00
Ageratum conyzoides	1.09	0.00	0.00	0.00
Conyza canadensis	0.95	0.00	0.00	0.00
Cuphea carthagenensis	0.94	0.00	0.00	0.00
Sphenomeris chinensis	0.92	0.00	0.00	0.00
Cyperus rotundus	0.82	0.00	0.00	0.00
Conyza bonariensis	0.81	0.00	0.00	0.00
Elaphoglossum crassifolium	0.72	0.00	0.00	0.00
Hedychium caronarium	0.65	0.00	1.59	0.00
Kyllinga brevifolius	0.61	0.00	0.00	0.00
Psidium guajava	0.58	1.00	0.00	0.00
Passiflora foetida	0.55	0.00	0.00	0.00
Desmodium sandwichensis	0.43	0.00	0.00	0.00
Kyllinga nemoralis	0.43	0.00	0.00	0.00
Ludwigia octovalvis	0.43	0.00	0.00	0.00
Pterium aqualinum	0.39	0.00	0.00	0.00
Ludwigia palustris	0.37	0.00	0.00	0.00
Stachytarpheta jamaicensis	0.37	0.00	0.00	0.00
Psychotria hawaiiensis	0.36	2.86	0.00	5.45

TABLE 1

Species	2-Year Post-Clearcut (%)	*Metrosideros*-Dominated Secondary Forest (%)	*Falcataria*-Dominated Secondary Forest (%)	Uncut Primary Forest Sampled in 2012 (%)
Commelina diffusa	0.33	0.00	0.00	0.00
Melochia umbellata	0.33	0.00	0.00	0.00
Blechnum occidentale	0.31	0.00	0.00	0.00
Erechtites valarianifolia	0.31	0.00	0.00	0.00
Alyxia oliviformis	0.29	5.25	1.59	0.00
Cyrtandra paludosa	0.26	0.00	0.00	0.00
Peperomia spp.	0.25	0.00	0.00	1.66
Setaria gracilis	0.22	0.00	0.00	0.00
Bidens pilosa	0.21	0.00	0.00	0.00
Hypericum degeneri	0.21	0.00	0.00	0.00
Aleurites moluccana	0.20	0.00	0.00	0.00
Antidesma platyphyllum	0.16	0.00	0.00	0.00
Bigonia hirtella	0.16	0.00	0.00	0.00
Coprosma mensiesii	0.16	0.00	0.00	1.15
Cordyline fruticosa	0.16	0.00	0.00	0.00
Isachne distichophylla	0.16	0.00	0.00	0.00
Melinus minutiflora	0.16	0.00	0.00	0.00
Hyptis pectinata	0.15	0.00	0.00	0.00
Mimosa pudica	0.15	0.00	0.00	0.00
Spermacoce assurgens	0.15	0.00	0.00	0.00
Macrothelypteris torresiana	0.14	0.00	0.00	0.00
Pleopeltis thunbergiana	0.14	0.00	0.00	0.00
Psilotum nudum	0.14	0.00	0.00	0.00
Axonopsis compressus	0.13	0.00	0.00	0.00
Coccinea grandis	0.13	0.00	0.00	0.00
Diospyros sandwichensis	0.13	0.00	0.00	0.00
Passiflora suberosa	0.12	0.00	0.00	0.00
Sadleria cyatheoides	0.12	0.00	0.00	0.00
Torrenia asiatica	0.12	0.00	0.00	0.00
Ascelpias curassavica	0.11	0.00	0.00	0.00
Centella asiatica	0.11	0.00	0.00	0.00
Fimbristylis dichotoma	0.10	0.00	0.00	0.00
Melastoma candidum	0.10	8.67	1.83	0.00
Sochus oleraceus	0.10	0.00	0.00	0.00
Asplenium lobulatum	0.09	0.00	0.00	0.00
Ageratina riparia	0.06	0.00	0.00	0.00
Desmodium incanum	0.06	0.00	0.00	0.00
Freycinetia arborea	0.06	0.00	1.59	3.86
Malvastrum coromandelianum	0.06	0.00	0.00	0.00
Myrsine lessertiana	0.06	0.00	0.00	0.00
Polygala paniculara	0.06	0.00	0.00	0.00
Polygonum aviculare	0.06	0.00	0.00	0.00
Rynchelytrum repens	0.06	0.00	0.00	0.00
Astelia menziesiana	0.05	0.00	0.00	0.00

Table 1

Species	2-Year Post-Clearcut (%)	*Metrosideros*-Dominated Secondary Forest (%)	*Falcataria*-Dominated Secondary Forest (%)	Uncut Primary Forest Sampled in 2012 (%)
Chamaesyce prostrata	0.05	0.00	0.00	0.00
Digitaria insularis	0.05	0.00	0.00	0.00
Dioscorea pentaphylla	0.05	0.00	0.00	0.00
Lactuca serriola	0.05	0.00	0.00	0.00
Oxalis corniculata	0.05	0.00	0.00	0.00
Paspalum scrobiculatum	0.05	0.00	0.00	0.00
Rhynchospora chinensis	0.05	0.00	0.00	0.00
Vernonia cinerea	0.05	0.00	0.00	0.00
Cerastrum fontanum	0.04	0.00	0.00	0.00
Drymeria cordata	0.04	0.00	0.00	0.00
Emilia fosbergii	0.04	0.00	0.00	0.00
Gnaphalium japonicum	0.04	0.00	0.00	0.00
Ilex anomala	0.04	0.00	0.00	0.00
Picris hieracioides	0.04	0.00	0.00	0.00
Plantago major	0.04	0.00	0.00	0.00
Broussaisia arguta	0.00	0.00	0.00	1.15
Dicranopteris linearis	0.00	16.90	0.00	3.82
Emilia sonchifolia	0.00	0.00	0.00	0.00
Erechtites hieracifolia	0.00	0.00	0.00	0.00
Falcataria moluccana	0.00	0.00	3.16	0.00
Melastoma spp.	0.00	3.92	1.59	4.79
Microlepia strigosa	0.00	3.93	4.98	4.86
Tibouchina herbacea	0.00	0.96	0.00	0.99
Unknown herb	0.00	0.00	3.16	0.00
Unknown vine	0.00	0.00	3.56	0.00
Vaccinium spp.	0.00	0.00	0.00	5.51
Zingiber zerumbet	0.00	0.00	0.00	2.27
Total	100.00	100.00	100.00	100.00

