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# Technical Report 72

# The Coastal Woodland of Hawaii Volcanoes National Park: Vegetation Recovery in a Stressed Ecosystem

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# Abstract

This study examined the recovery of vegetation in non-littoral low elevation native scrub and forest along the east Kalapana Extension, Hawaii Volcanoes National Park, island of Hawaii, following emigration of human settlers and the eradication of feral animals, especially goats (*Capra hircus*). Research methods included quantification of plant species cover in relevés, population and stand structural analysis using belt transects, and examination of aerial photographs from 1954, 1965, and 1977. Structural analysis was used to describe the relationship between native and introduced woody plant populations, and their status under differing canopy cover and on a variety of substrates. Native woody species were the overall dominants.


# Introduction

Rock (1913) has characterized the lower leeward forest in Hawaii as "richer in species as far as tree growth is concerned than the rain forest." He also states that "not less than 60% of all indigenous tree species can be found and are peculiar to the dry regions or lava fields of the lower forest zone." Observations of many native dry forests in Hawaii now seem to discount Rock's statements. These areas are generally depauperate in native woody species. This is because, throughout Hawaii, the lower elevation vegetation zones have been under the greatest stress due to human activity. Contributions to this loss of species include development, burning, agriculture, logging, grazing and browsing by feral ungulates, and the invasion of introduced plants and insects.

The lowland scrub and dry forest of Hawaii Volcanoes National Park (HAVO) is in a region impacted by lava flows, earthquakes, human settlements, and feral ungulate disturbances. Polynesians settled the area beginning 1275 A.D. (Hawaii Natural History Association 1965) and remained there until the 1940s (former National Park Ranger K. Roberts pers. comm.). Goats were first reported from the area in the 1840s (Pickering 1841). Disturbance was continuous until the mid-20th century when, in 1938, the Park annexed the region as the Kalapana Extension (Stone 1959). While settlers emigrated from here since the later 19th century (Allen 1979), goats remained (Konani in Stone 1959). During the 1960s road construction through the coastal area of the Extension resulted in westward movement of many goats (K. Roberts pers. comm.). However, it was not until 1970 and the implementation of a National Park Service organized feral ungulate eradication program (Baker and Reeser 1972) that almost total elimination of the animals occurred. Human and goat impact to the area is now greatly reduced allowing the vegetation to reproduce and develop almost undisturbed.

Elimination of human and ungulate disturbance provides the opportunity to investigate the status and potential future development of native plant communities of the E. Kalapana lowland. Successional changes were recorded for the herbaceous and low-scrub communities of the western lowland of the Park subsequent to goat removal (Mueller-Dombois 1979). Similar responses have not been documented in the forest and scrub of the eastern lowland. Relatively high resilience of native Hawaiian vegetation has been documented through the research of Wirawan (1972) and Mueller-Dombois *et al.* (1981). This study serves as a further investigation of the relative endurance of native species and communities in Hawaiian dry forests in spite of a history of heavy disturbance and the invasion of many introduced plant species.

The National Park Service (NPS) resources management policy is to preserve and restore, where necessary, the native character of the Park's ecosystems without interfering with the natural processes of succession and evolution (National Park Service 1985). One important step toward restoring natural ecological processes was the removal of feral goats from this ecosystem. Before implementing measures for introduced plant control, Park managers needed to know the dynamic balance of native and introduced species in the existing communities.

The present study is part of a broader program to provide scientific information about the biological communities and ecosystems in HAVO that started with the first major synthesis by Doty and Mueller-Dombois (1966), who mapped the Park's vegetation and ecosystems. A special focus in this program is to expand the scientific understanding necessary to carry out the Park's policy of introduced species control.

# Background

## Dynamic Relationships Between Native and Introduced Species in Island Ecosystems: Concepts

The controversy regarding the lack of resiliency of native plant species on islands versus invading plant species began with Darwin's (1859) observations of island biota published in *The Origin of Species.* He suggests that the struggle for survival is more severe on continents than on islands implying that continental species have evolved a greater ability to survive interspecific competition. Hooker (1867), in support of Darwin, attributes the success of European weeds on islands to such superior competitive abilities. More recently, Degener (1973) asserts that the continuing success of introduced plant invasion results from the weaker competitive ability of native plants. Elton (1958) and Harris (1965) identify the simplicity of island plant communities as the reason for their vulnerability to continental species invasion. Similarly, Fosberg (1963) defines native island ecosystems as being limited in diversity with reduced interspecies competition and a tendency toward greater instability when isolation is broken down. Carlquist (1974) concurs and adds that islands have been "refugia for species extinct on continents."

Wallace (1891) supports Darwin's theory of inferior competitive abilities of native island plant species. However, he qualifies his support by emphasizing the role played by humans in the disturbance of native vegetation. In New Zealand, Allan (1936) claims "local extermination of (native) vegetation occurs not merely through the presence of alien vegetation but, by humans armed with axe...horses, cattle and goats." Watts (1966), in the Barbados Islands, and Amor and Piggin (1977), in Australia, found that alien species are rarely able to invade undisturbed plant communities. They say that the success of a species invasion depends upon disturbance and modification through human factors. Harris (1965), working on Antigua, and Lee (1974), on Guam, both conclude, in part, that continental invaders are not necessarily greater agressors which drive out native species.

Observations of the disturbed Nicaraguan forests led Belt (1873) to speculate that if humans were withdrawn from the area, the native forest would slowly regain the ground lost. There are a number of others who also believe the removal of disturbances will allow native vegetation to reclaim the area lost to continental invaders. Allan (1936) states that if all introduced fauna were removed there is evidence indicating that indigenous plants would overtake introductions. Eventually the introduced plants would survive as subordinate members of the resulting ecosystem from which feral mammals were removed. Egler (1942) agrees with Allan and presents a model of *Leucaena leucocephala* as an introduced nurse species preparing disturbed habitats for native species reintroduction. Egler (1942), Fagerlund (1947), and later Watts (1966) consider that most aliens are pioneers in plant succession while indigenes are frequently tolerant and more competitive in later stages. Similarly, Hatheway (1952) predicted that in the absence of anthropic disturbance most introduced species would be replaced by natives which then would perpetuate themselves indefinitely.

A follow-up study of Hatheway's plots performed by Wirawan (1972) twenty years later, reveals that aliens are not always overtaken by natives on land relieved of herbivore pressure. During this study nearly all introduced as well as native species named by Hatheway were present. Wirawan concludes that the interaction of native and introduced plants may not lead to the superiority of either group.

Mueller-Dombois (1981) concurs with the view of Wirawan as a result of the International Biological Program (IBP) research conducted in the Hawaiian Islands. He initially states that many island species "are not so easily displaced as one would expect if the (Darwin, Hooker *et al.*) hypothesis was entirely valid" (Mueller-Dombois et al. 1981, p. 516). Rather, they propose that these species offer resilience to introduced invaders. Mueller-Dombois qualifies the statement and takes exception with Egler and Hatheway's thesis saying such a thesis necessitates that indigenous biota have the ability of climax species in that with time and without anthropic disturbance aliens would be displaced by natives. Mueller-Dombois thus believes that many indigenes "have retained their pioneering characteristics responsible for making them successful colonizers in the first place" (p. 516). He concludes by saying there is no evidence that the evolutionary stresses on islands are less vigorous and that competition among indigenes is any less harsh than among biota that evolved in continental ecosystems

Direct competition between native and alien plants is not the sole consideration when determining the invasive capabilities of plants. Insects and plant diseases may aid in the spread of introduced plants or the suppresion of natives. Fungal and bacterial diseases apparently are not a problem in Hawaii's forests at present (Gardner pers. comm.). However, endemic plants have been directly affected by serious outbreaks of a succession of invading alien herbivorous insects (Beardsley 1980). Wirawan (1972) found that the immigrant moth, *Alucita objurgatella* (Walsingham), was curtailing *Canthium odoratum* (alahe'e) regeneration through infestation of the plant's embryos. The alien tree *Schinus terebinthifolius* (Christmas berry) then invades the plots and suppresses *Canthium* growth. *Psylla uncatoides* an alien psyllid, infests the introduced *Acacia confusa* (Formosan koa) lightly, while it often heavily attacks the endemic *A. koaia* (koaia) (Leeper and Beardsley 1973). Finally, Beardsley (1980) warns that the introduced black twig borer (*Xylosandrus compactus* (Eichoff)) constitutes a serious threat to native trees in certain dry forests.

Davis (pers. comm.) hypothesizes that there is suppression of native tree growth by native insects as a result of human-induced disturbance. He cites the example of native koa cerambycid beetles attacking healthy saplings when cattle were freed on the Strip Road, island of Hawaii. The cattles' extreme damage to koa created more dying trees and therefore more breeding sites for the beetles. Their numbers increased greatly and they began to feed on healthy young trees as well the normally fed-upon dying trees. Davis additionally gives examples in which *Metrosideros* ('ohi'a) logging slash fosters population increases of the native 'ohi'a cerambycid, whereupon healthy 'ohi'a are also attacked, suppressing the trees' growth.

## Vegetation Recovery Following Feral Ungulate Removal: Selected Examples

Goats and cattle have disturbed vegetation on many oceanic islands through the centuries. Their eradication or removal has been accomplished on a number of these islands. Vegetation recovery following goat eradication on Catalina Island, California, was monitored by Coblentz (1976). He found that native species depleted or eliminated during high goat activity were re-establishing. There was also a notable regeneration of native island species on Isla Santa Fe (Barrington Island) in the Galapagos following complete removal of goats from the island (Hamann 1975). Howard (1965) reports that goats were exterminated on Three Kings Island, New Zealand after 56 years of establishment and within five years a floristically rich plant community developed. The number of vascular plant species increased from 118 to 151 during this recovery period.

In Australia, however, a study performed by Harrington (1978) quantified scrub recovery in an area from which goat and sheep were excluded for three years. During that time it was the unpalatable shrubs that increased in cover most rapidly. Previously, Taylor (1968) reported that following feral mammal removal from subantarctic islands off New Zealand, introduced plant species increased their range. According to Taylor (1968; pers. comm. 1982), when introduced animals have been isolated on islands for over 100 years there is the possibility of changes in the genetic adaptation of the affected plant species.

Vegetation recovery in Hawaiian forest and scrub ecosystems following feral mammal removal has been quantified for several locations. Native dry forest recovery in the coastal lowland of northwest O'ahu was analyzed by Wirawan (1972). His purpose was to investigate predictions made 20 years previously by Hatheway (1952) regarding the recovery of a disturbed dry forest in Hawaii. In 1947, all wild cattle were removed from a portion of the Mokule'ia Forest Reserve. Soon after, Hatheway (1952) established plots within and next to the Reserve and quantified the vegetation present. During 1971-72, Wirawan relocated Hatheway's plots and surveyed the vegetation. After twenty years of recovery, he found an increase in vegetation cover throughout the area. Most of the natives found by Hatheway were still present, as well as a few not mentioned by him. Every alien species recorded by Hatheway was also found plus a few additional species. Introduced species in the community were subordinate to the natives. Wirawan found that native plant species were regenerating and maintaining themselves as the dominant woody species. An exception, the native tree *Canthium odoratum*, was weakened by an alien insect *Alucita objurgatella.*

In the mountain parkland of HAVO the recovery of *Acacia koa*, the dominant native tree species of this ecosystem, was studied by Spatz and Mueller-Dombois (1973). Within an exclosure koa grew in dense clumps, while outside goats continued to feed on the plant and trample its shallow roots. It was concluded that koa recovers quickly following the exclusion of goats. However, Spatz and Mueller-Dombois found that there was a change in forest structure, a consequence of the long period of goat disturbance; koa within the exclosure exhibited denser sucker growth than in undisturbed conditions.

Plant community recovery following feral mammal removal may depend upon several factors: 1) the length of time of feral mammal disturbance, 2) the species of animal involved, 3) the successional stage of the original vegetation, and 4) the climate and vegetation zone. Therefore, each situation should be studied individually. A vegetation recovery study in the coastal woodland of HAVO may add a further perspective to the question of resiliency of the area's native vegetation.

## The Study Area in Relation to Hawaiian Vegetation Zonation Schemes

The Hawaiian Islands encompass sufficient climate and substrate types to support a variety of vegetation zones. The vegetation of the island of Hawaii, and HAVO in particular, spans from strand to alpine desert. Hillebrand (1888) proposed a simplified vegetation scheme containing only four zones plus bogs. Two of the zones encompass the Park's coastal woodland:

1. Lowland zone--open country near the shore; includes littoral species
2. Lower forest zone--up to 1000 to 2000 feet elevation

Rock (1913) expanded the zonation scheme to six "botanical regions." Although he details the vegetation zones of several areas on Hawaii, the area of this study is not mentioned. When compared floristically and elevationally to other similar locations in Rock's system, the Kalapana Extension of the Park includes the following zones:

1. Strand vegetation--coastline vegetation
2. Lowland region--up to 1000 feet elevation (section a. dry region)
3. Lower forest region--1000 to 2000 feet elevation (section b.--leeward side: dry, mixed species).

