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Stand Analysis of an Invading Firetree (*Myrica faya* Aiton) Population, Hawaii[1]

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ABSTRACT: Since 1971, the exotic firetree (*Myrica faya*) has been invading a native ohia tree (*Metrosideros collina* subsp. *polymorpha* Rock) habitat in the 1959 Kilauea Iki devastation area, Hawaii Volcanoes National Park. Ninety-six trees of the invading population were analyzed as to structural and fruiting characteristics.

Data were collected from two permanent transects that were designed to provide for continued study of the firetree and ohia community.

Initial findings reveal that the present firetree spread depends on an outside seed source, and successful seedling establishment is dependent on favorable microhabitat conditions beneath ohia trees. As yet, no competitive replacement of ohia trees by firetrees has been observed. On the contrary, firetrees over 2 m tall that had grown up and into ohia tree crowns were exhibiting poor vigor. Additionally, there is a high positive correlation between firetree loss of vigor and diameter increase beyond 4–5 cm.

Preliminary observations suggest that firetree seed dispersal depends on birds, primarily, the exotic Japanese white-eye (*Zosterops japonica*).

FIRETREE (*Myrica faya* Aiton), an aggressive, noncommercial, exotic species that is native to the Azores, Madeira, and Canary Islands, has been spreading rapidly in Hawaii for approximately 80 years. This tree was introduced in Hawaii for reforestation in the late 1800s, but by 1944 it had become so aggressive in colonizing agricultural and forested land that the Board of Agriculture and Forestry was pursuing a control program to eradicate it (Neal 1965).

DISTRIBUTION AND CONTROLS

Firetree concentration is dense on the islands of Maui and Hawaii, however, the major efforts of control have been on the island of Hawaii. In 1961 Kawasaki (1961) reported that the major concentrations on the island of Hawaii were along the Hamakua coast from Laupahoehoe to Honokaa, then *mauka* (toward the mountain side) to the Parker and Kukaiau Ranches. Areas in order of highest density of trees were pastures, croplands, uncleared areas, and wastelands. In the humid Hamakua climate firetrees grow to over 50 ft high, forming dense canopies with an understory devoid of other plant life. A smaller population covering 300–400 acres in the Olaa Forest near Hawaii Volcanoes National Park (HVNP) was also reported in the 1961 survey.

In a 1966 survey Kawasaki (1966a) estimated that the Olaa Forest infestation had increased to 4500 acres, including 1500 acres on forest reserve land and 25 acres in HVNP. Two additional infestations were observed in the national park: (1) a 50-acre site on the northeast rim of Kilauea Crater; and (2) a 150-acre site at the intersection of the Chain of Craters Road and the Ainahou Escape Road. A single plant reported growing on the barren southwest rim of Kilauea Caldera was eradicated by a local resident (Kawasaki 1966b). At this time the

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HVNP started a control of firetree, but lack of sufficient funds and labor limited the effort.

Invasion of firetree on the island of Hawaii has increased exponentially. A 1970 survey revealed that more than 40,000 acres of the island were infested with firetree (Walters and Null 1970). The 225 acres that were infested in HVNP in 1966 had increased to approximately 9000 acres in 1977. (Donald Reeser, personal communication). Infested acreage varied from light (1 tree/acre) to heavy (1000 trees/acre) concentrations, with the major distribution being in the seasonal dry forest section of the park. From 1967 to 1974, 62,776 firetrees were removed from the park, and from 1975 to 1978, and additional 30,884 were destroyed, making a total of approximately 100,000 trees removed over a 10-year period, and yet the plant continues to spread (Smathers 1976). The National Park Service (NPS) considers the firetree invasion an unnatural phenomenon that threatens and impairs the natural and historic quality of the park vegetation.

The United States Forest Service (USFS) and the Hawaii State Board of Forestry (HSBF) consider firetree to be an aggressive exotic with no commercial value, which is occupying land that should be utilized for agriculture and commercial forestry purposes. The State of Hawaii has conducted a control program for nearly 20 years, but funding and labor availability have caused considerable fluctuations in this effort. Herbicides are the primary means of control. Of the various herbicides used, Tordon 22K has proved the most successful in giving complete canopy kill and 99 percent control of sprouting (Kim 1969, Walters 1973, Walters and Null 1970).

The USFS has conducted experiments in establishing commercial type trees on sites where firetrees were removed with herbicides. Of several commercial species planted, only the Australian toon tree seemed to be promising for reforestation (Walters 1970). However, Null (1967) in an earlier evaluation of the cost and effectiveness of controlling firetree with Tordon 22K showed that it cost \$92.75/acre, which was considered a high price to pay for the program. One may wonder whether there is a cheaper way or whether the control of firetree is worth the cost.

Controls in HVNP consist of uprooting small trees and using Kuron herbicide (2–4,5 TP) on medium and large trees. In addition to chemicals, several species of insects have been tested for control of firetree, but none has been successful (Krauss 1964).

ECOLOGICAL EVALUATION

As yet no comprehensive ecological evaluation has been made of the long-term impact of firetree upon the native vegetation. It seems reasonable that such a study should be conducted, considering the long period firetree has been colonizing the island ecosystems. In addition, the complete eradication of firetree is not likely. The latter is especially true in wild lands where agriculture and forestry are not practiced. Such a study should reveal the ecological role that the firetree has assumed in relation to the native species, as well as in relation to other exotic species now naturalized to Hawaii. Information of this type would provide resource managers with a better knowledge of how to evaluate the firetree's presence relative to their agencies' missions and policies.