spp., were also present, though in low numbers (Table 1). The nonnative shrub, *C. hirta*, was present within the 2-year post-clearcut site, but not to the degree that it occurred in the three forest stands. Native species comprised 33% of the understory species in the 2-year post-clearcut site, and 77% percent consisted of nonnative species.

The two secondary forests, one dominated by *M. polymorpha* and the other dominated by *F. moluccana*, were most similar to one another within the group of stands (Figure 3) but differed from each other in notable ways. Species with high IVs *M. polymorpha*-dominated secondary stands included *C. hirta* (33), *Dicranopteris linearis* (17%), *Nephrolepus multiflora* (9%), *Melastoma* spp. (9%), *P. cattleianum* (8%), *Alyxia stellata* (5%), *Microlepia strigosa* (4%), and *Ciboteum* spp. (4%). Native species comprised 50% of understory species in the *M. polymorpha*-dominated secondary stands, and 50% consisted of nonnative species (Table 1).

Understory species exhibiting high IVs *F. moluccana*-dominated secondary stands included *C. hirta* (53%), *P. cattleianum* (11%), *Ciboteum* spp. (5%), *Microlepia strigosa* (5%), and *Nephrolepis multiflora* (5%). Twenty

native species accounted for 20% of understory species in *F. moluccana*-dominated secondary stands, and 80% were nonnative species. Whereas the nonnative shrub *C. hirta* dominated the understory of the *F. moluccana*-dominated secondary stands, it was co-dominant along with the native fern *Dicranopteris linearis* in *M. polymorpha*-dominated secondary stands (Table 1).

There was a significant shift in IVs of understory species from 2 years after clearcutting to the *M. polymorpha*-dominated forest and *F. moluccana*-dominated forest 27 years after clearcutting (Table 1). This was likely due to greater number of early successional species contributing to total cover in the 2-year post clearcut samples being absent or less prominent in secondary forest stands. An exception was *C. hirta*, which was relatively abundant in 2-year clearcut (12% of total) but much more abundant in *M. polymorpha* stands (51%) and in *F. moluccana*-dominated secondary forest stands (85%). *M. polymorpha* also demonstrated the ability to persist from early seedling establishment in the clearcut area to become one of the dominant secondary successional stand types 27 years later (Table 1).

Woody Species' Patterns and Dynamics

Similar to understory vegetation, Importance Values (IVs) of frequency, density and dominance (i.e., basal area) of woody species in the uncut primary forest measured in 1987 and 2012 as well as in secondary forests revealed clear delineations between stand types related to disturbance and successional stage (Figure 4). Collective IVs of the uncut mature forest measured in 1987 were most similar to those of the same uncut forest measured in 2012, and uncut forest IVs were more similar to those of *M. polymorpha*-dominated secondary forests than to the *F. moluccana*-dominated secondary forest (Figure 4).

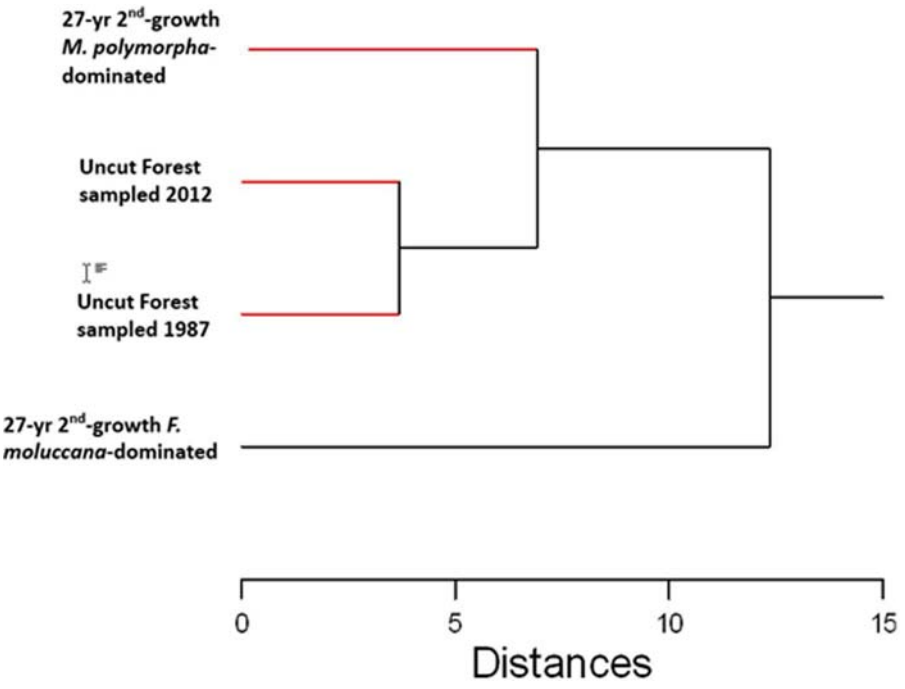

FIGURE 4. Cluster analysis of IV values of woody vegetation in *Metrosideros*-dominated and *Falcataria*-dominated secondary forests, the 2-year post-clearcut site, and uncut primary forest in the Ki Ula forest of Kalapana, Puna District, Hawaii Island.