Vegetation zones as defined by Robyns and Lamb (1939) are related to climatic factors, primarily rainfall, rather than elevation. Thus climate determines the zones and the "climax formations." Robyns and Lamb mapped nine climax formations for the island of Hawaii. Three of those are found within the Kalapana Extension, but only the following one with its subzones encompasses the study area: the coastal lowland zone with its subzone of the coastal scrub up to 1500 feet elevation on the leeward side; a xerophytic scrub formation.

In 1942, Ripperton and Hosaka presented a vegetation scheme comprised of ten zones based, in part, on climate. While they named all ten zones for the dominant species, only four zones were dominated by introductions; two of these (zones A and B) relate to the study area. In general, these two zones are dominated by *Leucaena leucocephala* (haole koa) and *Psidium guajava* (guava). Although these species are not dominant in the study area, they indicate the plant community degradation of most of Hawaii's lowland. Krajina (1963) modified Ripperton and Hosaka's system into 14 zones using the biogeoclimatic zonation scheme he developed (which includes animals, soils, and geologic substrate as well as climate and vegetation). Krajina's scheme does not differ from Ripperton and Hosaka's for the study area.

Fagerlund and Mitchell (1944) used Robyn and Lamb's (1939) treatment to describe the following seven zones:

I. Coastal lowland
   a. wet
   b. dry

II. Transition forest

III. Montane forest

IV. Parkland

a. plateau
b. montane

V. Subalpine shrub

VI. Alpine

VII. Bog

All but IVa and VII occur within the Park, but only Ib relates to the study area. Stone (1959), while surveying the plant species of the Kalapana Extension, defined the forest formations as coastal lowland forest, coastal lowland scrub, and semi-desert. The first two relate to the study area.

In 1974, Mueller-Dombois and Fosberg published a series of 1:52,000 scale vegetation maps for HAVO. They compiled the maps in 1966 using 1954 aerial photographs. Accompanying the maps is an outline of 31 vegetation types in six environmental sections (alpine, subalpine, montane seasonal, montane rainforest, submontane seasonal, coastal lowland). The detailed level of this classification system is obvious in that the coastal woodland alone contains seven vegetation type subdivisions within the zone.

The following section will explain why the study area has an anomalous vegetation zone, leeward or dry costal woodland, in light of its climate and substrate differentiations.

# Description of the Study Area

## Geography

The island of Hawaii, geologically the youngest island of the Hawaiian archipelago, is located at the southeast extreme of the island chain (Figure 1). Hawaii Volcanoes National Park extends from the top of Mauna Loa to the sea in the southern portion of the island. The study area is in the eastern lowland of the Park. The topography of this area consists of pali (cliffs) with gentle slopes or level areas above and below the pali. The elevation of the study area ranges from sea level to 80m elevation inland at the eastern Park boundary. Fourteen kilometers westward along the Chain of Craters Road is the study area's western boundary. The elevation here ranges from 120m to 500m (Figure 1, shaded portion). This area delineates the leeward woodland, an area of open canopied short-statured trees. Above it is the transition to mesic forest and below is semi-arid grassland.

## Geology and Soil

The study area is located downslope of the volcanically active east rift of Kīlauea Volcano. Thus, there are young lava flows in the region. Overall the area's substrate ranges in age from 400 to 1500 years (Holcomb 1980). Additionally, earthquakes and earth tremors of the past and the present have caused large cracks and upheavals in the landscape. Pāhoehoe is the widespread substrate. Upon flowing downhill, lava may develop into sharp, rubbly ʻaʻā. ʻAʻā is also found in isolated spots on the flatland. Very little topsoil or ash is found on any of these substrates. Mueller-Dombois (1980) established four major habitat types for the entire coastal lowland of the Park:

1. Pali with ʻaʻā rock rubble, including other ʻaʻā flows;
2. Pāhoehoe on level or somewhat sloping ground
   a) very recent (1969 - 1974),
   b) highly permeable but not very recent,
   c) with fine soil in cracks or fissures,
   d) with fine soil in pockets extending beyond cracks on somewhat sloping ground;
3. Discontinuous shallow ash blanket deposit over lava rock with up to 50% rock outcrop; and,
4. Continuous deep ash deposits without any significant rock outcrop (with two sub-divisions).

Habitats 1 and 2 make up the majority of the study area. Some areas fit into habitat 3 as well. Generally, habitat 4 is found in the western lowland.

Soil survey maps (Sato *et al.* 1973) identify the study area as ʻaʻā and pāhoehoe lava with no soil covering. Generally, ash or soil is found only in the cracks and pockets of pāhoehoe flows. Soil depths range from 0-25cm.

## Climate

Mueller-Dombois (1980) described the eastern Kalapana Extension as having a Mediterranean rainfall regime, because the area is exposed to wet winters and dry summers. The climate diagrams reflecting this pattern (Figure 2) are constructed according to the method of Walter (1971). Only climate diagram A is in the study area, while diagram B is just west of it in the semi-arid grassland (Figure 3). Climate diagram A represents the wettest portion of the study area. Rainfall in the lowland woody vegetation zone averages 1500 mm/year. As one travels west (toward a more leeward exposure), rainfall decreases. Thus, at each elevation there is a northeast to southwest decrease in precipitation reflecting the shift from windward to leeward exposure. The mean annual temperature ranges from 24°C at sea level to 22°C at 305m elevation (Mueller-Dombois 1980) placing the coastal lowland in the warm tropical zone.

## Vegetation

Vegetation types in the eastern coastal woodland of Hawaii Volcanoes National Park were mapped by Doty and Mueller-Dombois (1966). To interpret the map, Mueller-Dombois constructed a profile diagram showing six major vegetation types. Four of these are represented in the study area. They include:

1. Scattered *Metrosideros* (ʻohiʻa) trees on ʻaʻä.
2. Low spreading shrubs on pähoehoe.
3. Arborescent shrubs on pali.
4. Forest.

A more detailed classification formulated later by Mueller-Dombois (1980), in combination with a map, gives seven major floristic vegetation types for the study area. They are:

1. *Tricholaena* (natal red top) grassland with scattered *Metrosideros* trees
2. *Andropogon* (broomsedge) grassland with scattered *Metrosideros* trees
3. *Metrosideros* and *Diospyros* (lama) trees with native shrubs (*Dodonaea viscosa* (aʻaliʻi), *Osteomeles anthyllidifolia* (ʻülei), etc.) and introduced shrubs *(Lantana camara, Indigofera suffruticosa* (indigo), etc.)
4. Closed lowland scrub with native trees and shrubs (*Canthium odoratum* (alaheʻe), *Wikstroemia sandwicensis* (ʻäkia), *Diospyros ferrea, Osteomeles anthyllidifolia*) and alien trees and shrubs (*Schinus terebinthifolius* (Christmas berry), *Psidium guajava* (guava), *Pluchea odoratum* (Indian pulchea), *Lantana camara*, etc.)
5. Open lowland scrub with similar dominants to number 4 but with more frequent grass covered openings consist of *Tricholaena* and *Andropogon*
6. Closed lowland forest, taller woody vegetation with main crown biomass greater than 5m high, in species composition similar to vegetation type 4
7. Open lowland forest with species composition similar to number 4.

Jacobi (1983), using aerial photographs and groundtruthing, mapped the vegetation of the Kalapana Extension as part of a larger U.S. Fish and Wildlife Service vegetation-type mapping project. Detailed vegetation-types for the study area consist of the following dry forest and scrub types:

1. A mosaic of dry, very scattered, scattered, open, and closed *Metrosideros polymorpha* and native trees with native/alien shrubs and alien grass understory
2. Dry, open *Aleurites moluccana* (kukui)/native tree groves with native/alien shrub, alien grass understory
3. Dry, scattered native trees with native/alien shrubs and alien grass understory

A comparison of closed and open lowland forest generally indicates that areas covered by open forest are associated with less rainfall. However, in this study area substrate is also very important. When rainfall is equal in adjacent open and closed forests, open forests are usually found on a more porous soil or rock (pähoehoe) in the study area.

Kïlauea Volcano, which formed southeast coastal Hawaii, is a basaltic volcano (Dana 1890). According to Stearns and MacDonald (1943), basalts are highly permeable and, depending on age and other factors, high permeability characterizes most of the lava in Hawaii. The porous lava substrate of Kalapana creates a xeric situation which belies the high precipitation reaching the ground. Thus, rather than forming a moist forest zone as would be predicted by Holdridge's (1967) life-zone chart, this area is edaphically much drier and thus is occupied by sclerophyllous forest and scrub. Within this dry forest/scrub area there are the four different lava types (described in the Geology and Soil section). These have differing water-catching and water-holding capacities. According to Mueller-Dombois (1980), the four substrate types and their variations found in the coastal lowland of the Park have their effect on vegetation primarily through their differences in soil-water relations. Most taller trees and denser growth are found on ʻaʻä. With its jumbled surface, ʻaʻä catches more water than the flatter pähoehoe and with its dense core holds more water than more porous pähoehoe. Pähoehoe therefore generally supports shorter life-forms. Exceptions are coarsely broken or hollow pähoehoe areas. These will support taller trees as does ʻaʻä lava.

## Fauna

Conant (1980) recorded nine species of birds in the eastern coastal woodland. One, Noio (Black Noddy, *Anous tenuirostris melangenys*), is a native seabird found exclusively along the coast. Kölea (Golden Plover, *Pluvialis dominica*), a migrant species, has an extended range up to the forest zone. Other native birds in this area are Pueo (Hawaiian Owl, *Asio flammeus sandvicensis*) and ʻIo (Hawaiian Hawk, *Buteo solitarius*) (Griffin 1980). As a part of the NPS Nënë (*Nesochen sandvicense*) reintroduction program, a pen providing shelter for two Nënë is presently located within the study area. Introduced passerines in the region include Japanese White-eye (*Zosterops japonica*), Northern Cardinal (*Cardinalis cardinalis*), House Finch (*Carpodacus mexicanus*), and Barred Dove (*Geopelia striata*) (Conant 1980). All four are seedeaters which occur throughout the lowland. Thus, they may influence the distribution of native and introduced plant species in the area.

There are four introduced mammals presently populating the area. Rats (*Rattus* spp.) and mice (*Mus musculus*) occupy a variety of habitats where, through their feeding habits, they pose a serious threat to small native birds and invertebrates (National Park Service 1985). They are also known to gnaw and debark trees. Mongoose (*Herpestes auropunctatus*) prey on eggs of ground-nesting birds. Nënë is an example of a ground-nesting bird which was more common in the past (Baldwin 1945). Programs to reintroduce the Nënë into the wild are failing due in part to egg predation by mongooses (Banko 1978). Pigs (*Sus scrofa*) roam throughout the lowlands. In Kïpahulu Valley, Maui, Yoshinaga (1980) found that by trampling and rooting, pigs destroy ground cover, seedlings and saplings of trees, and create bare spots which are usually invaded by weeds. Diong (1982) also working in Kïpahulu Valley, found guavas (*Psidium cattleianum*) to be a food source of the pig which then disperses the seeds.

The eastern lowland of Hawaii Volcanoes National Park contains a rare ecosystem within both the Park and the Hawaiian Islands. The general concentration of human activities (settlements, agriculture, livestock introduction) near the coast has left this ecosystem with the greatest number of introduced plant species as compared to other Park ecosystems (Mueller-Dombois 1980). The eastern Kalapana Extension is unique in that the National Park status of the area has served to protect the ecosystem in recent years. Thus, unlike other lowland dry forests in Hawaii such as lower Auwahi on Maui, Mokulëʻia on Oʻahu, and lower Manukä on Hawaii, introduced disturbances here have been greatly reduced.

## Brief History

The eastern Kalapana lowland was first settled in approximately 1275 A.D. with the construction of Wahaʻula Heiau (Hawaii Natural History Association (HNHA) 1965). Remnants of human built structures have been found in Pülama, Kamoamoa, Lae ʻapuki, Pänau nui, and Kealakomo (Figure 1). These names refer to Hawaiian land divisions (ahupuaʻa) extending from mountain to ocean (Emory *et al.* 1959, HNHA 1965). All have been cited as settlements (Ellis 1825, Lyman 1924, HNHA 1965) and are within the study area.

Recently formed lava substrates with minimal soil precluded much variety of agriculture in the study area. The land, however, was extensively planted with sweet potatoes. Hawaiians formed rock piles of lava (Lyman 1924) for cultivation of this crop. The Hölei Pali bisects the study area and "hölei" translates as a variety of sweet potato (Pukui and Elbert 1971). Archaeological artifacts, generally sweet potato planting mounds, are noted as the darkened expanses on Ladd's (1974) archaeological map of the area (Figure 4).