Firetree's seemingly aggressive habit, characterized by horde invasion and quick development of a closed-canopy forest, can be threatening to the native biota and therefore distressing for resource managers. Yet these same habits can characterize a species that may not have a long-term presence or occupy a dominant position in a climax community. In addition, it has never been determined how firetree seeds are disseminated, and whether the plant can become reestablished in areas where it was previously eradicated.

There is now an excellent opportunity to study firetree as it invades a series of ecosystems in Hawaii. Since 1971, firetree has been invading the devastation area of the 1959 Kilauea Iki Crater eruption site in HVNP,

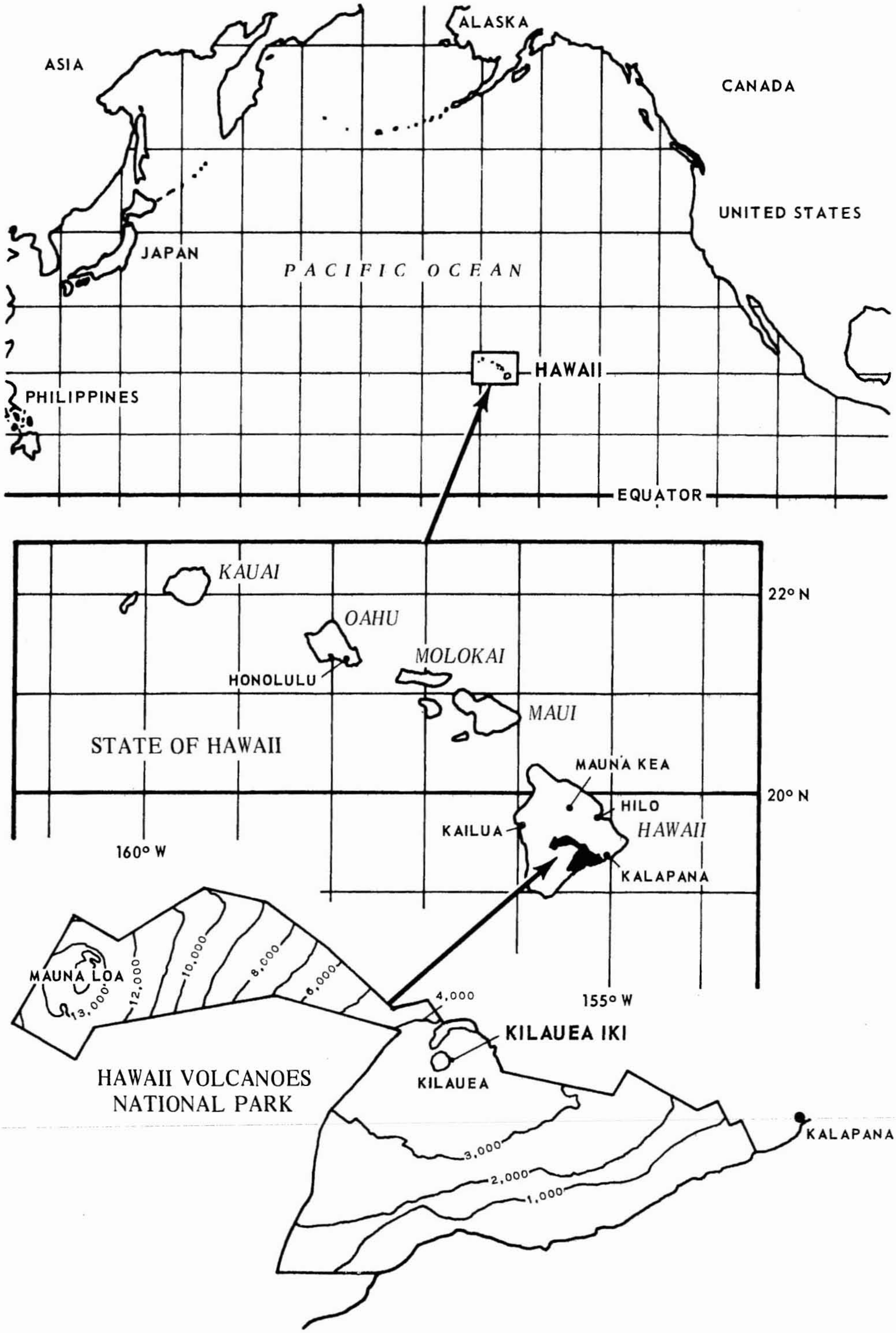

FIGURE 1. Map showing location of Kilauea Iki Crater in reference to Hawaii Volcanoes National Park and the Pacific basin.

where a similar comprehensive ecological study by the senior author has been underway for nearly 20 years (Figure 1) (Smathers and Mueller-Dombois 1974). A main objective of the devastation area study is to determine the competitive relationship between native and exotic plants as they colonize recent volcanic substrates. Results of this study have thus far shown that exotic and native plants have both a competitive and complementary relationship. In all habitats native woody plants eventually have been capable of replacing or holding their own with exotics (Smathers and Mueller-Dombois 1974). Because of the success of this project, part of the devastation area has now been set aside for concentrated study of the invading firetree population.

STUDY AREA

In December 1959 Kilauea Iki, a pit crater on the summit of Kilauea Volcano, erupted and deposited a blanket of pumice over an area of 500 hectares. Later the entire area, which is at approximately 1200 m elevation, became known as the *devastation area*. The latter name was given to the area because of widespread destruction of both a montane rain forest and a seasonal dry forest. With its variety of climates, substrates, and contiguous populations of native and exotic plants, the area provided a unique opportunity to study the formation of new plant communities.