Dominant native trees, *M. polymorpha* and *P. hawaiiensis* as well as the nonnative tree *P. cattleianum*, exhibited IVs quite similar to the uncut forest measured in 1987 and 2012 as well as the *M. polymorpha*-dominated 2nd-growth stands. *M. polymorpha* exhibited IVs of 28%, 33%, and 54%, respectively, for these forests. *M. polymorpha* IVs in the *M. polymorpha*-dominated secondary forest were nearly double those the uncut forest (Table 2).

Subcanopy constituents, *P. hawaiiensis* and *Cibotium* spp. exhibited IVs in the *M. polymorpha*-dominated 2nd-growth forest that were approximately half the value (14%) of those exhibited by those species the uncut forest (24% and 27%). *Cibotium* spp. expressed IVs in the *M. polymorpha*-dominated secondary forest that were also significantly less (6%) of those exhibited by the uncut forest (19% and 10%). *P. cattleianum* expressed very similar IVs (between 17% and 18%) across the three forest stands (Table 2).

Collectively, woody species exhibited IVs in the *F. moluccana*-dominated secondary forest stands differed substantially from those of other forest stands (Figure 3) due to the extreme dominance of *F. moluccana* and *P. cattleianum* in this stand type (Table 2). High IVs in the *F. moluccana*-dominated secondary forests were expressed by *F. moluccana* (40%) and *P. cattleianum* (25%). Native forest species exhibited much lower IVs; *M. polymorpha*, *P. hawaiiensis*, and *Ciboteum* spp. expressed IVs of 11%, 6%, and 3%, respectively (Table 2).

Forest Soil Seedbank

The majority of seeds and spores that germinated from soil samples collected from the uncut forest were nonnative ferns in the genera *Christella*, *Adiantum*, and *Nephrolepis* (Table 3). *C. hirta*, *Buddleia asiatica*, *Rubus rosifolius*, and *P. cattleianum* were prominent nonnative species germinating from the sampled forest soils. *C. hirta* seedlings were abundant in both sun and shade treatments. *Rubus rosifolius*, *Buddleia asiatica*, *Pluchea symphytifolia*, and *Ageratum conyzoides* exhibited higher germination levels in the sun treatment, while *P. cattleianum* demonstrated a very uneven distribution and density pattern with a slight preference for shade (Table 3).

Native woody species, *M. polymorpha* and *Pipturus albidus*, were also present in both

TABLE 2

Importance Values (IVs) of Woody Species in the Uncut Primary Forest and Secondary Forests in the Ki Ula Forests Above Kalapana in the Puna District of Hawaii Island

Genus species	Uncut Primary Forest Sampled in 1985 (%)	Uncut Primary Forest Sampled in 2012 (%)	*Metrosideros*-Dominated Secondary Forest (%)	*Falcataria*-Dominated Secondary Forest (%)
Metrosideros polymorpha	27.55	33.35	54.45	11.32
Psychotria hawaiiensis	23.58	26.89	13.85	5.65
Psidium Cattleianum	17.86	18.39	16.73	25.43
Cibotium spp.	19.31	10.37	5.99	2.93
Antidesma platyphyllum	4.90	1.19	0.00	0.00
Psidium guajava	2.54	0.00	0.00	2.29
Diospyros sandwic ensis	1.87	0.00	0.00	0.00
Pipturus albichus	1.23	0.00	0.00	0.90
Coprosma menziesii	0.38	0.00	0.00	0.00
Wikstroemia phillyreifolia	0.38	0.81	0.00	0.00
Aleurites moluccana	0.38	0.00	0.00	1.77
Falcataria moluccana	0.00	0.00	0.00	39.66
Other native spp.	0.00	4.33	1.44	0.00
Other nonnative spp.	0.00	4.68	7.53	10.05
Total	100.00	100.00	100.00	100.00

TABLE 3

Germinants (Mean + SE) From Soils Collected From Uncut Forests of Ki Ula in Puna District of Hawaii Island

Genus Species	Sun Treatment Seedlings (0.5 m^2)	Shade Treatment Seedlings (0.5 m^2)	Total Sampled Seedlings (16 m^2)	Seedlings ha^{-1}
Fern spp.[a]	95.44 ± 12.27	67.00 ± 0.95	2599	812,188
Clidemia hirta	27.00 ± 20.04	54.50 ± 40.27	1306	408,125
Buddleia asiatica	15.13 ± 2.48	7.44 ± 1.86	364	113,750
Pipturus albidus	12.69 ± 2.60	16.25 ± 2.66	453	141,563
Rubus rosifolius	6.13 ± 0.74	7.88 ± 1.05	224	70,000
Psidium cattleianum	4.19 ± 1.96	5.06 ± 2.08	148	46,250
Metrosideros polymorpha	1.63 ± 0.53	1.94 ± 0.62	57	17,813
Ageratum conyzoides	1.13 ± 0.22	0.06 ± 0.06	19	5,938
Aster. spp.[b]	0.38 ± 0.15	0.63 ± 0.18	16	5,000
Andropogon virginicus	0.31 ± 0.12	0.06 ± 0.06	6	1,875
Cyperus spp.	0.06 ± 0.06	0.00 ± 0.00	1	313
Desmodium spp.	0.06 ± 0.06	0.00 ± 0.00	1	313
Bigonia hirtella	0.00 ± 0.00	0.19 ± 0.19	3	938

[a] Fern species of the genera *Christella*, *Adiantum*, and *Nephrolepis*.
[b] Species in the genera *Erechtites* and *Crassocephalum* of the family Asteraceae.

forest soil seedbanks and showed little preference for sun or shade treatment; a total of 57 *M. polymorpha* seedlings germinated from the forest soils, germinating equally in the sun and the shade flats. Extrapolation of *M. polymorpha* germinant values from forest soil samples indicate that the soil seedbank could result in seedling densities up to nearly 18,000 individuals ha^{-1}.