Information about the activities of pre-Cook Hawaiian settlers in Kalapana is limited except for some ruins found in the study area, the traditional practices still continued, and stories are passed along. Once Europeans arrived, records became available as documented chronologies. Ellis (1825), during his journey around the island of Hawaii, mentioned the more agreeable aspect of the land upon reaching the eastern coastal lowland of Kalapana from barren Kealakomo (Figure 1). He noticed clumps of *Hibiscus tiliaceus* (hau), *Cordia subcordata* (kou), groves of coconut and kukui planted from Pänau to Kamoamoa, as well as the cultivated region of Kapa'ahua, just east of the study area. In the uplands of Poliokeawe, Ellis found plantations of sweet potatoes. While travelling through Kamoamoa, Lyman (1924) noted large patches of sweet potatoes planted among the lava. He also observed coconut and sugar cane in Pülama and tobacco in Kalapana. No other agricultural crops have been named for this region.

There is no mention of burning within the study area in the literature. However, some burning most likely occurred in the past. Fires for clearing and agricultural purposes have been documented elsewhere in Hawaii (Ladd and Yen 1972, Kirch and Kelley 1975, Kirch 1982, Clark and Kirch 1983). It is likely that the agricultural needs of the early Polynesian settlers and the need for pili grass (*Heteropogon contortus*) for roof thatching would require periodic burning of the woodland. McEldowney (pers. comm.) notes that these settlers needed wood for cooking and building, thus large-scale burning was most likely not the case. Still, Helen Pe'a LeHong (lifelong resident of Kalapana) tells of the expanses of pili grass from Panau nui to Kamoamoa at the turn of the century. This area is now a woodland. Goats most likely had a part in the maintenance of this former grassland, but perhaps prior to goat invasion, fire already prevented woodland recovery.

Harvesting parts of native plant species was probably also practiced: 'ulei for fish net frames, a'ali'i for dye and timber, 'äkia for cordage and fish poison, alahe'e for digging sticks and dye, and lama as a sacred wood for use in rituals and building of temples (Lamoureux 1976). The harvesting was probably done on a small scale and was thought to have caused little disruption of the species composition in the native lowland forest (Bryan 1930).

The Polynesians introduced about 28 plant cultivars to Hawaii (Handy and Handy 1972). According to Knapp (1975), a few have become weedy while most have not. Polynesian introductions present in Kalapana include 'ulu (*Artocarpus communis*), noni (*Morinda citrifolia*), tï (*Cordyline terminalis*), niu (*Cocos nucifera*), and kukui (*Aleurites moluccana*), none of which have become weedy. In contrast, Wester (unpublished list) presents a compilation of first sightings of European adventives in Hawaii. Many of those in the study area were not sighted until the late 19th to early 20th century (e.g. *Lantana camara* in 1858 and *Schinus terebinthifolius* in 1909).

In the upland rainforest (outside the study area), the pulu industry was flourishing in the 1800s. Pulu is the Hawaiian name for the soft hair covering the apex of tree fern (*Cibotium glaucum*) stipes and trunks. This material was used to stuff pillows and mattresses. Work available in the industry was thought to be a major cause for emigration of native people from the eastern coastal lowland to the upland (Allen 1979). Approximately seventeen families lived in Kealakomo in 1859; twenty years later only five families remained. Emigration to Hilo and Honolulu was another reason for a reduction in the area's population. Additionally in 1868, a series of catastrophic events: volcanic eruptions, earthquakes and a tsunami, had devastating effects on the landscape along the southeast coast of Hawaii. These natural disasters, in which the coastline sank 1.5 to 2.5m, may have been the final reason for abandonment of Kamoamoa Village and other coastline settlements (Emory *et al.* 1959).

There were no goats reported in Kalapana until the 1840s when Pickering (1841) mentioned seeing one. Marques (1906) reported goats to be abundant and widespread on the island of Hawaii by 1850. Goat ranching in the Panauiki and Lae'apuki ahupua'a began in 1862 (Allen 1979). By the turn of the twentieth century goat round-ups were held twice a year in the Pänau - Kealakomo region. Helen Pe'a LeHong (pers. comm.) tells that during the early twentieth century families living in the area harvested thousands of goats each year for food and trade.

Cattle, as well as horses and donkeys, were introduced by Captain Vancouver in the 1790s, and became established in the eastern Kalapana coastal lowland during the late 19th century. Rycroft had a cattle ranching operation around 1886 in Kamoamoa (Allen 1979). Another rancher, Cheung Peu, reportedly had 1,000 head of cattle in Kamoamoa by 1889 and still another rancher, Pe'a, had the same number in Panauiki by 1899 (See Pe'a place in Figure 1). However, one former resident (Kaipo Roberts, former Park Ranger, pers. comm.) feels the land could not have supported such numbers of cattle. Perhaps the figures available to Allen (1979) were exaggerated. The animals were provided with only two water holes, one a well at Lae'apuki and the other a man-made water hole at Pülama. In addition, the area was considered to be poor pastureland (Hoogs *et al.* 1943). The low carrying capacity of the land was verified by the poor condition of cattle which were said to be stunted and undernourished (Allen 1979). Ranching came to an end in Kalapana during the 1940s soon after the National Park Service annexed the area as part of the Kalapana Extension (in 1938). Horses and donkeys were also removed from the area at that time by Park Service order (K. Roberts pers. comm.).

Goats, however, flourished. As settlers continued to leave the Kalapana region, goats were able to roam freely. Former resident Sam Konani remarked "people died out or moved from Pülama and today (no date) the place is deserted, only goats run around there now." (Emory *et al.* 1959).

In 1965 the Chain of Craters Road was connected with the eastern coastal lowland. The period of road building activity resulted in the goats migrating westward away from human activity. Morris (1969) estimated 5,000 to 10,000 goats to be in the Park at that time. A goat eradication program had been ongoing in the region since the early twentieth century (Baker and Reeser 1972), however, it was not until 1970 that a comprehensive plan was developed to systematically eradicate goats by fencing them out of the area. Following implementation of the plan, goat numbers in the Park were greatly reduced. By 1976, they were almost eliminated from the eastern lowland and today there are no goats below 5,000 ft. within the park.

Certain changes in vegetation structure since goat eradication are becoming apparent according to some observers. Mueller-Dombois (1980), in comparing his 1966 and 1980 maps of the coastal lowland, found that *Heteropogon contortus* (pili) grassland with chamaephytes has changed to open lowland scrub with *Tricholaena repens* and *Andropogon virginicus.* Warshauer and Jacobi (1973) mentioned a structural size gap and regeneration of woody species in the area just a few years after goat removal. Yen (1971), an archaeologist, who previously (in 1959) surveyed the study area, noted the growth of tree species on the coastal plain (near Waha'ula Heiau). He explained that while working in the area in 1959 no clearing was required; a different situation if such work were presently undertaken. Finally, LeHong shared her thoughts about the change in the study area following goat eradication. She clearly preferred the fields of pili over the "alien" (sic) bushes now present.

## Vegetation Research in the Coastal Lowland of Hawaii Volcanoes National Park

There has been little quantitative research performed in the vicinity of the study area. Although descriptive in content, Hoogs *et al.* (1943) survey of the area and Stone's (1959) botanical report of the Kalapana Extension as well as Warshauer and Jacobi's (1973) biological report of Pülama and Kamoamoa aided greatly in formulating a recent historical account of a little described region.

Newell (1968) and Rajput (1968) presented the first quantitative work done in the area. They quantified plant species cover according to the Braun-Blanquet cover abundance scale in numerous relevés and transects throughout the Park. Newell analyzed species distribution through synthesis table formation. For the coastal lowland she described one alliance, two associations, and two subassociations. When superimposed on parameters such as tree presence, substrate, elevation, slope, the following groupings represent ecological relationships in the area:

| | |
|---|---|
| Alliance I. | *Waltheria indica - Chrysopogon aciculatus* |
| Association 1. | *Lantana camara - Cassia leschenaultiana* |
| Subassociation 1. | *Psidium guajava - Fimbrystilis cymosa* |
| Subassociation 2. | *Cassia leschenaultiana - Lantana camara* |

Association 2. *Eragrostis tenella - Ageratum conyzoides*

A study by Mueller-Dombois and Spatz (1975) was undertaken in the western lowland of the Park. Here three exclosures were built, one in 1968 at Kūkala'ula and two in 1971 at Pu'u Kaone. These were monitored on a semi-annual basis to study the pattern of vegetation recovery in detail. The Kūkala'ula site was an annual grassland on massive pāhoehoe at the study's inception. Within three years, the vegetation within the exclosure changed to predominantly perennial bunchgrasses. In addition, a native vine, *Canavalia kauensis*, which had not been previously recorded in the literature (St. John 1972), became dominant.

Mueller-Dombois and Spatz (1975) established the early recovery sequence of plants during this study. The formerly dominant *Eragrostis tenella* was rapidly displaced by perennial grasses, particularly *Tricholaena repens*. Later the large mat-forming grass *Melinis minutiflora* appeared and several low-growing woody plants (chamaephytes) also became important.

Continued monitoring of the site by Mueller-Dombois (1981) revealed that certain species recovered rapidly only to die back within a few years and then begin recovery anew (e.g., *Canavalia kauensis*). Other species, molasses grass, increased in cover continuously while still others, *Eragrostis tenella* (love grass), decreased. Thus, when disturbance is removed, consistent recovery is not to be expected in a situation such as that at Kūkula'ula. Rather, a dynamic, perhaps endogenously controlled, community change may occur. Mueller-Dombois (1981) suggests that the oscillating changes within a group of the persisting species may relate to life-cycle dependent death of the affected population.

During the mid-1970s goats were greatly reduced in number throughout the Park, thereby allowing recovery to occur outside the Kūkula'ula exclosure. The site has now been monitored for over a decade and although the area's climate could support growth of woody vegetation, no tree species have appeared within the exclosure or its vicinity. This has been explained by the heavy browsing and grazing pressure previously exerted by the goats during their 150-year occupation of the area (Mueller-Dombois and Spatz 1975). Until trees become established (through seed dispersal), succession here will be "arrested" in a mixed shrub-vine-bunchgrass stage (Mueller-Dombois 1979).

The Pu'u Kaone exclosures are located on a different substrate than Kūkala'ula. Deep ash supported a perennial introduced grassland of *Chrysopogon aciculatus* (pilipili'ula) and *Cynodon dactylon* (Bermuda grass) at the inception of the Mueller-Dombois and Spatz study. Different perennial grasses (*Tricholaena repens* and *Melinis minutiflora*) became more abundant and woody shrubs increased in number during the recovery period. However, as in Kūkula'ula, no native tree species appeared (Mueller-Dombois and Spatz 1975). This effect may be due to the depletion of seed supply through browsing and grazing of native seedlings by goats.

This project is similar to the above studies in its investigation of the recovery abilities and species composition of a formerly stressed vegetation. However, a quantitative analysis has never been performed in the east Kalapana Extension of the Park. In this area, woody vegetation persists despite a long period (approximately 135 years) of feral goat occupation as well as human settlement and agriculture. Thus, an ecological analysis of all woody species present may yield substantial vegetation recovery and baseline information suitable for future studies and decision-making for Park management.

# Methods And Materials

## Relevé Analysis

The relevé method as described by Mueller-Dombois and Ellenberg (1974) was employed to sample the vegetation. Relevés are vegetation plots of measured minimal area (according to community type and species diversity) in which species cover is estimated in height strata. In this study the vegetation was vertically stratified as follows:

T1 layer - trees ≥ 5m tall,
T2 layer - trees 2 to 5m tall,
Shrub layer - all plants 0.6 to 2m tall
Herb layer - all plants 0 to 0.5m tall.

This stratification is based on the general height ranges of foliar biomass in different developmental stages and life-forms within this region. For each species in each layer a Braun-Blanquet cover abudance estimate (Braun-Blanquet 1932, Mueller-Dombois and Ellenberg 1974) was made. These layers also define forest versus scrub for the study area. Woody communities generally less than two meters in stature were defined as scrub sites. Woody vegetation cover dominated by individuals with crowns more than two meters in height constituted a forest. Relevé sizes of 10 x 10m were used for scrub and 20 x 20m for forest communities.

Relevés were centrally placed in community types recognized form aerial photographs in combination with extensive ground reconaissance. Forest and scrub relevés were chosen for several apparent comunity types occurring on differing substrates. The dominant substrate in the study area, pahoehoe, was of various subtypes (flat, chunky, and upheaved). A smaller portion was located on ‘a‘a, generally along the pali. In addition, relevés were chosen along an elevational gradient from near sea level to 425m elevation. Along this gradient, separate comparisons were made within forest and scrub vegetation. In total, forty-two relevés (20 scrub and 22 forest) were sampled (Figure 5)

Data collected from relevés were analyzed in order to prepare a synthesis table, dendrographs and a life-form spectrum.