Immediately after the eruption, a study was begun of plant invasion and recovery within six habitats (Figure 2). These were recognized by kinds of substrate and remains of the former vegetation. A series of permanent photographic stations, belt transects, and quadrats was established to record the chronological sequence of plant succession and recovery. The results of this study have provided information heretofore unknown on the phytosociological relationships of native and exotic plants (Smathers 1976, Smathers and Mueller-Dombois 1974).

During the 15-year observation period (in 1974) a small population of firetree seedlings was recorded in the western part of habitat 6 near Byron Ledge. It is estimated that the initial invasion started about 1971.

The habitat is easily recognized because it has a large number of surviving native ohia (*Metrosideros collina* subsp. *polymorpha* Rock) trees with a pumice layer that varies from approximately 30 cm to 3 m in depth (habitat 5, Figures 3, 4). It is in the lee of the cinder cone that formed during the 1959 eruption and slopes gently in a southwesterly direction. This habitat is somewhat protected from the prevailing northeasterly tradewinds. However, it receives greater insolation in the lower sectors because of decreased cloud cover. The approximate mean annual air temperature is 17.0°C and the mean annual rainfall is approximately 2700 mm. Mean evaporation rate from Livingston atmometers was 6.0 cm^3/day/week with a mean deviation of 2.7. The climate is characterized by humid mild winters and warm dry summers (Smathers and Mueller-Dombois 1974).

METHODS

A survey was made of the firetree infestation pattern in habitat 5 to determine its boundary, homogeneity, and direction of invasion before placement of transects for stand analysis. Two permanent belt transects at right angles to one another were then established in the infested area. It was not possible to determine direction of invasion, as size classes (height and diameter) were found evenly distributed throughout the populated area. One transect, C-C′, which was 180 m long and consisted of contiguous 10 × 10 m plots, was originally established in 1960 for the devastation area study. The other transect, W-W′, was 70 m long and consisted of 10 × 20 m contiguous plots (Figure 2).

Ninety-six firetrees were sampled within the transects for height, basal diameter, vigor, and fruiting characteristics. A vigor rating of good was given to those specimens with dark-green foliage, mature fruits, and strong terminal growth. A rating of average

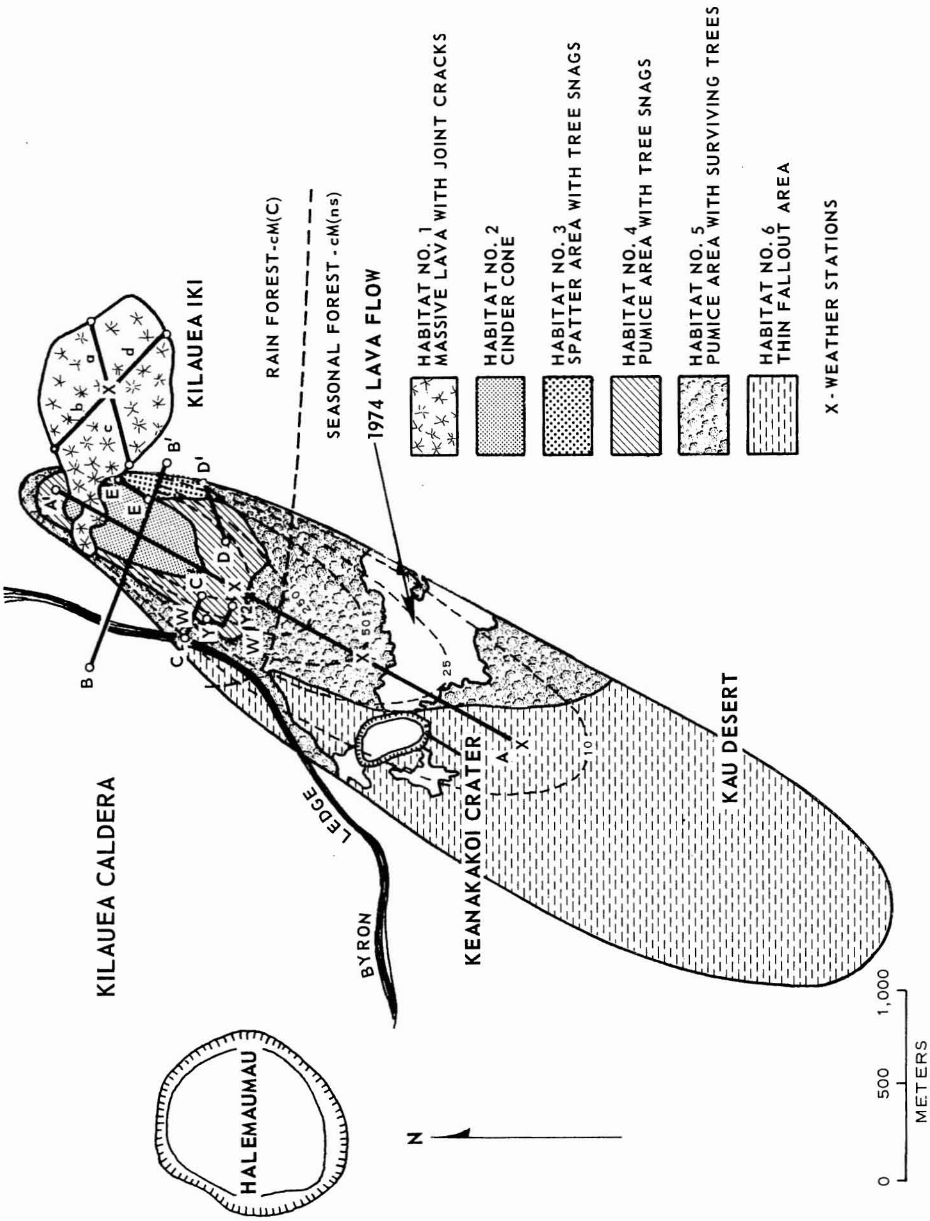

FIGURE 2. Habitat types of the 1959 Kilauea Iki eruption site (crater floor and pyroclastic deposit).