Many native and nonnative species that germinated from sampled forest soils were also present and often abundant as early pioneers in adjacent clearcut area surveyed 2 years after the clearcut event (Table 3).

DISCUSSION

The unfortunate destruction of 400 hectares of rare and nearly pristine lowland Hawaiian rainforest provided a valuable research site for primary and secondary succession. While having the full complement of native species, the intact forest showed signs of past disturbance based on the presence of nonnative species. The keystone Hawaiian tree species, *M. polymorpha*, was most dominant in this stand, followed by *P. hawaiiensis* and the two *Ciboteum* tree ferns. The only nonnative tree species expressing a high level of importance in this forest was *P. cattleianum*. As would be expected, the number of *M. polymorpha* individuals decreased over successional time (i.e., from 1987 to 2012) while the size of trees increased, resulting in a net increase of basal area. *P. hawaiiensis* saw an increase in the number of smaller sized individuals. The density and dominance of the two *Cibotium* species as well as *P. cattleianum* decreased over this successional time period. Decline of *Cibotium* could be associated with an increase of the wild pig population in this ecosystem (Cole and Litton 2014).

Early succession across the clearcut site included a large number of species (103). Nonnative species accounted for 76% of the total, with *Pipturus albidus* being the only native species exhibiting high cover and frequency values. Most of these early successional light loving species did not persist into later phases of secondary succession. Twenty-seven years after the clearcutting event this site was covered by two distinct forest types, one dominated by *M. polymorpha* and the other dominated by *F. moluccana*. Whereas *P. cattleianum* was present equally in both secondary forest types, *M. polymorpha*, *P. hawaiiensis*, and the *Cibotium* species were

only found in small numbers in the *F. moluccana* dominated forest. It is interesting to note the increase of the nonnative understory species, *C. hirta*, in understory dominance from the newly clearcut area (12%) to the *M. polymorpha* dominated forest (51%) and the *F. moluccana* dominated forest (85%).

Our results regarding the early stages of secondary succession 2 years following the clearcut event were similar to secondary succession documented elsewhere for tropical systems, but contrasted from plant community patterns documented for early-stages of primary succession in similar ecosystems of Hawaii. Guariguata and Ostertag (2001) characterized the very early stages of early succession following disturbance in lowland wet and moist Neotropics as a dynamic and dominated by light-loving grasses, shrubs, and forbs. Ohtsuka (1999) documented early stages of secondary succession following agricultural abandonment in Sabah as dominated initially by a few therophytic species that were rapidly replaced by perennial grasses and shrubs, with pioneer tree species establishing approximately three years following abandonment.

Our results following two years of secondary succession which was comprised of more than 100 native and nonnative plant species differs from prior studies of primary succession in Hawaii (Atkinson 1970, Aplet and Vitousek 1994, Kitayama et al. 1995, Aplet et al. 1998, Raich et al. 2000) which is characterized by a gradual pattern of increase in species richness, above ground biomass, and soil organic matter. The resulting vegetation is dominated by native species, controlled by temperature and precipitation, and tightly constrained by availability of nitrogen among other nutrients (Vitousek et al. 1993). The highly exposed, nutrient-poor young lava substrates typically undergo an initial multi-year period in which they are exclusively colonized by lichen species rather than higher plants (Kurina and Vitousek 1999). All introduced nonnative species, excepting those capable of symbiotic N fixation (Vitousek and Walker 1989), are unable to colonize young lava flows until sufficient nutrients have accumulated over multiple decades (Hughes and Denslow 2005). In contrast, the originating disturbance of clearcutting and bulldozing studied here left significant amounts of aboveground biomass and soil organic matter on site, including pools of available soil N that were accrued during the 200–400 years of prior primary succession. Thus, it is not surprising that many native and nonnative pioneer species were able to take advantage of the abundant light and soil nutrient availability during initial stages of secondary succession immediately following the clearcut event. It is similarly not surprising that relatively few of these initial pioneer species, among them *M. polymorpha*, were able to persist through the stages of secondary succession.

Further, studies of early secondary succession studied elsewhere (e.g., Ohtsuka 1999, Guariguata and Ostertag 2001) accurately describe our results, with the qualification that most species present during the early successional stage were introduced, nonnative species. A notable exception was the abundance of the native pioneer shrub, *Pipturus albidus* which exhibited the highest importance value of all species 2 years following the clearcut event. *P. albidus* is a bird-dispersed small tree or shrub that exhibits facility to establish in disturbed areas where light is abundant (Kandert et al. 2021). The relative abundance of *P. albidus* may have provided a strong native compositional, structural, and functional component to the initial stages of secondary succession.

In addition, our results indicate robust recruitment by the keystone Hawaiian forest species, *M. polymorpha* into the clearcut area. *M. polymorpha* exhibited 804 seedlings ha^{-1} across the 1985 study of the clearcut area, a similar number to the 806 stems ha^{-1} documented in the uncut primary forest during 1987 sampling. *M. polymorpha* ranked twelfth among IVs of the 110 species encountered after 2 years of post-disturbance secondary succession. *M. polymorpha* expresses many characteristics of a pioneer species, including the ability to colonize newly formed lava flows with small wind dispersed seeds that are produced throughout the year and germinants

that demand high light environments (Drake 1998, Cordell et al. 2009). *M. polymorpha* propagules may have come from wind dispersed seed after the deforestation event (Cordell et al. 2009), as well as the forest soil seedbank which exhibited the potential to germinate as many nearly 18,000 seedlings ha^{-1}. Regardless of propagule source, *M. polymorpha* established and persisted in the highly diverse and competitive post-disturbance environment in the clearcut area.