## Synthesis Table Analysis

The floristic data collected from each of the 42 relevés was analyzed using a computer program version of the Braun-Blanquet technique originally developed by Ceska and Roemer (1971), and applied to other studies in Hawaii by Mueller-Dombois and Bridges (1975).

## Dendrograph Analysis

The same relevé data were additionally analyzed by the dendrograph technique of McCammon and Wenninger (1970) which graphically presents the information of a similarity matrix. The matrix results from a mathematical comparison of all combinations of relevé pairs. Clusters of relevés are generated by joining them at different levels of similarity. A threshold (or cluster cut-off point) of between 25% and 50% is recommended to isolate ecologically meaningful clusters (Mueller-Dombois and Ellenberg 1974).

## Life-Form Spectra

The Raunkiaerian life-form classification (Raunkiaer 1937, Mueller-Dombois and Ellenberg 1974) was used to group plants of similar structure and function. These similarities indicate that species of the same life-form type may utilize environmental resources in a like manner. Thus, plants of the same life-form type occupy similar general ecological niches and can be competitors for the same habitat resources.

The plants species of the study area can be classified into seven general life-form types. The following criteria determine the plants' category at maturity (Gerrish and Mueller-Dombois 1980): phanerophytes (p) - are woody species that grow taller than 50 cm and have branches greater than 1 cm in diameter. Phanerophytes can be subclassified as nano (low shrubs or small trees), or meso (larger trees). These same individuals can also be categorized as sclerophyllous (hard-leaved) or malacophyllous (soft-leaved). Chamaephytes (Ch) - are woody plants or herbaceous evergreen perennials whose mature shoot system can grow taller, but usually dies back to about 50 cm or less during unfavorable seasons. Branches are usually less than 1 cm thick. Hemicryptophytes (H) - are perennial herbaceous plants whose shoot system dries up during the unfavorable season to a green remnant usually covered by dry foliage. Geophytes (G) - are herbaceous perennials with subterranean storage organs and whose shoot systems may be shed entirely during the unfavorable season. Therophytes (T) - are annual plants which die after seed production. Lianas (L) - are rooted in the ground but depend upon other plants for support. Epiphytes (E) - are plants growing on others for support while deriving no nourishment from them. Parasites (Pa) - are vascular plants which contain little or no chlorophyll and are heterotrophic, thus they derive nourishment from other plants on which they root.

The life-form spectra consist of histograms representing the percent shoot or crown cover of each life-form category within the community. Two steps were employed in the calculation:

1) the mean Braun-Blanquet cover amount, represented in the synthesis table, is used to convert species cover-abundance to percentage values as follows:

r = 0.1%,
+ = 0.5%,
1 = 3.0%,
2 = 15.0%,
3 = 38.0%,
4 = 63.0%,
5 = 88.0%.

2) The appropriate percentages are added for the relevés included in the life-form spectrum and the mean percentage value calculated.

## Structural Analysis

During the initial field reconnaissance, the first plots were selected incorporating the following factors: elevation range in the study area is from 3m to 425m; substrate, although dominated by pähoehoe lava, also includes ‘a‘ä and pali talus, as well as varieties of pähoehoe (chunky, upheaved, and flat); canopy cover in the forested stands ranged from 25% to almost 60%. Forests were defined as those stands which were greater than two meters tall and which had a woody vegetation cover of more than 25%. Twenty-two sample stands were chosen (Figure 5).

At each sample stand structural measurements were taken along a belt transect. These belts were 10m wide and were divided at 5m intervals into 5 x 5m subplots. Woody plants were classed as 0.6 to 2m tall, and 2 to 5m tall, and 5m tall. Basal diameter (bd) was used as the measurement instead of diameter at breast height (dbh) because diameter was taken of very low statured plants (0.6m tall). Individuals less than 0.6m tall were called seedlings and divided into three classes: 0-20cm, 20-40cm, 40-60cm. Every individual was counted.

A meter tape was laid out along a compass direction and served as the center line of the belt transect. On either side of this line, 5 x 5m subplots were established. Measurements began in the subplot closest to the starting point. Trees and shrubs over 0.6m tall were measured for bd and seedlings were scored in the three height classes. Subplots were sampled on alternating sides of the transect until at least 30 trees of the dominant species were counted. Thus, the transects could vary in length according to the spacing of the trees. The shortest transect was 20m long and the longest was 120m long. Although at least 30 trees were measured for each species, quite often the count was increased to more than 60 individuals.

The structural analysis data for major woody species in each of the 22 sample stands were plotted to reflect individuals per 1,000 square meters for each basal diameter class. Most woody species measured were short-statured and did not exhibit a broad basal diameter range, thus a narrow diameter class interval of 4cm was used in presenting the data. Two exceptions were:

1) The first class was chosen to be 0-2cm. This narrow range was used because two different life stages, seedlings and juveniles, would otherwise be included in the broader 0-4cm interval class which would not accurately represent the ecological character of the population.

2) Trees with diameters of 50cm and greater were grouped in 10cm intervals. This broader categorization was useful for representing the few bigger individuals of the larger-sized species (‘öhi‘a and kukui).

Histograms were grouped according to canopy cover and substrate type. Canopy cover was considered to be open when it ranged from 25% - 50% and semi-open when it ranged from 50% - 60%. Very few stands had closed canopies (greater than 60%), thus the term semi-open was chosen to describe denser forest sites. This canopy classification applied to all woody species taller than 2m. Substrate type was classified as flat pähoehoe, upheaved pähoehoe, chunky pähoehoe, and ‘a‘ä. Flat pähoehoe refers to an even rock surface with few cracks. Such surfaces have little water catchment ability or rooting space. In contrast, upheaved pähoehoe refers to broken and upended rock surfaces. These have large cracks and cavities for water catchment and plant establishment. A third type, chunky pähoehoe, is broken into large blocks which are tilted. During rains these act as inverted funnels creating microhabitats particularly favorable for tree growth. ‘A‘ä is quite a different lava type in its physical makeup, although not necessarily different in composition. In the study area it is represented by sharp, clinkery lava rubble. Rainwater penetrates easily but is held by a dense core of lava at approximately one meter below the rubble. There are many spaces to support plant rooting in this type of substrate.

One or more sample stands can represent a species population. If a group of stands on the same substrate type and with similar canopy cover had similar structural histogram curves for a species, such a grouping of stands was treated as one population.

To test the significance of apparent differences between populations, the Kolmogorov-Smirnov Test (K-S Test) was applied to the basal diameter class histograms. This is a conservative test which is used for detecting equality of discrete distributions (Steel and Torrie 1980). This test gives no information on stocking levels instead it compares curve shapes, in this case diameter class distributions.

### Aerial Photographic Analysis

The vegetation of the study area was examined from three sets of aerial photographs. The first set was taken in 1954, during the period of goat occupation. The second set was made in 1965; goat numbers were still high in all but the most coastal portions of the area. The third set was taken in 1977. By this time goats had been eliminated from the eastern Kalapana coastal area for about five years. The photographs were used to determine changes in tree and shrub cover over a 23-year span while goat numbers in the region decreased.

Seven plots of easily recognizable woody communities in the study area were chosen from the photographs (Figure 6). These were selected to meet specific requirements. Primarily, they had to be recognizable in all three sets of photographs. Since photo quality is not identical for the three sets, areas reflecting the least variation in clarity were most acceptable as study sites. Secondly, within these areas, locations were selected that had, in most cases, been studied in detail on the ground. Finally, plots in a variety of community types, substrates, and elevations (as described in structural analysis methods) were selected.

The approximate scale of each photo set varied. The 1954 set was at 1:12,000, the 1965 set was at 1:24,000 and the 1977 set was at 1:45,000. Canopy outlines were easily spotted on the photos but, height and species could not be determined with the exception of kukui and ʻōhiʻa. From field observations it was known that the other trees were predominantly ʻākia, alaheʻe, lama, guava, strawberry guava, and Christmas berry. Certain points were located that could be exactly relocated on each photo set. These were used as starting points for the placement of a dot grid. A 2.54 x 2.54 cm clear plastic dot grid (256/inch sq.) was placed over the community chosen and using eight power magnification for viewing, crown interceptions were counted. This procedure was done three times for each plot and the mean calculated.

Since each aerial photo series is at a different scale and there are variations within each photo, a conversion factor was necessary for each set. Using topographic quadrangles and locating landmarks recognizable on both the quads and the aerial photos, the distance between two points was measured on the quad and on each photo. Using the quad map as the standard, a conversion factor was formulated to enable comparison in cover between the three chronological sets of photos. The formula used with sample distance follows:

on quad on photo of unknown scale
<u>10 cm x 5 cm</u>
1:24,000 1/x = scale of 1:12,000

# Results

### Synthesis Table Analysis

The synthesis table with threshold values of 50/10 produced the most distinctive relevé order and species groupings. Therefore, this is the table examined herein. The relevé order (Table 1) can be most broadly divided into two groups: scrub and forest. The first 21 relevés are all scrub sites with the exception of relevé 22. Although a forest relevé, it is an open ʻōhiʻa dominated site with co-dominants which are also found in scrub sites, including broomsedge and aʻaliʻi. These species were generally of low cover in other forest sites. The next 21 relevés are all forest sites. Thus, there is a general division in species composition between the two broad community types.

Inspection of the species groups reveals overlap between forest and scrub. Subsequently, a more appropriate break in the data set was found to be associated with substrate. Generally, the first 15 relevés have a substrate of chunky or broken pähoehoe, the next 6 are less broken or flat pähoehoe. The group of 7 relevés which follows is indistinct with 3 different substrate types. This is called the transition group and contains a cross section of all major species groupings. The last 14 are in the 'a'ä group. Two of these forest sites (34 and 37) are on pähoehoe, however they are adjacent to 'a'ä flows and are perhaps within the influence of the rubbly substrate. Moreover, both of these relevés have chunky pähoehoe substrate with soil pockets, possibly providing conditions similar to 'a'ä for the vegetation. At a more general level, the first 27 relevés (from 02 to 31) comprise the pähoehoe group and the last 15 (from 23 to 33) comprise the 'a'ä group.

Only forest stands were found on 'a'ä. Relevé groupings were not associated with elevation differences. Location of relevés along an east-west gradient did correspond to groupings in certain cases. Five main differential species groups are represented in the 50/10 synthesis table (Table 1). In addition, the remaining untitled list of species are all others measured within the study area in descending order from ubiquitous to rare.

The Waltheria group, occurring only on pahoehoe, characterizes 27 relevés of the study area (from 02 to 31). Three native species comprise the group: *Waltheria americana* (hi'aloa), *Wikstroemia sandwicensis* ('akia), and *Heteropogon contortus* (pili). Hi'aloa is a low growing shrub widespread in open areas (i.e. in all 20 scrub relevés and in seven open forest relevés). 'Akia is an endemic low-statured tree. Its juvenile stage (i.e. shrub layer) is included in this group. The distribution of 'akia is more restricted than that of hi'aloa being conspicuously absent from the 6 western sites (relevés 02, 06, 12. 18, 20, and 22) (Figure 5) which are also located at higher elevations ($\geq$ 190 m). Pili is considered indigenous by St. John (1972). It is widespread and occurs in twelve scrub relevés and in four open forest relevés.

The *Canthium odoratum* (alahe'e) shrub group consists of four differential species: alahe'e, *Desmodium triflorum* (beggarweed), 'äkia and *Psidium guajava* (guava). The group characterizes 26 relevés of which 11 are forest and 15 are scrub. Except for alahe'e (shrub layer), the other species in this group have low cover in each relevé (%) but are widespread. Alahe'e is a small native tree which is as prevalent in scrub as it is in the open forest. The associated species, 'äkia (herb layer) and two introductions, guava (herb layer) and beggarweed, were frequently observed growing in the shade of larger woody species, in this case alahe'e. All four species were found exclusively in the east and middle sectors of the study area.

The alahe'e tree group is composed of four species: alahe'e (tree layer), 'äkia (tree layer), *Diospyros ferrea* (lama) (tree and herb layers), and *Indigofera suffruticosa* (indigo) (shrub layer). This differential group is found in 17 relevés: 15 forest and 2 scrub. Both scrub relevés are in the extreme eastern portion of the study area where vegetation is of greater stature. In terms of substrate, 8 relevés are on 'a'ä and 9 on differing types of pähoehoe. All 4 species are woody and only indigo is non-native.

The *Oplismenus hirtellus* (basketgrass) group contains three introduced species associated with disturbed forests. Besides basketgrass, the shrub form of *Psidium cattleianum* (strawberry guava) and the vine *Passiflora edulis* (passionfruit) comprise this group. The relevés included are all forest sites on 'a'ä.

The *Aleurites moluccana* (kukui) group consists of two species, the aboriginal introduction kukui (herb, shrub, and tree layers) and an endemic *Stenogyne* (mint) species. Five relevés describe kukui groves which generally contain few other species. All of these are forest sites on 'a'ä.