was given to those exhibiting green foliage, both mature and immature fruits, and medium terminal growth. A rating of poor included specimens with numerous pale-green to chlorotic leaves, defoliated branches, fruit falling before maturity, and terminal dieback. Associated plant species were recorded as to their location (beneath, above, interlocking, etc.) in relation to each firetree. Parameters of density, frequency, and percent cover were determined for the various height and diameter ranges. Unusual growth forms were also recorded.

An invasion pattern similar to that of the

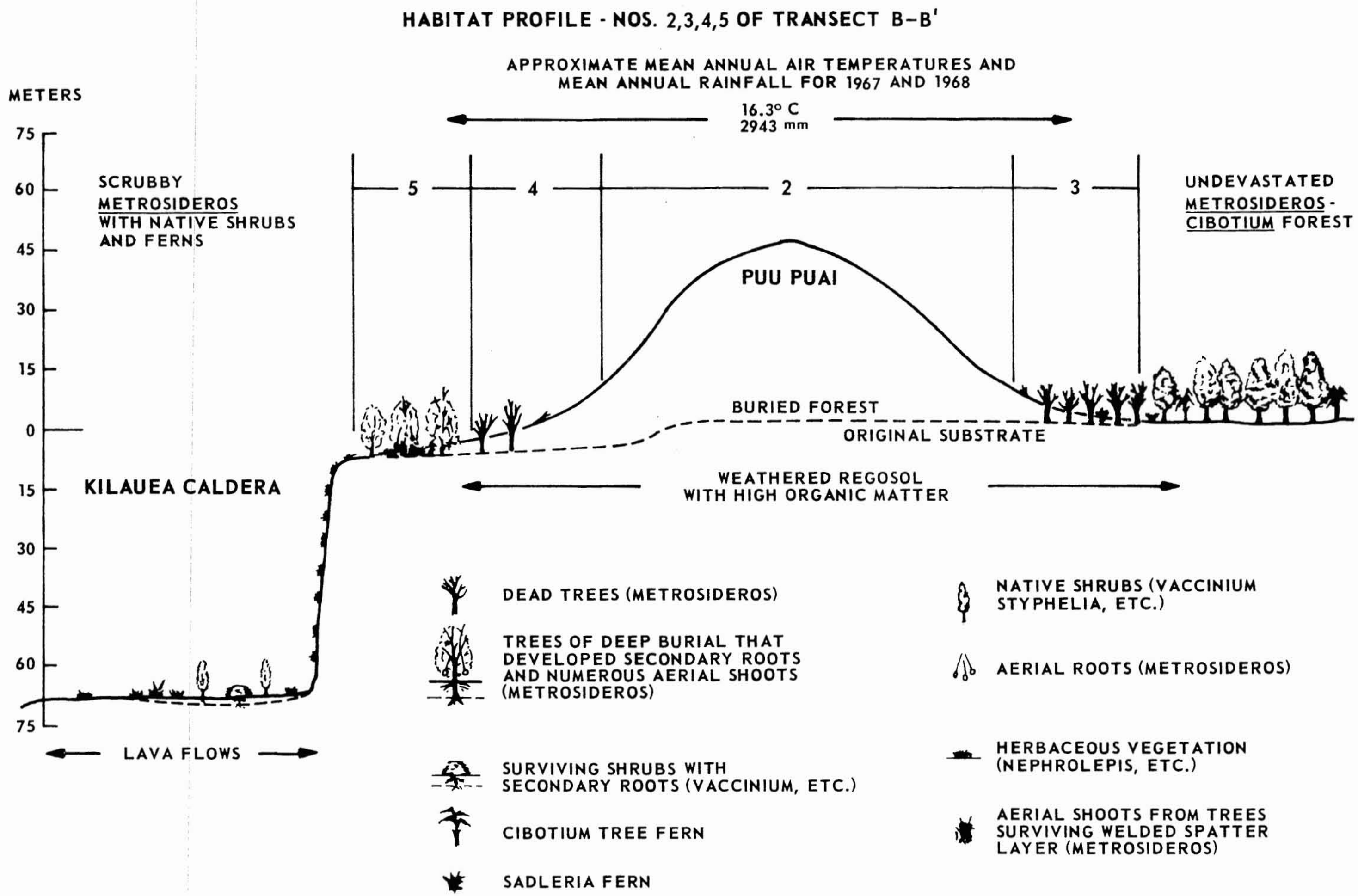

FIGURE 3. Northeast–southwest profile of eruption extending from Kilauea Iki Crater to upper Kau Desert.

FIGURE 4. Scene of habitat 5 with surviving ohia trees where firetrees invaded (left arrow). Habitat 4 pumice area with tree snags where native and exotic shrubs have invaded (right arrow). Photographed February 1978.

firetree was observed during an earlier tree invasion of the devastation area study (Smathers and Mueller-Dombois 1974). In the third year after the 1959 eruption, a weedy, exotic shrub, *Buddleja asiatica* Loureiro, began to invade the area in hordes. By the seventh year it had an 86 percent frequency of occurrence in habitat 3. Over 90 percent of the shrubs were established under surviving ohias in habitat 3 or by dead ohia snags in habitat 4 (Figure 2). Rainfall and fog interceptor studies (Smathers and Mueller-Dombois 1974) revealed that the surviving trees and snags intercepted large volumes of water that were concentrated at their bases. *Buddleja asiatica* readily became established in these microhabitats, but whenever a snag fell, *B. asiatica* quickly developed poor vigor and eventually died. By the ninth year *B. asiatica* had begun to die back throughout all habitats, even where it had originally started under surviving ohias.