M. polymorpha demonstrated the ability to perform as a native pioneer species in a secondary succession context, as it became successfully established within the clearcut area, and outcompeted other pioneer species to develop into virtually monospecific forest stands across much of the clearcut area. After 27 years of secondary succession, only 13 of the 110 species encountered in the 2-year post clearcut sample area were present in the *M. polymorpha*-dominated secondary forest. Hughes et al. (2022) documented the remarkable growth of these 2nd-growth *M. polymorpha* forests, noting that their rates of aboveground carbon accumulation were on par with the highly productive and resilient secondary forests of continental tropical systems (Poorter et al. 2016).

The relative abundance of *Dicranopteris linearis* in the understory of *M. polymorpha*-dominated secondary forests may also have been a factor in subsequent suppression of nonnative understory species. *D. linearis* has been characterized, by virtue of its thick mat-forming growth form, as playing an important role in resisting invasions by nonnative species into recovering forest stands such as those described here (Russell et al. 1998) without appearing to substantively hinder *M. polymorpha* stand development (Hughes et al. 2022).

C. hirta was the only nonnative species to persist as a dominant understory species in *M. polymorpha*-dominated 2nd-growth stands. Although this species is a notably troublesome nonnative invasive shrub species in Hawaii and elsewhere (DeWalt et al. 2004, DeWalt 2006) and is capable of suppressing recruitment of *M. polymorpha* seedlings in Hawaiian forests (Zimmerman et al. 2008), its abundance in this understory did not appear to hinder recovery and growth of *M. polymorpha*-dominated 2nd-growth stands.

Landscape-scale assessment of georeferenced 2013 imagery indicated (Figure 2) that *F. moluccana*-dominated stands occupied approximately 5%, with *M. polymorpha* stands occupying the remaining 95% (note; a guess until tomorrow), of the clearcut area located on 200–400-year-old lava flows sampled here. Where *F. moluccana* was present in the clearcut area, it was able to successfully suppress *M. polymorpha* stand development, and conversely, where *M. polymorpha* occurred, they were able to suppress *F. moluccana* stand establishment and development. Grossman (1992) noted the presence of scattered *F. moluccana* individuals across the research site that had been left by the chipping operation and anticipated this species could play an important role in future forest succession dynamics across the site (Grossman, 1992). Subsequent *F. moluccana*-dominated secondary forest establishment did occur, likely a result of initial colonization of open, high-sunlight areas required by this shade-intolerant, pioneer tree species (Soerianegara et al. 1994, Hughes et al. 2012). Where *F. moluccana* stands did become established, *M. polymorpha* re-establishment and growth was suppressed and understory conditions promoted the invasion of the invasive nonnative species *P. cattleianum* and *C. hirta*. Results agree with those of Hughes and Denslow (2005) that invasion by *F. moluccana* into *M. polymorpha*-dominated stands led to wholesale mortality and subsequent suppression of that native tree species. Prior studies in Hawai‘i (Asner et al. 2008, Mascaro et al. 2012, Hughes et al. 2014) also predicted that *M. polymorpha*-dominated and *F. moluccana*-dominated secondary succession to be mutually exclusive, as our results clearly indicate.

The nonnative tree, *P. cattleianum* (strawberry guava), also rapidly colonized large portions of the clearcut area (Grossman 1992). It was not the target species for woodchips, so in addition to seed germination could root sprout from stems left intact across the clearcut area. *P. cattleianum* is capable of

forming dense clonal thickets after invading understories of intact forests even in the absence of overstory disturbance (Huenneke and Vitousek 1990, Asner et al. 2008, Zimmerman et al. 2008, Barbosa et al. 2017). *P. cattleianum* establishment is reported to exhibit high stem densities on lava flows >200 years old where soil N availability is sufficient and to form dense subcanopy stands on younger lavas where well-established, nonnative, N-fixing, canopy-dominant trees like *F. moluccana* prematurely increase soil N availability (Hughes and Denslow 2005, Zimmerman et al. 2008, Hughes et al. 2014). This is consistent with our results demonstrating *P. cattleianum* relatively high IVs across all stand types except in the *F. moluccana* dominated stands. To date, *P. cattleianum* has invaded, and continues to invade, hundreds of thousands of hectares, displacing endemic and endangered native Hawaiian species in the process (Smith 1985, Zimmerman et al. 2008, Asner et al. 2009).

The fidelity of the two time-period samplings of the uncut primary forest to one another was remarkable. Importance values for most of the common species were similar, indicating that this particular native dominated forest remained somewhat resistant to change from nonnative invasion. The relative abundance of several key native subcanopy and understory species (i.e., *Freycinetia arborea*, *Coprosma menziesii*, *Peperomia* spp., *Vaccinium* spp.) encountered during the 2012 sampling of understory vegetation also provided strong evidence of the native integrity of this forest over time.

The seed bank study demonstrated the majority of early successional vegetation could have originated from seed that was already in place, thus agreeing with earlier studies showing initial floristic composition often starts from the cutover vegetation (Egler 1954). Although only 28% of the total species composition of the adjacent clearcut area were represented in the forest soil bank, this group of species represented 70% of the total importance values for all species. The other 72% of the species colonizing the cutover area were coming in as "relay floristics", implying these native forests are particularly vulnerable to disturbance, as the nonnative successional species are waiting in the seedbank or easily dispersed propagules (Gomez-Pompa and Vazquez-Yanes 1972, Kellman 1980).

That 57 *M. polymorpha* seedlings germinated from sampled forest soils indicates that a substantial number of viable *M. polymorpha* seeds in the soil bank could assist in the rainforest regeneration process. Although Burton and Mueller-Dombois (1984) concluded that light is probably not a severe limitation to *M. polymorpha* germination on the forest floor, the lack of seedlings in the uncut primary forest signifies that some disturbance must be required to release these seeds from dormancy.