The balance of the synthesis table contains much information about the study area. Among the species too widespread to qualify as differentials are *Lantana camara* (lantana), *Cassia leschenaultiana* (partridge pea), and broomsedge. The introduced lantana persists with seedlings or vegetative offshoots in almost every relevé. The introduced herb partridge pea is more prevalent on pähoehoe than 'a'ä, and the recently introduced bunchgrasses, *A. glomeratus* (bush beardgrass) and broomsedge are also widespread in the scrub relevés.

## Dendrograph Analysis

Various mathematical indices are used to generate similarity matrices and dendrographs. In this case, two dendrographs were generated, one by using Jaccard's index (Figure 7), the other by using Motyka's quantitative modification of Sorenson's index (Figure 8). The indices are detailed in Mueller-Dombois and Ellenberg (1974).

The threshold level in the Jaccard dendrograph was set at 27% where it segregated five clusters (A, B, C, D, and E in Figure 7). Little useful additional information is rendered if the clusters are subdivided at a more discriminating threshold value.

Cluster A in the Jaccard dendrograph is, at the 27% level of similarity, composed of seventeen relevés which all occur on pähoehoe; only 3 of these are forest relevés. All are located in the eastern or central portion of the study area. Cluster B, consisting of 8 relevés (3 forest, 5 scrub) also relates to sites on pähoehoe. However, the majority of the B cluster relevés are on chunky pähoehoe and are all in the western sector of the study area.

Species differences separating clusters A and B are revealed through examination of the synthesis table. Cluster A is confined to the alahe'e shrub group of the synthesis table, while cluster B contains none of the species within this group.

Cluster C consists of only 3 relevés, all of which are pali forest relevés on 'a'ä or pali talus. They represent chiefly kukui groves.

Cluster D and E are quite similar to one another. If the threshold was set at 25% rather 27%, D and E would be one cluster. Together they contain 14 relevés (10 on 'a'ä and 4 on pähoehoe with soil pockets). These similar clusters generally compare in species composition with the alahe'e tree group of the synthesis table. All, with the exception of relevé 5, are forest relevés.

Motyka's quantitative modification of Sorenson's method results in a dendrograph with a different arrangement of clusters (Figure 8). With the threshold drawn at 25%, 5 clusters emerge once again. Cluster A is the largest with 20 relevés (9 forest, 11 scrub). With the exception of 3 relevés (39, 28, 23), all are on pähoehoe. However, no other relationships can be detected. There is no clear species grouping pattern related to cluster A, although 15 of the 20 relevés are in the hi'aloa group of the synthesis table.

Cluster B consists of 3 scrub relevés on pähoehoe. All 3 are dominated by *Melinis minutiflora* (molasses grass) with introduced shrubs lantana and guava.

Cluster C contains 11 relevés (7 scrub, 4 forest). All have a pähoehoe substrate and are in the alahe'e shrub group of the synthesis table (except relevé 34).

Cluster D is restricted to the pali. Comprised of 3 relevés, this cluster is characterized by sites on 'a'ä or pali talus in the western sector of the study area, and with kukui as the dominant species. All 3 sites are adjacent to one another in the synthesis table.

Cluster E consists of 5 forest relevés on 'a'ä. All are neighbors in the synthesis table. This appears to be the appropriate group also for relevé 34 from cluster C.

Summarizing, the 5 dendrograph clusters can be interpreted as representing the study area vegetation as follows:

| | |
|---|---|
| Cluster A. | Native scrub on pähoehoe |
| Cluster B. | Mixed scrub on pähoehoe |
| Cluster C | Kukui groves on 'a'ä or pali talus |
| Clusters D and E. | Native forest on 'a'ä |

## Life-Form Spectra

The 62 species of vascular plants in 42 relevés of the study area were classified into 21 life form types (Table 2). Four life-form spectra were developed from the 4 major dendrograph clusters using quantitative data of Sorenson. Spectrum A (Figure 9) is cluster A in the dendrograph and represents the 17 relevés on pähoehoe which are included in the native-dominated scrub communities. Most biomass is concentrated in the native woody nanophanerophytes (or low shrubs) and the caespitose hemicryptophytes (or grasses). Introduced species are present in both categories but as subordinates. Natives are exclusive as scapose, sclerophyllous, meso- and microphanerophytes as well as reptant chamaephytes, while introductions are exclusive as malacophyllous mesophanerophytes, reptant hemicryptophytes, and caespitose geophytes.

Spectrum B (Figure 10) is cluster B of the dendrograph representing 8 relevés on pähoehoe which are confined to the western portion of the study area. This spectrum reflects the scrub community dominated by non-native species: for example, introduced caespitose hemicryptophytes and introduced reptant chamaephytes as the ground cover with native meso- and nanophanerophytes (larger trees and low shrubs).

Spectrum C (Figure 11) (cluster C in the dendrograph), is composed of three forest relevés on 'a'ä. All are kukui groves with accompanying lantana and introduced ground cover species. Introduced species by far dominate this spectrum. While natives are exclusive to the scapose meso- and microphanerophytes, they are of low cover.

Finally in spectrum D (Figure 12), clusters D and E in the Sorenson dendrograph represent 14 relevés, mostly on 'a'ä, which comprise the native-dominated forest community with introduced species dominant in the ground cover. Only natives are represented as scapose sclerophyllous mesophanerophytes and by far dominate scapose microphanerophytes and caespitose nanophanerophytes. Introductions dominate caespitose hemicryptophytes, reptant geophytes, and malacophyllous scapose mesophanerophytes.

## Structure of Major Native Woody Populations

Alahe'e is a very common species within the study area. Distributed over 14 of the 22 stands on 3 substrate types, the species is prolific on all substrates. The greatest number of individuals with the broadest diameter range (0-26 cm) was found in 9 'a'ä stands. Eight alahe'e stands are open, while six are semi-open (Figure 13). Both canopy types have high seedling numbers: 1106/1000m$^2$ vs. 1832/1000m$^2$, respectively. However, more alahe'e trees/1,000m$^2$ are found in semi-open stands. The species appears to be shade tolerant since it has more sapling-sized individuals in the denser canopy stands, herein called semi-open. However, the K-S Test (Table 3) showed no significant difference between the populations.

Lama was found in 13 stands. The species was recorded on 2 upheaved and 3 flat pähoehoe stands with soil. In addition, 8 'a'ä stands contained lama. The 5 pähoehoe stands could be grouped since all exhibit similar diameter ranges (0 - 22cm) and low reproduction. In the 8 'a'ä stands, lama populations are more widely represented forming a histogram which is clearly decreasing, signifying continuous reproduction (Figure 14). Lama growing on 'a'ä, has a significantly different structural representation than on pähoehoe where it is sparser and smaller (K-S Test, $p = .05$). Lama was more commonly found in open woodland than semi-open (8 vs. 5). However, reproduction in the open stands was significantly less than in semi-open (25 seedlings/1000m$^2$ vs. 450/1000m$^2$) (K-S Test, $p = .05$). While the diameter range was identical (0-34cm), the numbers within each class are markedly different in the 2 types of stands. Open stands had less than 10 saplings included in the mode of the histogram while the denser semi-open stands had 20 times as many. This self-sustaining species is apparently shade tolerant or a more successionally advanced tree able to germinate and grow to maturity under an almost closed forest canopy.

A'ali'i, a native shrub, was measured in 8 plots. This plant sets fruit abundantly and has a high germination rate as demonstrated by the numerous individuals in 3 of the 4 substrates (Figure 15). Of the areas surveyed, only 1 stand on flat pähoehoe contained a'ali'i. Numbers of individuals within the stand are quite low when compared with more broken substrates. On chunky and upheaved pähoehoe as well as on 'a'ä, the species grows prolifically. An exception is stand 25. Here the introduced mat-forming molasses grass provides an obvious barrier to a'ali'i. Seeds can rarely reach the soil and if some do succeed and germinate, the seedlings generally die from lack of light. All a'ali'i containing stands characteristically have open canopies. The species is probably shade intolerant because it is rarely found growing under semi-open canopies and then only in very low numbers.

'Öhi'a was sampled in 5 open forest stands on pähoehoe (Figure 16). The diameter range is broad

(0 - 90 cm) and the histograms exhibit more than one mode. The 2 chunky pähoehoe stands contain a majority of individuals in the small diameter class (2cm - 6cm), however the numbers decline quickly. There are almost no seedlings in any of the stands. Thus, at present 'öhi'a appears not to be maintaining itself in the E. Kalapana lowland. The histograms suggest that recruitment is probably complete in the stands measured.

'Akia is a low-growing tree present in 11 sample stands. Two of these were on upheaved pähoehoe, 4 on flat, and one on chunky pähoehoe. Four others were sampled on 'a'ä. Reproduction is high on flat pähoehoe (Figure 17). On 'a'ä, no seedlings were found in two plots (23,27), while many were found in two others (29,36). The species appears most frequently in the lower elevation portions of the study area where woody vegetation is shorter and more open.

When reproduction and survival are compared for open versus semi-open canopy, a clearer picture emerges of the 11 stands containing 'akia. Eight are open with a mean number of seedlings of $241/1000m^2$. The histogram is continuous and represents a sustaining population. The 3 stands with semi-open canopies contain very few individuals, no seedlings, and a discontinuous, narrow-ranged histogram (having very few basal diameter classes). The K-S Test shows no significant differences between curve shapes. However, once again, this may be due to the tests inability to account for numerical differences.

## Structure of Major Introduced Woody Populations

Kukui was found in 6 stands only on 'a'ä. Two stands (26 and 27) are distinct from the remaining 4 (K-S Test, $p = .01$) (Figure 18). They exhibit a diameter range of 0 - 22 cm and low numbers of individuals in each class. Seedlings average only $9/1000m^2$. The species does not maintain itself continuously. There are fewer individuals in the smaller size classes indicating a unimodal, normal distribution. The other 4 stands (28, 30, 35, 42) have a completely different size structure with a distinct mode in the smaller diameter classes (saplings). From here, the curve flattens abruptly exhibiting an inverse J-shape. The seedling number is also quite high ($517/1000m^2$). These two groups reflect the different communities in which kukui is found. Sites 26 and 27 are within mixed native-introduced communities, while 28, 30, 35, and 42 are chiefly kukui groves.

All 6 stands have semi-open canopies. When these histograms are examined, they demonstrate more than one mode. The seedling height histograms further support the possibility that the regeneration of kukui occurs in the form of waves or cohorts. The numbers of taller seedlings are consistently greater than those of the shorter seedlings.

Lantana, a low growing shrub, was measured in 15 stands (Figure 19); eight on 'a'ä, 4 on upheaved or chunky pähoehoe and 3 on flat pähoehoe. More individuals were found in the 'a'ä stands, but this difference does not appear to be significant. According to the canopy cover classification, 9 stands were in open forest and 6 in semi-open. Reproduction and self maintenance trends are similar for both canopy classes.

Strawberry guava was sampled in 7 stands. Five of these were on 'a'ä (Figure 20). There are numerous individuals on this substrate in the 0 - 10 cm diameter range including many seedlings. The 2 remaining stands on pähoehoe exhibit distinct, though not significantly different, growth patterns for the species. Stand 25 is on chunky pähoehoe with some soil. Rooting in the stand indicates feral pig activity. These animals seem to feed on and distribute strawberry guava fruits here in a manner similar to that described for Kïpahulu Valley by Diong (1982). Such pig activity favors the spread and increase in numbers of individuals of strawberry guava. However, the mat-forming introduced molasses grass is the stand's major ground cover. The thick mat may prevent seeds from reaching the soil or may result in insufficient light for seedling growth. No seedlings were recorded at this location. Stand 31 is near 25 with the same basic characteristics except molasses grass is absent. In this stand strawberry guava seedlings are numerous ($621/1000m^2$).

The separation of the strawberry guava containing sample stands into open and semi-open canopy groups indicates that the species fares well in shaded conditions. The open stands (relevés 25, 31, 38, 39) have fewer individuals, while the semi-open stands (relevés 26, 27, 34) have many more individuals in all corresponding size classes. Since curve shapes are similar for both habitat types, no significantly different maintenance trends were detected between populations using the K-S Test.

Guava, a mid-sized tree, was measured in 13 stands; eight on 'a'ä, 5 on pähoehoe (Figure 21). This species thrives on 'a'ä as indicated by its broad diameter range (0 - 22 cm) and the abundance of seedlings ($185/1000m^2$). The 5 pähoehoe stands have a diameter range of 0 - 18 cm with very few in each class and an average of 30 seedlings/$1000m^2$. As with strawberry guava, the K-S Test revealed no significant differences in species histogram shapes by substrate type.

A comparison of guava stands with open versus semi-open canopies demonstrates a significant difference in histogram shapes (K-S Test, $p = .01$). Generally, guava is self-sustaining and appears to reproduce more abundantly in open stands. In contrast to strawberry guava, the open stands of guava have more individuals per size class than the semi-open stands.