RESULTS AND DISCUSSION

The terms *seedling*, *shrub*, and *small tree* are used for the following approximate height and diameter ranges: seedling = diameter < 2 cm, height up to 1.8 m; shrub = diameter 2–3 cm, height 1.3–3.6 m; small tree = diameter > 4 cm, height > 2 m.

Stand Structure and Vigor Characteristics

By totaling both transects in Table 1 (C-C′ and W-W′), it may be noted that the greatest

TABLE 1

STRUCTURE AND VIGOR OF FIRETREE POPULATION, HABITAT 5

BASAL DIAMETER RANGE (cm)	NUMBER OF TREES	NUMBER WITH BASITONIC BRANCHING	VIGOR CLASS NUMBER OF TREES/ % OF DIAMETER RANGE			NUMBER ASSOCIATED WITH OHIA		NUMBER ASSOCIATED WITH SPECIES OTHER THAN OHIA	NUMBER GROWING IN OPEN
			O (POOR)	+ (AVERAGE)	++ (GOOD)	NUMBER INTERLOCKING WITH OHIA	NUMBER GROWING UNDERNEATH OHIA		
TRANSECT C-C′, 18 PLOTS, 10 × 10 m, TOTAL SAMPLE AREA 1800 m²									
< 2	9	0	0/0	6/66.7	3/33.3	2	7	0	0
2– 3	17	5	1/5.9	14/82.4	2/1.2	11	6	0	0
4– 5	11	2	3/27.3	6/54.5	2/18.2	7	3	0	1
Subtotals	37	7	4/10.8	26/70.3	7/18.9	20	16	0	1
TRANSECT W-W′, 7 PLOTS, 10 × 20 m, TOTAL SAMPLE AREA 1400 m²									
< 2	23	0	1/4.3	7/30.4	15/65.2	8	10	2	3
2– 3	18	4	3/16.7	10/55.6	5/27.8	14	3	1	0
4– 5	15	4	11/73.3	2/13.3	2/13.3	13	2	0	0
6– 7	2	0	1/50	1/50	—	2	0		
8– 9	—	—	—	—	—	—	—	—	—
10–11	1	0	1/100	—	—	1	0	0	0
Subtotals	59	8	17/28.8	20/33.9	22/37.3	38	15	3	3
BOTH TRANSECTS COMBINED, 25 PLOTS, 3200 m² TOTAL COVER									
Totals	96	15	21	46	29	58	31	3	4

FIGURE 5. Firetree seedlings (< 2 cm diameter) growing beneath ohia tree. Photographed February 1978.

number of trees (61, in blocked areas) is in the 2–5-cm basal diameter range; the second greatest number (32) is in the < 2-cm seedling range; and the next lowest number (2) is in the 6–7-cm range. This number trend in diameter ranges indicates that firetree is invading the area. In addition, these data indicate that diameters increase with age.

Considering that the first seedling was observed in habitat 5 in 1971, the oldest trees are less than 10 years old.

Of the 96 firetrees examined in Table 1, 89 (58 interlocking plus 31 growing underneath) were directly associated with the native ohia trees by being rooted beneath their crowns. In the < 2-cm diameter range, 27 seedlings having a height range of 0.20–2.00 m grew beneath ohia trees, and 10 of these over 1 m tall (2 in C-C′ plus 8 in W-W′) were beginning to interlock with the lower ohia branches. In the 2–3-cm range, 34 shrubby firetrees were growing beneath ohia trees, and 25 of these (11 in C-C′ plus 14 in W-W′) were interlocking with ohia branches. In the 4–5-cm range and up to the 4-m height range, 25 small trees grew beneath ohias, with 20 exhibiting strong interlocking of branches with ohia (7 in C-C′ plus 13 in W-W′). In the 6–7-cm range, all had interlocking of most branches with both ohia and firetree canopies growing together as one. The data in Table 1 show that firetree seedlings become established beneath ohia trees (Figure 5) and then grow upward and into the ohias' crowns with interlocking branches (Figure 6). One could assume that this behavior of firetree toward ohia would appear to end in competitive replacement of the latter. However, in only one firetree–ohia interlock situation did an ohia exhibit low vigor. In contrast, the firetree was not faring as well, as shown in Table 1 (blocked areas). In transect C-C′ its vigor is from average to good in the < 2-cm range. However, this condition shifts in the 2–3-cm range, where 82.4 percent of the firetrees exhibited average vigor, and on reaching the 4–5-cm range, average vigor has decreased to 54.5 percent and 27.3 percent of the trees exhibit poor vigor. In transect W-W′ a similar relationship exists, with poor vigor continuing to increase with diameter range.

The data show that firetree in the study area habitat tends to lose vigor as it increases in size. Cause of the vigor loss may be a lack of available soil water. The recent pumice soil is exceedingly dry regardless of the high rainfall (2700 mm) for habitat 5. Available water for plants ranges only from 2 percent to 3 percent. Thus, there is less water available in this new volcanic material than in most sands, and plants in open areas will have water for growth only for a short period after showers (Smathers and Mueller-Dombois 1974).