This research underscores the threat of nonnative species to the persistence of the Hawaiian native rainforest. Nonnative tree species, like *F. moluccana* and *P. cattleianum* can outcompete native species and permanently alter natural successional processes and the resulting secondary forest composition. *F. moluccana*, in particular, will dominate the forest canopy and suppress the establishment of native tree species.

CONCLUSIONS

The 1985 clearcut of the Ki Ula forests of Kalapana, Hawaii was motivated by the demand of fuel for energy production and associated monetary profits. The importance and value of protecting rare native ecosystems was not part of these motivations, but ultimately succeeded in stopping the destruction. The only apparent benefits of the clearcut event were the public awakening to the intrinsic value of Hawaii's native forests and insight into their vulnerability, functioning, and capacity to persist, which in turn underscored the need for research to advance our understanding of Hawaiian rainforest secondary successional dynamics to help inform and sustain successful management of these ecosystems into the future.

Results confirm the ability of the *M. polymorpha* rainforest not only colonize new lava substrate, but also to revegetate sites following anthropogenic disturbance. *M. polymorpha* stands were shown capable of

successfully establishing across deforested sites but require management intervention to ensure aggressive nonnative trees are managed to allow the establishment and early development of recovering native forest species. In *M. polymorpha* dominated secondary forests, stem densities were nearly 5 times greater than in the uncut primary forest measured at the same time (i.e., 2012) while basal area values averaged 62% of those of the uncut forest after only 27 years of secondary succession (Hughes et al. 2022). This illustrates the ability of *M. polymorpha* to reestablish and grow quickly where it gains an initial "foothold" at a site. The impressive rate of *M. polymorpha* recovery was attributable to a combination of factors: relatively well-developed soils that provided a fertile substrate for widespread and rapid recruitment, and abundant seed sources afforded by adjacent intact *M. polymorpha* dominated forests and the soil seed bank. This last factor underscores the need to maintain as much native-dominated forest as possible to sustain Hawaii's native biodiversity.

In contrast, where localized stands of the nonnative invasive tree, *F. moluccana*, had become established, *M. polymorpha* stem densities and basal area were less than 12% of those in *M. polymorpha*-dominated 2nd-growth stands and basal area values were only 7% of those exhibited by the extant uncut forest (Hughes et al. 2022), confirming that nonnative forest constituents such as *F. moluccana* and *P. cattleianum* are serious impediments to continued existence of Hawaii's native forests.

Results presented here may offer both encouragement and guidance to land managers desiring to reestablish *M. polymorpha* dominated forests in areas that have suffered significant recent mortality. Reestablishment and rapid aboveground C accumulation by *M. polymorpha*-dominated second-growth forests of Hawai'i is possible, even following loss of mature *M. polymorpha* individuals and stands in highly disturbed areas. However, reestablishment will likely only occur where populations of nonnative species can be effectively controlled during early stages of secondary succession to allow for successful recruitment and growth of *M. polymorpha*.

If the ultimate objective is to reestablish the native Hawaiian rainforest with the full complement of understory as well as overstory native rainforest species, forest management will be required. This management must include the physical control of nonnative tree species, at least until the native trees become well established. Ideally introduction of these species should be addressed to ensure fewer introductions, and existing mature tree seed sources should be destroyed.

The clearcutting of this stand of Hawaiian lowland rainforest should never have been allowed to occur. This was the result of a zoning system that allowed short-term financial interests to significantly impact the integrity and sustainability of important native Hawaiian ecosystems. These antiquated policies must be identified and updated to reflect our increased knowledge regarding the importance of these ecosystems which require more focus on conservation and management rather than the short-term economic profit individuals can acquire through resource extraction.

ACKNOWLEDGMENTS

The authors deeply and sincerely thank the late Dr. Dieter Mueller-Dombois for his contribution in stopping this clearcutting activity and having the foresight to encourage our research on this site to advance our understanding of the ecology and management of Hawaii's forests. For the 1985 component of this research, we recognize and appreciate support from the Estate of James Campbell for their support of this research. We thank Lani Stemmerman for her enthusiasm to address any botany and taxonomy questions, Mallikarjuna Aradhya for statistical advice and field support, Jesse Grossman for his cheerful field support regardless of sun or rain, and Christine Pieper for her helpful review and edits to this manuscript.

For the 2015 component of this research, we thank Jon Marshall for invaluable GIS and graphic assistance, and K. Hiraoka, M. Murphy, L. Bufil, E. Bufil, A. Cantan, A. Kaha, N. Wilhoite, I. Sagaga, Z. Winter, C. Rogers, J. Puni, N. Friday, and N. Zimmerman for their valuable field assistance. We also thank the Hawai'i Island Branch of the Division of Forestry and Wildlife, Department of Land and Natural Resources (DOFAW-DNLR), and the Office of Hawaiian Affairs (OHA) for permission to conduct field work in the Kalapana Forest landscapes. We thank E. Lee for helpful assistance and access to study sites through his property.
We also thank the two anonymous reviewers who provided helpful and insightful comments and advice that greatly improved upon earlier versions of the manuscript.

Literature Cited

Aplet, G. H., and P. M. Vitousek. 1994. An age-altitude matrix analysis of Hawaiian rain-forest succession. J. Ecol. 82(1):137–147

Aplet, G. H., R. F. Hughes, and P. M. Vitousek. 1998. Ecosystem development on Hawaiian lava flows: biomass and species composition. J. Veg. Sci. 9(1):17–26

Asner, G. P., R. F. Hughes, P. M. Vitousek, D. E. Knapp, T. Kennedy-Bowdoin, J. Boardman, R. E. Martin, M. Eastwood, and R. O. Green. 2008. Invasive plants transform the three-dimensional structure of rain forests. Proc. Natl. Acad. Sci. U.S.A. 105:4519–4523.