Christmas berry is a low bushy tree measured in only 3 stands (Figure 22). All 3 were of open canopy. They contained 200 seedlings/$1000m^2$ and showed high mortality as evidenced by the low numbers in successively taller size seedling classes. Perhaps the species is exhibiting a form of autotoxy in which adult individuals can eradicate proximal seedlings following their initial period of growth.

## Community Structure

The structural analysis data (stem cover for each woody species) was used to determine forest community types. The goal was to describe forest communities according to stem cover of native versus introduced woody species. A ratio of native to introduced species' stem cover (N/I) was calculated for each height class. Height classes are those used in the fieldwork and are as follows: 0.6 - 2m = class 1 (shrubs), 2 - 5m = class 2 (short trees), and 5m = class 3 (taller trees). Using these guidelines, 4 forest communities were described for the study area:

1. Lowland mixed native/introduced stands
2. Upland mixed native/introduced stands
3. Upland native stands
4. Kukui stands

## Lowland mixed native/introduced forest stands

This type included the greatest number of structurally analyzed stands (10) (Figure 23). Substrates varied: 4 stands were on flat pähoehoe; 4 on 'a'ä, and, two on upheaved and chunky pähoehoe. Most (7) of these had open canopies (2% crown cover). All stands occurred below 100 m elevation and all contained guava and usually lantana as the more important introduced species. In addition, Christmas berry, indigo, and kukui were found in one or more stands. The native component was consistently alahe'e, lama, 'akia with occasional a'ali'i, 'öhi'a or ulei.

The ratio of native species stem cover to introduced species stem cover (N/I) was calculated for each height class. In all but 3 stands (32, 41 and 35) native species had a greater stem cover than the introduced species (N/I ratio = 1:3.1). However, none of the introduced species were maintaining themselves. Thus, exclusion of natives was not likely. Stand 41 contains greater coverage by introduced species in the two taller size classes. The N/I ratio in favor of introduced species is 1:1.5 and 1:1.6. Also in this stand, neither the native nor the introduced species exhibited sufficient seedling numbers for population maintenance. Stands 32 and 35 were open-canopy stands on flat pähoehoe at very low (12m) elevation. Perhaps moisture availability is low in these stands thus preventing sufficient regeneration for replacement of the older life stages.

Stand 35 was also dominated by introduced species. This stand is of semi-open canopy on 'a'ä. Two introduced and 2 native species were present. The 2 introductions, guava and kukui, grow to canopy heights of greater than 5m. Kukui, especially, grows taller and broader than either of the 2 native species present (lama and alahe'e). Thus, introduced species had greater stem coverage than natives in all height classes of stand 35. In the 7 other stands of this community type, native species dominated. Although in some of these stands introduced species were reproducing in large quantities, the natives consistently had a higher ratio of stem cover.

## Upland mixed native/introduced forest stands

This group contains 5 stands (Figure 24). Substrate for all 5 is ‘a‘ä or pali talus. Three stands have semi-open canopies. All stands are above 226m elevation. Seven introduced species were found in these stands, most consistently strawberry guava, guava, and lantana. *Eugenia cumini* (Java plum), kukui, koa haole and indigo were also occasionally found. Five native species are present, most commonly lama, alahe‘e, a‘ali‘i, and ulei. One stand with a few ‘akia was also included in this community type.

Native species dominated in all stands except number 26. In this stand there was substantial pig activity. Five introduced species (koa haole, strawberry guava, guava, kukui, lantana) dominated the sole native species present, lama. All species, except the shrub lantana which would be expected to remain slender, had broad diameter ranges indicating their long-term establishment in the area.

## Native upland stands

This group consists of 4 open stands (Figure 25); 2 on upheaved pähoehoe and 2 on chunky pähoehoe. The minimum elevation was 344m. Each stand contained only 1 introduced species, either lantana or strawberry guava. The native component was consistently ‘öhi‘a and a‘ali‘i with less frequent *Styphelia tameiameiae* (pükiawe), alahe‘e, and ‘akia. Native species dominated in all three height classes. No introduced species were present in height class 3, and very few were present in class 2.

Lantana, the introduced component in two stands (22 and 33), exhibited low cover and poor regeneration. Strawberry guava was the sole woody introduced species in the two remaining stands (25, 31). This species was regenerating well in stand 31, but not in 25. The mat-forming grass, molasses grass, occurred in stand 25 where it may prevent the regeneration of strawberry guava. The presence of pigs and their rooting activities may account for the low cover of native species in height classes 1 and 2 of both stands (25 and 31).

In all 4 stands, the structural histograms of ‘öhi‘a demonstrated more than one mode (Figure 26).

## Kukui stands

This was the most restricted community type in terms of cover in the study area. Two sample stands had semi-open canopy. Elevation ranged from 78 to 375m. Lantana and guava were the other introduced species in this community. Native species were found in only 1 of the 3 stands and in very low quantity; they included lama, alahe‘e, and a‘ali‘i. *Cassia bicapsularis* (kalamona), which occured in stand 28, could not be measured for its diameter distribution because the stem bases were hidden in a thicket of lantana. Introduced species dominated in all 3 size classes (Figure 27), with the greatest trunk cover in height class 3 (5cm). Minimal basal area cover was measured for the native species in 2 stands (9.4$m^2$ in 28 and 72$m^2$ in 42). Thus, these stands will probably continue to be dominated by introduced species. For all 3 stands of kukui the structural histograms demonstrated more than 1 mode (Figure 28).

## Aerial Photographic Analysis

Seven sites were located on aerial photographs to analyze changes in woody vegetation cover from 1954 to 1977 (Figure 6). Analysis of crown cover on aerial photographs was compared with the data collected during the structural analysis fieldwork. This comparison revealed the following trends in selected communities (Figure 29):

1. Mixed species canopy increase;
2. Kukui canopy decrease but with associated regeneration; and
3. ‘Öhi‘a canopy decrease.

## Trend 1

Sites 1, 6, and 7 are within mixed forest. The canopy of each plot has increased over the 23-year examination period (Figure 29, sites 1, 6, and 7). Sites 1 and 7 had slightly greater increases from 1965 - 1977 (during and following the goat eradication program), 1.2 and 1.8 ha, than before the program's initiation (1954-1965). Site 6 had little canopy change. It may be significant that site 6 is within a campground area built during the 1960's. It is possible that vegetation development is restricted due to consistent human impact therein (i.e., cutting, trampling).

Structural analysis data within the site provided the specific information needed to infer the part played in canopy change by native and introduced species. Structural analysis stand 37 is within site 1. Two introduced species and 3 native species were measured in stand 37. The introduced species, guava and lantana, were not of sufficient height to be detected on aerial photographs. The structural histograms of the native species, ʻakia and alaheʻe indicate ongoing reproduction while the histograms of lama represent a remnant population with very few juveniles. Thus, it is chiefly the canopy of alaheʻe and ʻakia that resulted in the cover increases from 1954 - 1977 (see Figure 29, site 1).

Site 6 contains sample stand 32 which was adjacent to the campground. Guava and 3 natives, alaheʻe, ʻakia, and lama were the major species. Once again, lama is a remnant population while the other three species are actively reproducing. Therefore, canopy increases can be attributed chiefly to the native species (alaheʻe and ʻakia) and subordinately to the introduced guava. It is noteworthy that this stressed location (through human activity at the campground) supports copious seedlings of the following introduced species: Christmas berry, lantana, and guava.

Site 7 encompasses two structural analysis stands (26 and 34). Stand 26 has 5 measured species with lama as the only endemic present. This species has irregular size structure and is reproducing (juveniles are present), however, no seedlings were found. A large amount of pig rooting was observed which may explain the absence of seedlings. Kukui, also shows an absence of seedlings. With a wide diameter range, very few in each class, and the greatest number in the upper diameter range, there are indications that this is a remnant population. While overall canopy cover increased in site 7, kukui's easily recognizable cover decreased. Three other introductions (guava, strawberry guava, and koa haole) are present in the canopy layer and are maintaining themselves. Thus, in site 7, introduced species account for the increase in canopy cover.

Structural analysis results for stand 34 are quite different from those of stand 26 which also contributed information for site 7. Two natives, alaheʻe and lama, and 2 introduced species, guava and strawberry guava were measured. All are maintaining themselves and all likely contributed to canopy increase during the 23-year period.

Summarizing, sites 1, 6, and 7 are representative of mixed forests. In all 3, native and introduced species co-exist. However, there are individual species within each group not faring well: lama is a remnant population in 2 stands as is kukui in one. Alien invaders, especially both species of guava, Christmas berry and lantana, are becoming established. Alaheʻe and ʻākia are the two enduring native species in these stands. Overall, canopy change in these 3 sites can be attributed to both natives and introductions.

## Trend 2

This second trend refers to a decrease in canopy cover of kukui with continued regeneration. It is found in site 3 which relates to 1 of the 3 kukui groves of the Holei pali (stand 28). The main canopy species, kukui, is maintaining itself with numerous seedlings and individuals in each diameter class up to 70 cm. However, according to the aerial photos the kukui canopy has receded over the 23 year period by 1.43 ha (0.06 ha per year). The kukui grove, which includes a wide range of diameters, is probably a generation stand or cohort which is now gradually senescing.

Site 4 contains forest stand 30 which is also a kukui grove. Once again, kukui is maintaining itself although not as consistently as stand 28. The canopy of this grove has also receded since 1954 (by 0.4 ha). Thus, in both sites 3 and 4 ground analysis demonstrates a maintaining population, while aerial photographs imply a decline. Gap-phase regeneration appears to be the mode of maintenance here although it is not evident from the aerial photographs alone.

Site 5 is a third kukui grove along the same pali as forest stands 28 and 30. Measurements did not show consistent change in canopy cover, but rather reflected slight increase for the first 11 years (0.08 ha). Subsequently, the area decreased in canopy by the same amount over the next 12 year period.

## Trend 3

This is a trend of ʻōhiʻa decrease. Site 2 is an area of widely spaced mature ʻōhiʻa greater than 5m in height. No juveniles less than 2m tall nor seedlings of ʻōhiʻa were found here. The area appears to have had no regeneration for a number of years. Photo observation of the site reveals a decrease in canopy cover over the 23-year period. Less trees are standing now than in 1954. Overall decrease is 1.3 ha (0.05 ha per year).

Summarizing, when combined with ground vegetation surveys (especially structural analysis) the method of serial comparison of aerial photographs has revealed trends not otherwise detectable. This combined method is useful in understanding changes within a region's vegetation when an historical series of ground surveys are not available.

The overall changes seen and verified by structural analysis and relevé measurements attest to the increased cover of native woody species in Kalapana. Introduced species also increased in cover during the 23-year period, although less than native species. The decrease of the ʻōhiʻa canopy may only reflect 1 phase of a long-term successional trend.

# Discussion

Synthesis table and dendrograph analyses of the 42 relevés suggest that species associations within the study area are correlated with substrate. Species associations separate according to scrub and forest formations and, more clearly, according to substrate (ʻaʻā vs. pāhoehoe). However, low species numbers comprising the associations reveal that these are more structural than floristic groupings. A total of 62 plant species are present in the relevés, and a mere 13 species form differentials in the 5 species groups as shown in the synthesis table (Table 1). These differentials tend to be developmental stages (herb or youngest stage, shrub or juvenile, and tree or mature stage) of a few major species: ʻakia, alaheʻe, lama, hiʻaloa, and kukui. And, with the exception of the kukui group, the groups separate as shrubs with herbs or trees with herbs. Thus, although associations are distinct according to community structure and substrate, they are not so much species-substrate associations as they are life stage-substrate associations.

The concept that native and introduced species represent different life-forms with introduced species occupying the pioneer position is not fully supported by the data from the 42 relevés. Native and introduced species separate according to life-form in most categories of the life-form spectra, however, in both the nanophanerophyte and hemicryptophyte categories there is overlap. Most of the species present, both native and introduced, are pioneers; although it is true that most aliens are herbaceous and may be more prone to seral displacement when overgrown by woody species. Assuming the continued absence of human impact, increased coverage by woody species is expected, for according to the accounts of former residents (Roberts and LeHong, pers. comm.), a steady increase in woody species has been observed since the reduction in goat numbers within the study area.