It is not known whether there is competition between the ohia and firetree root systems. Surviving ohia were rooted in the old soil layer prior to the 1959 ash fallout layer (Figure 3). In localities where the ash fallout was over 0.5 m, a secondary root system had developed on the buried ohia trees, thus there could be competition between the two trees for water and nutrients. In any case, ohia would still have the advantage by having a rooting system in the old soil, which still receives water filtering through the new soil.

Undoubtedly, there is some competition for light between the interlocking foliage of ohia and firetree, but this does not seem to be as important to loss of vigor as the soil water relationship. This assumption is supported by the fact that firetrees growing in isolation without closely neighboring trees also show similar symptoms of lack of vigor.

Quantitative Characteristics

Additional quantitative characteristics of height, density, frequency, and percent cover are shown in Table 2. Frequency was determined as the number (percent) of times firetree was recorded in 18 of the 10 × 10 m contiguous plots in transect C-C′ and in 7 of the 10 × 20 m plots of transect W-W′. Cover was expressed as a percentage of the total firetree crown cover in the total area covered by each transect. In transect C-C′, the 2–3-cm range had the highest density and frequency, and had the second highest percentage of cover, thus showing its dominance in the community structure (stratification). In transect W-W′, the < 2-cm class had the highest density (1.64/100 m^2) and frequency, but the 2–3-cm and 4–5-cm ranges had the same frequency and also the highest percentage of cover (3.88 and 5.72, respectively). The higher total density, frequency, and percent cover of the W-W′

FIGURE 6. Firetree shrub (6.3 cm diameter, 2.8 m tall) growing up and into ohia tree with interlocking crowns. Photographed February 1978.

TABLE 2

QUANTITATIVE CHARACTERISTICS OF FIRETREE POPULATION, HABITAT 5

BASAL DIAMETER RANGE (cm)	NUMBER OF TREES	HEIGHT RANGE (m)	DENSITY IN 10 × 10 m PLOTS	FREQUENCY (%)	COVER (% OF TOTAL COVER)
TRANSECT C-C′, 18 PLOTS, 10 × 10 m, TOTAL COVER 1800 m²					
< 2	9	0.34–1.80	0.50/100 m²	38.9	0.48
2– 3	17	1.30–3.20	0.94/100 m²	50.0	2.79
4– 5	11	2.10–4.00	0.61/100 m²	33.3	3.22
Subtotals	37	—	2.05/100 m²	72.2	6.49
TRANSECT W-W′, 7 PLOTS, 10 × 20 m, TOTAL COVER 1400 m²					
< 2	23	0.20–2.00	1.64/100 m²	85.7	0.88
2– 3	18	1.85–3.60	1.29/100 m²	85.7	3.88
4– 5	15	2.40–4.00	1.07/100 m²	85.7	5.72
6– 7	2	2.80–4.10	0.14/100 m²	28.6	0.76
8– 9	0	—	—	—	—
10–11	1	4. 0	0.07/100 m²	14.3	1.22
Subtotals	59	—	4.21/100 m²	100.0	12.46
BOTH TRANSECTS COMBINED, 25 PLOTS, 3200 m² TOTAL COVER					
Totals/averages	96	—	3.13/100 m²	86.1	9.48

transect as compared to the C-C′ transect is due to wider spacing of ohia trees in C-C′ than in W-W′. These parameters tend to confirm the close dependency that firetree has on ohia for its establishment in habitat 5. Thus, there were more available microhabitats (beneath ohia crowns) in transect W-W′ for firetree to colonize.

Flowering and Fruiting Characteristics

Data on fruiting are shown in Table 3. The following information on flowering and fruiting was also obtained in August 1977. Most noticeable was the drying up of male flowers and green immature fruits developing on several plants. Also, considerable defoliation was occurring on the branches of three plants that bore both male flowers and fruits. Approximately one-fourth of the fruits observed were purple, which indicated they were mature. With the exception of defoliation, the flowering and fruiting cycle of firetree in Hawaii probably approximates that in the plant's native habitat. In Madeira and the Canary Islands, Krauss (1964) observed firetrees in June with abundant male flowers and immature green fruits. However, he noted that the male flowers were drying up. From July to September he reported that most of the green fruits had turned purple, and by November there were many mature fruits, with some on the ground.

Fruiting starts with the devastation area firetrees in the 2–3-cm range. Three of the 17 trees in transect C-C′ had fruits, while three of the 18 trees in transect W-W′ had fruits. The percentage of trees with fruits increased with diameter size (blocked areas in Table 3). At the 4–5-cm range, 14/26 of the trees had fruits (C-C′ and W-W′ combined). At the 6–7-cm range all the trees had fruits. There were no seedlings beneath those trees that bore fruit, even though the ground beneath some trees was covered with fruits. Twenty-four percent of all trees had fruits, which consisted of 4/96 with immature fruits, 6/96 with mature fruits, and 13/96 with both mature and immature fruits.