Asner, G. P., R. F. Hughes, T. A. Varga, D. E. Knapp, and T. Kennedy-Bowdoin, 2009. Environmental and biotic controls over aboveground biomass throughout a tropical rain forest. Ecosystems 12:261–278. http://dx.doi.org/10.1007/s10021-008-9221-5

Atkinson, I. A. E. 1970. Successional trends in the coastal and lowland forest of Mauna Loa and Kilauea Volcanoes, Hawaii. Pac. Sci. 24:387–400.

Barbosa, J. M., G. P. Asner, R. F. Hughes, and M. T. Johnson. 2017. Landscape-scale GPP and carbon density inform patterns and impacts of an invasive tree across wet forests of Hawaii. Ecology 27(2):403–415.

Burke, M. J. W., and J. P. Grime. 1996. An experimental study of plant community invasibility. Ecology 77(3):776–790.

Burton, P. J., and D. Mueller-Dombois. 1984. Response of *Metrosideros polymorpha* seedlings to experimental canopy opening. Ecology 65(3):779–791.

Cole, R. J., and C. M. Litton. 2014. Vegetation response to removal of non-native feral pigs from Hawaiian tropical montane wet forest. Biol. Invasions 16:125–140.

Cordell, S., R. Ostertag, B. Rowe, L. Sweinhart, L. Vasquez-Radonic, J. Michaud, T. C. Cole, and J. R. Schulten. 2009. Evaluating barriers to native seedling establishment in an invaded Hawaiian lowland wet forest. Biol. Conserv. 142: 2997–3004.

Crawley, M. J. 1987. Pages 429–453 *in* A. J. Gray, M. J. Crawley, and P. J. Edwards, eds. What makes a community invasible? Colonization, succession, and stability. Blackwell Scientific, London.

Curtis, J. T., and McIntosh, R. P. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. Ecology 32:476–496.

D'Antonio, C. M. 1993. Mechanisms controlling invasions of coastal plant communities by the alien succulent, *Carpobrotus edulis*. Ecology 74:83–95.

DeWalt, S. J. 2006. Population dynamics and potential for biological control of an exotic invasive shrub in Hawaiian rainforests. Biol. Invasions 8(5):1145–1158

DeWalt, S. J., J. S. Denslow, and J. L. Hamrick. 2004. Biomass allocation, growth, and photosynthesis of genotypes from native and introduced ranges of the tropical shrub *Clidemia hirta*. Oecologia 138(4):521–531.

Drake, D. 1998. Relationships among the seed rain, seed bank and vegetation of a Hawaiian forest. J. Veg. Sci. 9:103–112.

Egler, F. 1954. Vegetation science concepts I. Initial floristic composition. Vegetatio 4:412–417.

Giambelluca, T. W., Q. Chen, A. G. Frazier, J. P. Price, Y.-L. Chen, P.-S. Chu, J. K. Eischeid, and D. M. Delparte, 2013: Online rainfall atlas of Hawai'i. Bull. Amer. Meteor. Soc. 94, 313–316. https://doi.org/10.1175/BAMS-D-11-00228.1

Giambelluca, T. W., X. Shuai, M. L. Barnes, R. J. Alliss, R. J. Longman, T. Miura, Q. Chen, A. G. Frazier, R. G. Mudd, L. Cuo, and A. D. Businger. 2014. Evapotranspiration of Hawai'i. Final report submitted to the U.S. Army Corps of Engineers—Honolulu District, and the Commission on Water Resource Management, State of Hawai'i.

Grossman, D. 1992. Early recovery of a Hawaiian lowland rainforest following clearcutting at Kalapana on the Island of Hawaii. PhD Dissertation, University of Hawaii.

Guariguata, M. R., and R. Ostertag. 2001. Neotropical secondary forest succession: changes in structural and functional characteristics. For. Ecol. Manage. 148:185–206.

Gómez-Pompa, A., C. Vázquez-Yanes, and S. Guevara. 1972. The tropical rain forest: a nonrenewable resource. Science 1:762–765.

Hobbs, R. J., and L. F. Huenneke. 1992. Disturbance, diversity, and invasion – implications for conservation. Conserv. Biol. 6(3):324–337.

Holden, C. 1985. Hawaiian rainforest being felled: wood chipping operation decried by scientists as sorry model for bioenergy development. Science 31:1073–1074

Huenneke, L. F., and P. M. Vitousek. 1990. Seedling and clonal recruitment of the invasive tree *Psidium cattleianum* – implications for management of native Hawaiian forests. Biol. Conserv. 53(3):199–211.

Hughes, R. F., and J. S. Denslow. 2005. Invasion by an N_2-fixing tree, *Falcataria moluccana*, alters function, composition, and structure of wet lowland forests of Hawaii. Ecol. Appl. 15:1615–1628.

Hughes, R. F., A. L. Uowolo, and T. P. Togia. 2012. Recovery of native forest after removal of an invasive tree, *Falcataria moluccana*, in American Samoa. Biol. Invasions 14(7):1393–1413.

Hughes, R. F., G. P. Asner, J. Mascaro, A. Uowolo, and J. Baldwin. 2014. Carbon storage landscapes of lowland Hawaii: the role of native and invasive species through space and time. Ecol. Appl. 24:716–731.