Rock (1913) claimed that no less than 60% of the indigenous tree species of Hawaii are peculiar to dry regions or lava fields. However, this study area contains fewer native dry forest species than other similarly impacted dry forests in Hawaii. Six major native tree and shrub species were surveyed in the relevés: ʻōhiʻa, ʻakia, alaheʻe, aʻaliʻi, lama, and ulei. Others in extremely low quantities adjacent to the relevés include: *Hibiscus tiliaceus* (hau), *Erythrina sandwicensis* (wili wili), *Myoporum sandwicense* (naio), and *Reynoldsia hillebrandii*. These species comprise only a portion of the potential species composition of this area. Warshauer and Jacobi (1973) and Warshauer (1974) have located additional endemic tree species in the vicinity of the study area, but these are extremely rare. Their species list includes *Cassia gaudichaudi, Pittosporum terminalioides,* and *Xylosma hillebrandii.*

In 1944, Fagerlund and Mitchell surveyed the vegetation of the Naʻulu Forest. This unique forest is located on a pali at the western end of the study area. Its location is orographically distinct and receives higher rainfall than the surrounding region. The Mauna Ulu flows of 1969-1974 decimated this forest. In addition to some of the above-mentioned species, Fagerlund and Mitchell found the following native trees in the Naʻulu Forest: *Alphitonia ponderosa,* *Bobea timinoides, Myrsine lessertiana,* and *M. sandwicensis* with high frequency. Less frequent were *Pleomele aurea, Myrsine lanaiensis, Rauvolfia sandwicense*, and *Tetraplasandra hawaiiensis.*

The data indicate that the study area is in an early successional stage and/or a degraded stage since woody species richness is low and the major life-forms are a low-growing woody group (nanophanerophytes) and an herbaceous group (hemicryptophytes).

Knowledge of the study area's past impacts (goats and human settlement) implies that degradation is partly responsible for its early successional stage and poor species diversity. However, the youth of the area's substrate should not be overlooked. It is suggested that the relative frequency of lava flows, subsidence, and earthquakes may hinder succession, thus forcing the vegetation to remain in an early seral state far longer than expected.

Holcomb (1980) states that 70% of Kilaeua Volcano is less than 500 years old and 90% is less than 1,000 years old. Since Kalapana's formation is under the direct influence of Kilaeua and its east rift zone, the land surface is of relatively recent volcanic origin. Holcomb's dating of lava in the Kalapana Extension estimates the major portion of the study area to be from 500 to 700 years old. In addition, there are small areas dated from the 18th century and as recently as 1990's; while one area is composed of lava 1500 years old.

It is well established that in temperate areas of the world succession from abandoned field to climax forest may take longer than 200 years (Whittaker 1975). It is suggested that for tropical forest to develop to climax stage from bare lava (thus including soil development) and with water as a limiting factor, a period at least twice as long may be required. Atkinson (1971) proposed that more than 400 years may be necessary for generally undisturbed primary succession to progress into a closed forest in a windward tropical location. Under the drier climatic and edaphic conditions found in the study area, succession to a climax forest probably requires additional time. A comparison of substrate age and time necessary for a climax community to emerge suggests that the low species richness of Kalapana's vegetation may be attributed as much to an overall youthful substrate as to past disturbance.

Native and endemic woody species richness in representative dry forest areas below 625 m in Hawaii can be compared with approximate substrate ages (Figure 30). Four selected locations: Kalapana, Hawai'i; Manuka, Hawai'i; Auwahi, Maui and Mokulē'ia, O'ahu, have endured similar human-induced disturbance factors: goats, cattle ranching, settlements and limited agriculture. Thus, it is substrate age and rainfall differences that should contribute to species richness discrepancies. Rainfall variation between sites is substantial. The study area of Kalapana has the greatest rainfall of 2000mm (at 3m elevation in the east) and 1630mm (19m elevation in the west) (DLNR 1976). Auwahi receives 680mm at 630m elevation. Manuka receives 1470mm (DLNR 1976), and Mokule'ia ranges from 630mm at sea level to 1600mm at 625m elevation (Wirawan 1972).

Despite the greater overall rainfall at the younger substrate locations (Kalapana and Manuka) which could be considered as driving a more rapid succession to dry forest, the general trend is one of increased species richness with substrate age. The dry forest of Kalapana contains 20 native or endemic woody species, while Manuka contains 23. Auwahi has 27 native woody species below 625m elevation, and the area of oldest substrate, Mokuleia, contains 44 native or endemic woody plants (Appendix C).

That low species richness of the Kalapana study area is partly due to its youthful substrate and not only to introduced disturbances appears to be a tenable hypothesis. Given sufficient time without land destruction by lava flows, upheavals or subsidence, native species richness within the eastern Kalapana lowland may increase. Although the continued activity of Kilauea Volcano to the west and east (Appendix D) effectively impedes seed migration due to the near barren state of the regions, favorable conditions also exist which may speed up succession within the Kalapana lowland. Abrupt elevation change leads to a more diverse mixed (dry and mesic species) transition forest in close proximity to the study area. This increases the probability that with time and minimal disturbance, additional seral species will filter into and become established in the lowland. Also, since large mammalian herbivores and humans no longer reside in this region and since human activities are now minimized because of the protected status of this area, the additional succession-arresting factor, i.e. disturbance, is now eliminated.

# Conclusion

The competitive abilities of native woody species in Hawaii should not be underestimated. The native woody species present in the study area probably represent only a portion of the original native dry forest in the vicinity. However, these species have endured the influx of foreign animals, human settlements, and introduced plant competitors, and have recovered to dominate the woody communities within a few years following removal of the recently introduced impacts. This is the sign of a resilient, not defenseless, native vegetation.

# Management Recommendations

The National Park protected status of this study area affords it a management advantage available to no other dry forest area in the State of Hawaii. Baning inundation of the study area by the current eruption of Kilauea's Kupaianaka vent; the following recommendations are proposed for the continued recovery of the area's native vegetation.

The Resources Management program concerned with mapping and control of introduced species should be extended to the study area by

1) controlling spread of *Eugenia cumini* (java plum) trees. These are concentrated above 200 m along the Kalapana Trail, but have been observed growing at sea level in Lae Apuki.

2) eliminating *Leucaena leucocephala* (haole koa). Found above 70 m along the Kalapana Trail, there are very few with a large potential for increase in cover as evidenced by the numerous seedlings in the trees' immediate vicinity. This species and *E. cumini* have barely been mentioned in this paper, however, data is available on them for the two plots in which they were measured.

3) Monitoring *Lantana camara*; this species appears to be under control now due to the biological control agent *Thecla bazochii*, but the ability of Lantana to reproduce by root shoots and the possibility of reduced effectiveness of the moth provides potential for *Lantana's* spread.

4) Controlling the spread of *Psidium cattleianum* (strawberry guava); these are also concentrated above 200 m elevation along the Kalapana Trail and in some areas exhibit dense growth.

Areas of continued disturbance, such as trails, roadways, and campgrounds require more intensive control of introduced species, especially *Schinus terebinthifolius* (Christmas berry) and *Melinis minutiflora* (molasses grass). It is in these areas that introduced species are local dominants which can suppress the recovery of native trees and herbs.

Pigs appear to play a part in the spread of *Psidium cattleianum* and *Eugenia cumini* in the study area as both species are prolific where pig densities are greater. Evidence of pig activity has also been found as low as 30 m elevation. Controlling the numbers of these animals in the study area and its vicinity is imperative. While there are no reports of goat presence in the study area for more than a decade, immigration from nearby populations of the very few left is always a possibility. Monitoring of this animal's numbers and distribution should continue.

Finally, fire prevention is of great importance in this dry area, for although native woody species are recovering and dominant, the introduced grasses and alien woody species present are generally more fire-adapted and have already demonstrated in at least one portion of the study area (near the former Na'ulu Forest) their ability to dominate following such a disturbance.

While there may be a certain fire resistance in the native woody vegetation, fire will set succession back to the grassland stage if it occurs at frequent intervals. Fire suppression allows woody plants to gain further dominance and also allows for the eventual development of scrub-grassland into woodland and forest.

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Table 1.

Synthesis Table for the 42 scrub and forest relevés of the study area. The differential species emerge as five major groups named for the first species in the group. These groups are correlated with substrate type in general and in some cases with forest or scrub formation.

SYNTHESIS TABLE (50/10)

| Relevé Numbers | 0 | 0 | 1 | 1 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 3 | 4 | 4 | 3 | 2 | 3 | 3 | 3 | 3 | 2 | 3 | 2 | 3 | 4 | 2 | 3 | 2 | 2 | 3 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Habitat | 2 | 6 | 2 | 8 | 0 | 2 | 1 | 3 | 4 | 5 | 7 | 8 | 9 | 0 | 4 | 5 | 6 | 7 | 9 | 1 | 3 | 1 | 4 | 2 | 0 | 1 | 1 | 3 | 8 | 6 | 7 | 9 | 9 | 4 | 7 | 5 | 2 | 8 | 0 | 5 | 6 | 3 |
| | SCRUB | | | | | | | | | | | | | | | | | | | | | FOREST | | | | | | | | | | | | | | | | | | | | |
| Substrate | Chunky Pahoehoe | | | | | | | | | | | | | | | Flat Pahoehoe | | | | | | Mixed Pahoehoe & A'Ā | | | | | | | A'Ā | | | | | | | | | | | | | |
| WALTHERIA AMERICANA SHRUB GROUP | + | + | 1 | 1 | 2 | 1 | + | + | + | + | 1 | 1 | 1 | 1 | 1 | + | 2 | + | + | 1 | 1 | + | + | + | 1 | + | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Waltheria americana (herb) | - | + | - | + | + | + | + | + | + | + | + | + | + | + | + | + | 1 | - | + | + | + | - | + | + | + | + | + | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Wikstroemia sandwicensis (shrub) | - | - | - | - | - | - | 2 | 1 | 2 | 2 | 1 | r | r | 1 | 1 | + | - | 2 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 2 | + | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - |
| Heteropogon contortus | 1 | 3 | - | - | - | 1 | 1 | - | 1 | - | 3 | 4 | 2 | - | 2 | 1 | 2 | - | - | + | + | 2 | 3 | - | 1 | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - |
| CANTHIUM ODORATUM SHRUB GROUP | - | - | - | - | - | - | - | + | + | 1 | + | - | - | - | 2 | + | - | 1 | 1 | + | 1 | 1 | 1 | 1 | 1 | 2 | - | 2 | 2 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | - | - | - | - | - | - |
| Desmodium triflorum | - | + | - | - | - | - | + | - | + | 1 | + | + | + | + | + | - | + | + | r | + | + | + | + | + | + | + | - | - | - | + | + | - | - | - | - | - | - | - | - | - | - | - |
| Wikstroemia sandwicensis (herb) | + | - | + | - | - | - | + | r | + | + | + | - | - | + | + | + | - | + | - | + | + | - | + | + | + | + | + | - | - | + | + | + | + | - | - | - | - | - | - | - | - | - |
| Psidium guajava (herb) | - | - | - | - | - | - | + | r | - | - | - | + | - | - | - | - | + | - | - | - | - | - | - | - | r | - | - | 1 | + | + | - | - | - | - | - | - | - | - | - | - | - | - |
| CANTHIUM ODORATUM TREE GROUP | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | + | 1 | 2 | + | 2 | 2 | - | 1 | 3 | - | 2 | 3 | 2 | 2 | 1 | 2 | 1 | - | - | - | - | - |
| Diospyros ferrea (tree) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | 2 | 1 | - | 2 | 1 | + | - | 4 | 1 | - | 2 | 2 | 3 | 1 | 2 | - | - | - | 4 | - |
| Indigofera suffruticosa (tree) | - | - | - | - | + | - | - | - | - | - | - | - | + | - | - | - | - | - | - | - | - | + | + | + | + | - | 1 | - | - | - | - | - | + | - | - | 1 | - | - | - | - | - | - |
| Wikstroemia sandwicensis (tree) | - | - | - | - | - | - | - | r | - | 1 | - | - | - | + | - | - | - | - | - | + | + | + | 2 | 2 | 2 | 2 | - | - | - | - | 2 | - | 2 | - | - | - | - | - | - | - | - | - |
| Diospyros ferrea (shrub) | - | - | - | - | - | - | r | - | + | - | - | - | - | - | - | - | - | - | 1 | - | - | + | - | - | - | - | 1 | + | - | - | 1 | - | - | 1 | 1 | - | - | - | - | - | - | 1 |
| OPLISMENUS HIRTELLUS GROUP | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | + | + | - | + | - | - | - | - | - | - | - |
| Psidium cattleianum (shrub) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 2 | - | r | - | - | 1 | - | + | + | - | - | - | - | - | + | 2 |
| Passiflora edulis | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | + | + | + | - | - | - | - | - | - | - | - |