The data show that firetree begins to produce seed at an early age, and that the seed crop continues to increase as the stand gets older. Thus, numerous seeds are available for the stand regeneration and outside dispersal. This prolific seed production and invasion pattern tends to characterize some

TABLE 3

FRUITING CHARACTERISTICS OF FIRETREE POPULATION, HABITAT 5 (AUGUST 1977)

BASAL DIAMETER RANGE (cm)	NUMBER OF TREES	NUMBER OF TREES WITH IMMATURE FRUITS	MATURE FRUITS	BOTH MATURE AND IMMATURE FRUITS (8 AUGUST 1977)	TREES WITH FRUIT
TRANSECT C-C′, 18 PLOTS, 10 × 10 m, TOTAL SAMPLE AREA 1800 m²					
<2	9	0	0	0	0/9
2– 3	17	1	0	2	3/17
4– 5	11	3	2	2	7/11
Subtotals	37	4	2	4	10/37
TRANSECT W-W′, 7 PLOTS, 10 × 20 m, TOTAL SAMPLE AREA 1400 m²					
<2	23	0	0	0	0/23
2– 3	18	0	0	3	3/18
4– 5	15	0	3	4	7/15
6– 7	2	0	0	2	2/2
8– 9	0	—	—	—	—
10–11	1	0	1	0	1/1
Subtotals	59	0	4	9	13/59
BOTH TRANSECTS COMBINED, 25 PLOTS, 3200 m² TOTAL COVER					
Totals	96	4	6	13	23/96

species that are not long-term colonizers. Whether this is true of firetree is yet to be determined.

It is not known what caused defoliation of terminal branches of three trees after they had produced flowers and fruits, although action of pathogenic fungi is a likely contributor. Soil dryness also could be a factor. These were relatively large trees ranging from 3.95 to 5.67 cm in diameter and from 3.1 to 3.9 m tall. Two of the trees exhibited poor vigor and one average vigor. This condition suggests a stress condition brought on by lack of available soil water. It could also indicate a response of conserving energy needed for fruit development.

The means of dispersal of firetree throughout habitat 5 is still unknown. As previously pointed out, it is not likely that the large number of seedlings are offspring from the small number of trees capable of producing mature fruit. Also, there is no invasion pattern characterized by a sequential trend of diameter ranges along a directional gradient. The spatially random distribution of diameter sizes suggests birds as the major dispersal agent. In addition, the fact that 93 percent of firetrees are established underneath ohia crowns suggests a strong correlation to the distributional pattern other than just microhabitat conditions for seed germination.

There is good reason to believe that birds are the main dispersal agents of firetree seed. While collecting field data, the investigators observed numerous Japanese white-eye (*Zosterops japonica*) foraging in the ohia trees. The white-eye is an exotic bird in Hawaii, being native to Japan, as its name implies. It has been observed to feed on insects, nectar, and fruits in Hawaii (Guest 1973). In Australia, Gannon (1936) reported that white-eye spread blackberry, lantana, and several other species of plants. Although white-eyes were never observed feeding on firetree fruits in habitat 5, its foregoing food habits make it a prime suspect. It seems logical that as Japanese white-eyes forage among the ohia flowers for nectar or insects, they could be depositing firetree seeds obtained from trees outside the devastation area. The presence of numerous firetree seedlings beneath ohia crowns, and often close to the trunk, tends to support the

FIGURE 7. Firetree with multiple branching at base of main stem (largest branch is approximately 3.5 cm in diameter and 2 m tall). Photographed February 1978.

assumption that seeds are being deposited by birds. Another exotic bird common to the area, that may also be capable of spreading firetree, is the red-billed leiothrix (*Leiothrix lutea*).

Growth Form Characteristics

Data are shown in Table 1. Firetrees in the 2–3-cm and 4–5-cm ranges exhibited a high degree of basitonic branching (multiple branching near base of main stem; Figure 7). The cause for this type of adventitious budding was not determined. A similar budding and branching developed at the base of firetrees that were burned in the park's Hiiaka Crater fire of 1967 (Smathers 1967). It seems likely that the basitonic branching is a response to a stressful condition. For example, one firetree specimen found in the 1974 survey of the devastation area (Smathers 1976) is believed to have survived the 1959 ash fallout (Figure 8). This tree had a stem 10 cm in diameter that appeared to have been burned off by the hot falling ash. It occurred approximately 10 cm below the 1959 ash level, underneath and close to the trunk of a surviving ohia tree. It had numerous branches that sprouted from the burned stump. These branches had been unable to penetrate the dense basal branches of the surviving ohia, and thus they had grown outward, prostrate on the ground, beyond the periphery of the crown and then upward. This growth response which occurred under a dense ohia crown could indicate a low shade tolerance under ohias with high crown density. A similar condition was also observed in transects C-C′ and W-W′, where a majority of firetrees grew into ohias with open crowns, while similar prostrate growth behavior occurred where the basal canopy was dense.

FIGURE 8. Firetree branches growing outward and upward from dense basal branches of ohia. Photographed February 1978.

CONCLUSIONS

The devastation study area provides a unique opportunity to study firetree ecology. Here, a population can eventually be studied under six different habitat conditions that range from rain to seasonal dry forest types.

At present, the firetree has been able to invade only the pumice habitat with surviving ohia trees (habitat 5). Here, the firetree population has developed a specific structural pattern (diameter and height ranges) that reveals its progressive invasion of the area since 1971. Both structural characteristics and the invasional pattern have been dependent on the presence of ohia trees providing suitable microhabitat conditions. The density and frequency of diameter ranges show that present population of firetrees is expanding where available ohia habitat exists. Although one-fourth of the trees are producing fruits, the great abundance of seedlings indicates that the major seed source is still outside the stand.

Although several factors have been evaluated, the results are preliminary. Present results suggest that the firetree population is not yet competitively replacing ohia trees, nor any other native vascular plant growing in the new volcanic material of the study habitat. In contrast, the firetrees show a decided loss in vigor as they develop into shrub and tree size, apparently a function of low availability of soil water for an increasing biomass.