Hughes, R. F., D. Grossman, T. G. Sowards, J. D. Marshall, and D. Mueller-Dombois. 2022. Aboveground carbon accumulation by second-growth forests after deforestation in Hawai'i. Ecol. Appl. 32(4):e2539. https://doi.org/10.1002/eap.2539

Kandert, S., H. Kreft, N. DiManno, A. Uowolo, S. Cordell, and R. Ostertag. 2021. Influence of light and substrate conditions on regeneration of native tree saplings in the Hawaiian lowland wet forest. Pac. Sci. 75(1):107–127

Kellman, M. 1980. Geographic patterning in tropical weed communities and early secondary successions. Biotropica 12: 34–39.

Kent, M. 2011. Vegetation description and data analysis: A practical approach. 2nd edition. Wiley-Blackwell, New Jersey. 448 pp.

Kitayama, K., D. Mueller-Dombois, and P. M. Vitousek. 1995. Primary succession of Hawaiian montane rain forest on a chronosequence of eight lava flows. J. Veg. Sci. 6:211–222.

Kurina, L. M., and P. M. Vitousek. 1999. Controls over the accumulation and decline of a nitrogen-fixing lichen, *Stereocaulon vulcani*, on young Hawaiian lava flows. J. Ecol. 87(5):784–799.

Mascaro, J. T., R. F. Hughes, and S. A. Schnitzer. 2012. Novel forests maintain ecosystem processes after decline of native tree species. Ecol. Monogr. 82:221–238.

Mueller-Dombois, D. 1985. The biological resource value of native forest in Hawai'i with special reference to the tropical lowland rainforest at Kalapana. 'Elepaio 45(10):95–101.

Mueller-Dombois, D., and H. Ellenberg. 1974. Aims and methods of vegetation ecology. John Wiley & Sons, New York, NY, USA.

Ohtsuka, T. 1999. Early stages of secondary succession on abandoned cropland in north-east Borneo Island. Ecol. Res. 14: 281–290

Poorter, L., F. Bongers, T. M. Aide, A. M. Almeyda Zambrano, P. Balvanera, J. M. Becknell, V. Boukili, P. H. S. Brancalion, E. N. Broadbent, R. L. Chazdon, D. Craven, J. S. de Almeida-Cortez, G. A. L. Cabral, B. H. J. de Jong, J. S. Denslow, D. H. Dent, S. J. DeWalt, J. M. Dupuy, S. M. Durán, M. M. Espírito-Santo, M. C. Fandino, R. G. César, J. S. Hall, J. L. Hernandez-Stefanoni, C. C. Jakovac, A. B. Junqueira, D. Kennard, S. G. Letcher, J. C. Licona, M. Lohbeck, E. Marín-Spiotta, M. Martínez-Ramos, P. Massoca, J. A. Meave, R. Mesquita, F. Mora, R. Muñoz, R. Muscarella, Y. R. F. Nunes, S. Ochoa-Gaona, A. A. de Oliveira, E. Orihuela-Belmonte, M. Peña-Claros, E. A. Pérez-García, D. Piotto, J. S. Powers, J. Rodríguez-Velázquez, I. E. Romero-Pérez, J. Ruíz, J. G. Saldarriaga, A. Sanchez-Azofeifa, N. B. Schwartz, M. K. Steininger, N. G. Swenson, M. Toledo, M. Uriarte, M. van Breugel, H. van der Wal, M. D. M. Veloso, H. F. M. Vester, A. Vicentini, I. C. G. Vieira, T. Vizcarra Bentos, G. B. Williamson, and Danaë M. A. Rozendaal. 2016. Biomass resilience of Neotropical secondary forests. Nature 530:211–214.

Raich, J. W., W. J. Parton, A. E. Russell, R. L. Sanford, Jr., and P. M. Vitkousek. 2000. Analysis of factors regulating ecosystem development on Mauna Loa using the Century model. Biogeochemistry 51:161–191.

Russell, A. E., J. W. Raich, and P. M. Vitousek. 1998. The ecology of the climbing fern *Dicranopteris linearis* on windward Mauna Loa, Hawai'i. J. Ecol. 86:765–779.

Smith, C. W. 1985. Impacts of alien plants on Hawaii's native biota. Pages 180–250 *in* C. P. Stone and J. M. Scott, ed. Hawaii's terrestrial ecosystems: Preservation and management. Cooperative National Park Resources Studies Unit, Honolulu.

Soerianegara, I., E. N. Lemmens, and R. H. M. J. Lemmens, eds. 1994. Plant resources of South East Asia No. 5 (1), Timber trees: major commercial timbers. PROSEA Foundation, Bogor.

USDA. 1955. Soil Survey Report. Soil Conservation Service in cooperation with the Hawaiian Agricultural Station.

Vitousek, P. M., and L. R. Walker. 1989. Biological invasion by *Myrica faya* in Hawaii: plant demography, nitrogen fixation, ecosystem effects. Ecol. Monogr. 59:247–265.

Vitousek P. M., L. R. Walker, L. D. Whiteaker, and P. A. Matson. 1993. Nutrient limitations to plant-growth during primary succession in Hawaii-Volcanos-National-Park. Biogeochemistry 23(3):197–215.

Wagner, W. L., D. R. Herbst, and S. H. Sohmer. 1999. Manual of the flowering plants of Hawai'i. University of Hawai'i Press, Honolulu, Hawaii, USA.

Wolfe, E. W., and J. Morris. 1996. Geologic map of the Island of Hawaii; Map I-2524-A. Miscellaneous Investigations Series; U.S. Geological Survey.

Woodcock, D. 2003. To restore the watersheds: early twentieth-century tree planting in Hawai'i. Ann. Assoc. Am. Geogr. 93:624–635.

Zimmerman, N., R. F. Hughes, S. Cordell, P. Hart, H. K. Chang, D. Perez, R. K. Like, and R. Ostertag. 2008. Patterns of primary succession of native and introduced plants in lowland wet forests in eastern Hawai'i. Biotropica 40:277–284.