The surviving ohia trees have created a mesic microhabitat beneath their canopy, in comparison to the xeric soil environment outside the canopy. An accumulating litter layer has formed beneath each tree; this layer is periodically moistened by rain and is protected from desiccation by crown cover. It appears that the microhabitat conditions beneath ohias favor firetree seed germination and seedling development up to a diameter range of 2–3 cm. Further growth is expected to reduce the soil water, and this condition could be reflected by loss of vigor. Thus, when the firetree reaches the 6–11-cm range, and soil water is practically unavailable for growth, vigor becomes poor. The fact that firetree has never invaded the dry, barren soil of habitat 4 tends to support the foregoing reasoning. In contrast, ohia seedlings have become established in habitat 4 as well as the open areas of habitat 5. However, no ohia seedlings were found beneath firetrees.

Since the ohia trees are survivors of the 1959 eruption, being rooted in the old soil, it would appear that their source of water is from a different soil stratum. Thus, the ohia is able to retain good vigor regardless of drought periods in the new soil. However, this may not be entirely the case. In some areas of habitat 5, where ohias survived deep pumice burial, they have developed secondary root systems along their buried trunks. It is likely that these secondary root systems are at the same level as those of the larger firetrees. Thus, available soil water competition could exist between the two trees. But here again, ohia would be able to draw soil water from its original root system during drought in the upper soil level. Further study of the soil water relationship between ohia and firetree root systems is needed to test this hypothesis.

The close interlocking of ohia and firetree crowns, which could eventually cause competitive replacement of one or the other, must be further evaluated. To evaluate the apparent close, physical, competitive relationship between ohia and firetree will require long-term observations on a permanent site. Data collected over an extended period of time will reveal whether firetree can competitively replace ohia, and in addition whether firetree can regenerate itself on the same site.

Kawasaki's (1961) observation that firetree forms a dense, closed canopy forest with nothing growing beneath—not even new firetree seedlings—suggests that it is a shade-intolerant species. This can be verified by long-term observations in permanent plots. In addition, it must be determined whether firetree can recolonize where it was previously eradicated by herbicides, or where it has been competitively replaced by natural succession, if this is shown to occur.

Although the present distribution of firetrees correlates with the foraging pattern of fruit-eating birds, it cannot be definitely stated that this is the dispersal agency. Considerable observations, seed viability, and germination study will be needed to test this hypothesis.

It is imperative that the firetree be observed in its native habitats (Azores, Madeira, and Canary Islands). This would provide a better understanding of its potential ecological role in the various ecosystems of Hawaii. It now appears that firetree is becoming naturalized in Hawaii, as have hundreds of other exotics in the past. It seems that the prudent course of action is to learn as much as possible about how it fits into the new vegetation. Knowledge of this type will provide a better understanding of what controls, if any, can be effective in eliminating or stabilizing firetree. This viewpoint is shared by some of the foremost ecologists who have studied exotic invasions. Elton (1977) put it very well when he stated that "we require fundamental knowledge about the balance between populations, and the kind of habitat patterns and interspersion that are likely to promote an even balance and damp down the explosive power of outbreaks and new invasions."

LITERATURE CITED

ELTON, C. S. 1977. The ecology of invasions by animals and plants. Chapman & Hall, London. 181 pp.

GANNON, G. R. 1936. Plants spread by the silvereye. Emu 35:314–316.

GUEST, S. J. 1973. A reproductive biology and natural history of the Japanese white-eye (*Zosterops japonica*) in urban Oahu. Island Ecosystems IRP/IBP Hawaii. Tech. rep. 29. University of Hawaii, Honolulu. 95 pp.

KAWASAKI, A. 1961. *Myrica faya* survey. Typescript with maps. State of Hawaii, Department of Agriculture. 4 pp.

———. 1966a. Survey of *Myrica faya* in volcano area Sept. 7–9, 1966. Typescript and map. State of Hawaii, Department of Agriculture. 2 pp.

———. 1966b. *Myrica faya*, volcano area. Typescript and map. State of Hawaii, Department of Agriculture. 2 pp.

KIM, J. Y. 1969. "*Myrica faya*" control in Hawaii. Down Earth 25:23–25.

KRAUSS, N. L. H. 1964. Insects associated with firebush (*Myrica faya* Aiton). Proc. Hawaii. Entomol. Soc. 18:405–411.

NEAL, M. C. 1965. In gardens of Hawaii. Bernice P. Bishop Mus. Spec. Publ. 50. 924 pp.

NULL, W. S. 1967. Evaluation report for conversion of *Myrica faya* forest type by chemical control and replanting Aug. 11, 1967. Typescript. State of Hawaii, Division of Forestry. 4 pp.

SMATHERS, G. A. 1967. Heake [sic] fire burn study in Hawaii Volcanoes National Park. Pages 73–75 *in* U.S. Department of Interior, National Park Service. Office of Natural Science Studies Annual Report, 1968.

———. 1976. Fifteen years of vegetation invasion and recovery after a volcanic eruption in Hawaii. Pages 207–211 *in* Proceedings of the First Conference in Natural Science, Hawaii Volcanoes National Park. University of Hawaii, Honolulu.

SMATHERS, G. A., and D. MUELLER-DOMBOIS. 1974. Invasion and recovery of vegetation after a volcanic eruption in Hawaii. National Park Service Science Monogr., ser. 5. 129 pp.

WALTERS, G. A. 1970. Selected timber species to replace killed firetree in Hawaii. USDA Forest Service Res. Note PSW-211.

———. 1973. Tordon 212 ineffective in killing firetree in Hawaii. USDA Forest Service Res. Note PSW-284.

WALTERS, G. A., and W. S. NULL. 1970. Controlling firetree in Hawaii by injection of Tordon 22K. USDA Forest Service Res. Note PSW-217.