Table 1. (Cont'd)

| | |
|---|---|
| ALEURITES MOLUCCANA TREE GROUP | - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - \|+ 3 3 4 3\|- 1 - |
| Aleurites moluccana (shrub) | - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - \|+ 1 1 2 2\|- - - |
| Aleurites moluccana (herb) | - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - \|- + - + +\|- - - |
| Lantana camara (herb) | r + - - - - - - r - - - - - - - + - - - - - + + + 1 + + - - + + r - + + - - - - + + - - - |
| Lantana camara (shrub) | 1 3 - + 3 1 1 1 1 1 + - + 1 1 + 1 1 + 1 + 2 1 2 - 1 - 2 1 - 1 1 - + - - 2 - 3 - 1 1 |
| Cassia leschenaultiana | + r + - + + + + + + + + + + + + 1 + + + + + + + + + - - + 1 - - - - - - - 1 + - + |
| Andropogon virginicus | 1 - 1 3 - 3 4 + 2 3 + - + 4 2 1 2 + 3 3 2 - + - - + 4 - 2 - 3 2 - - - - - + - 3 - 4 |
| Psidium guajava (shrub) | - - - + + - - + 1 1 + + 1 + - + + 1 + + + + + 2 - 1 - 1 2 - 1 1 - + - 1 - - - - 1 - |
| Phymatosorus scolopendria | - - - - - - + - - + + + - r - + - - + + + + + + + 1 - 1 + 3 - + 4 1 + 5 - + + - 1 - |
| Osteomeles anthyllidifolia (shrub) | - - - - - - - - - - - - - - - - - - 1 1 2 r 1 - 2 1 2 - - + 3 + + 2 - - - - - - + - - |
| Chrysopogon aciculatus | - - + - + + + - + 1 + + + + + + 1 + + + + + - + + + - - - + + + - - - - - - - - - 1 |
| Dodonaea viscosa (shrub) | 3 - 2 2 - 3 - 1 - - r - + - 2 2 3 + - - 1 r r - 1 - 2 - 2 - 1 3 + - - - 1 - - 2 - 3 |
| Nephrolepis multiflora | - - + - - + + + + + - + 1 + - - 1 - - + + - - - - - 1 1 - - - - - + + + + + 1 1 + 1 1 - |
| Canthium odoratum (herb) | - - - - - - - - - + - - - r + - - - - - + + + + + + + - + + + + + + 1 + + + - - - - - |
| Bare Lava | 1 1 2 - - 2 1 1 3 1 + 1 - 1 - - - - - 1 - 1 - - - 2 - 2 1 1 1 + - 1 - - 4 3 - - - - |
| Tricholaena repens | - 1 1 2 3 - - - - - + + 2 + 1 - 1 + 1 - - - + 2 1 3 - - - - - - - - - - 2 + + - - 2 |
| Andropogon glomeratus | 4 - 1 2 - + - 3 - + - - - + 1 - - - + - 2 - - - - + + - 1 - 1 2 - r - - - 1 - 3 - 1 |
| Dodonaea viscosa (herb) | + - + + - 1 - + - - - - - - + + + - - - + - - - + - + - + - - - - - - - - - - - - 1 |
| Passiflora foetida | - - - - - - - - - r r + - - - r - - r - - r - - r r - + - 1 r - + r + - + + + - 1 - |
| Melinis multiflora | - - + 2 3 + - 4 - - 1 - - - - - - + 4 - - - + - - - - - - - - - - - - - - + - - 3 - 1 |
| Desmodium uncinatum | - - - - - - + - + 1 - - - + - - - + - - - r - + - r 1 - - r - - - 1 - - - - - - - + - |
| Psilotum nudim | - - - - - r r r - - - - - - - - - + - - - r - - - - - - - r - r + + - + - + - + - - r |
| Schinus terebinthifolius (herb) | - - - - - - - - - - - - - - - - - - + + - + + + - + - + - + - - - - - - - - - - - - |
| Diospyros ferrea (herb) | - + - - - - - - - - - - - - - - - - - - - + + + - - - - - - - - - - - + - + - - - - - - |
| Stachytarpheta jamaicensis | - - - + - - - - - - - - - - - + 1 + - - + - - - - - + + - 1 + 1 + - - - - - + - + - - |
| Emilia sonchifolia | - r r - + - r - - - - - - r r - - - - r - - - - - + - - - - - - - + + - - - - - + - - - - |
| Rock Outcrop | - - - 2 3 - - - - - - - - - - - - 2 - 1 - - - + - 1 - 1 - - - - - - - - - - 1 - 2 - - 2 |
| Conyza canadensis | + - r - - - - - - - - - r - r - - - + - - - - - - - - - r - - r r + - - - - - - - - - - |
| Psidium guajava (tree) | - - - - - - - - - - - - - - - - - - - - - - + 1 - 1 - 1 2 - - 1 - 1 - 1 - - - - - 1 - |
| Schinus terebinthifolius (shrub) | - - - - - - - - - - - - - - - - - - 1 1 - r 1 - - 1 - - - - - - - - - - - - - - - - - |
| Metrosideros polymorpha (tree) | - - - - - 3 - r - - - - 1 - - - - - - - - + 2 - - - r 2 - - - - - - + - - - - - - - - - |
| Pluchea odorata (shrub) | - - - + - r - - r r - 1 - - - - - - - - - - - - - - - - + - - - - - - - - - - - - 3 - 2 |
| Indigofera suffruticosa (shrub) | - + - - + - - - - - - - - - - - - - - 1 + + + - + - - + r - - - - r - r - - + + - - |

**Table 1. (Cont'd)**

| Relevé Numbers | 02 | 06 | 12 | 18 | 20 | 22 | 01 | 03 | 04 | 05 | 07 | 08 | 09 | 10 | 14 | 15 | 16 | 17 | 19 | 11 | 13 | 21 | 24 | 32 | 40 | 41 | 31 | 23 | 38 | 36 | 37 | 39 | 29 | 34 | 27 | 35 | 42 | 28 | 30 | 25 | 26 | 33 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Habitat | SCRUB | | | | | | | | | | | | | | | | | | | | | FOREST | | | | | | | | | | | | | | | | | | | | |
| Substrate | Chunky Pahoehoe | | | | | | | | | | | | | | | Flat Pahoehoe | | | | | | Mixed Pahoehoe & A'Ā | | | | | | | | A'Ā | | | | | | | | | | | | |
| Arundina bambusaefolia | r | - | + | + | - | - | + | - | - | - | - | - | - | - | - | - | - | - | - | + | + | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - |
| Styphelia tameiameia (shrub) | - | - | - | - | - | + | 1 | + | r | 1 | - | r | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | + | - | - | - | - | - | - | - | - | - |
| Spathloglottis plicata | 1 | - | - | - | - | - | + | r | - | r | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | r | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Pleopeltis thunbergiana | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Schinus terebinthifolius (tree) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | 1 | - | 2 | - | - | - | - | - | - | - | - | - | - | r | - | - | - | - | 2 |
| Morinda citrifolia (herb) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Setaria geniculata | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | + | - | + | + | - | - | - | - | - | - | - | - | - | - | - | - |
| Lantana camara (dead) | - | - | - | - | - | - | - | - | - | - | - | 1 | + | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Ipomoea congesta | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Dodonaea viscosa (tree) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | + | - | - | - | 2 | - | 1 | + | - | - | - | - | - | - | - | + | - | - |
| Cassia bicapsularis (herb) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Cassytha filiformis | + | - | - | - | - | - | - | - | - | + | + | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Osteomeles anthyllidifolia (herb) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | + | - | - | + | + | - | - | - | - | - | - | - | - |
| Eugenia cumini (shrub) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | r | - | - | - | - | - | - | - | - | - | - | - | - | + | - | - | + | + | - | - | - |
| Abrus precatorius | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | r | - | 1 | - | - | - | - | - | - | - | - | - | - | r | - | - | - | - | - | - | - |
| Bidens pilosa | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | r | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Eugenia cumini (herb) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | + | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | + | - | - | - | - | - | - | - | - |
| Stenogyne sp. 2 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - |
| Leucaena leucocephala (herb) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | r | - | - | - | - | - | - | + | - | - | - | - | - |
| Morinda citrifolia (shrub) | - | - | - | - | - | - | - | - | - | r | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Cassia bicapsularis (shrub) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | r | - | - | - | - | 1 | - | - | + | - | - | - | - | - |
| Lantana camara (tree) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | + | - | - | - | - | - | - | - | - | 2 | - |
| Bare Ground | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Psidium cattleianum (tree) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 2 | - | - | - |
| Artocarpus communis (tree) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Eugenia cumini (tree) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | 2 | - | - | - | - | - | - | - |
| Oxalis corniculata | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 3 | - |
| Cocculus ferrandianus | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | + | - | - | - | - | + | - | - |
| Ageratum conyzoides | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | + | - | - | - | 1 | - | - | - | - | - | - | r | - | r | - | - | 2 | - |
| Metrosideros polymorpha (herb) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Hyparrhenia rufa | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | + | - | - | - | - | - | 2 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | + | - | r | - |
| Metrosideros polymorpha (dead) | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | + | - |
| Cocos nucifera (tree) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |

**Table 1. (Cont'd)**

| | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Indigofera suffruticosa (herb) | - | + | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | + | - | - | - | - | - | - | - | + | - | - | - | - | - | - | - | - | - |
| Machaerina angustifolia | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | r | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Styphelia tameiameiae (tree) | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Styphelia tameiameiae (herb) | - | - | - | - | - | - | - | - | - | + | - | - | - | - | - | - | - | + | - | - | - | - | - | - | - | - | + | - | - | - | - | - | + | - | - | - | - | r | - | - | - | - |
| Osteomeles anthyllidifolia (tree) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | + | - | - | - | - | - | - |
| Cordyline terminalis | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Morinda citrifolia (tree) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Pluchea odorata (herb) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | + |
| Mucuna gigantea | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Sesuvium portulacastrum | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Psidium guajava (dead) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | + | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Asplenium nidus | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | + | - | - | - | - | - | - | - | - |
| Metrosideros polymorpha (shrub) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | + | - | - | - | - | r | r | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Erythrina sandwichensis (tree) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | r | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Psidium cattleianum (herb) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | + | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Doryopteris sp. | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | + |
| Peperomia sp. | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | + | - | - | - | - | - |

r = rare, 1 or 2 individuals
\+ = very few, scattered

1 = < 5% cover
2 = 5-25% cover
3 = ≥25-50% cover
4 = ≥50-75% cover
5 = ≥75-100% cover

**Table 2.**

Species of the coastal woodland vegetation of the Kalapana Extension, Hawai'i Volcanoes National Park study area listed by life-form, origin, and life-form spectrum. N = native, I = introduced, (A) = aboriginal introduction. The vegetation types were derived by using the dendrograph technique and applying the results to formulate life-form spectra. They are symbolized in the life-form spectra as follows:

A. Open scrub dominated by native species
B. Open scrub dominated by introduced species
C. Semi-open introduced *Aleurites moluccana* groves
D. Semi-open forests dominated by native species

| Origin | Species by Life-Form | Spectra |
|---|---|---|
| **Sclerophyllous, Mesophanerophyte, scapose** | | |
| N | *Metrosideros polymorpha* | A, B |
| N | *Diospyros ferrea* | A, C, D |
| N | *Erythrina sandwichensis* | D |
| I(A) | *Cocos nucifera* | C |
| **Malacophyllous, Mesophanerophyte, scapose** | | |
| I(A) | *Aleurites moluccana* | C, D |
| I | *Eugenia cumini* | A, D |
| I | *Psidium guajava* | A, B, D |
| I(A) | *Artocarpus communis* | C, D |
| **Sclerophyllous, Microphanerophyte, scapose** | | |
| N | *Canthium odoratum* | A, C, D |
| N | *Wikstroemia sandwicensis* | A, B, D |
| I | *Psidium cattleianum* | B, D |
| **Malacophyllous, Microphanerophyte, scapose** | | |
| I(A) | *Cordyline terminalis* | B, D |
| I(A) | *Morinda citrifolia* | D |
| I | *Leucaena leucocephala* | D |
| **Malacophyllous, Microphanerophyte, caespitose** | | |
| I | *Schinus terebinthifolius* | A, C, D |
| I | *Cassia bicapsularis* | C, D |
| **Sclerophyllous, Nanophanerophytes, caespitose** | | |
| N | *Dodonaea viscosa* | A, B, C, D |
| N | *Osteomeles anthyllidifolia* | A, B, D |
| N | *Styphelia tameiameiae* | A, B, D |
| I | *Lantana camara* | A, B, C, D |
| I(A) | *Indigofera suffruticosa* | A, B, D |
| **Suffruticose Chamaephytes** | | |
| I | *Stachytarpheta jamaicensis* | A, B, C, D |
| I | *Cassia leschenaultiana* | A, B, C, D |

**Table 2. (Cont'd)**

| Origin | Species by Life-Form | Spectra |
|---|---|---|
| **Fruticose Chamaephytes** | | |
| I | *Pluchea odorata* | A, B, C, D |
| **Herbaceous Chamaephytes, caespitose** | | |
| N | *Stenogyne sp.* | C, D |
| N | *Machaerina angustifolia* | D |
| N | *Waltheria americana* | A, B, D |
| I | *Desmodium uncinatum* | A, D |
| I | *Setaria geniculata* | A, B |
| **Herbaceous Chamaephytes, reptant** | | |
| N | *Peperomia sp.* | A, B, C, D |
| N | *Sesuvium portulacastrum* | A, D |
| I | *Melinis minutiflora* | A, B, C |
| | *Oplismenus hirtellus* | C, D |
| I | *Paspalum conjugatum* | A, C, D |
| **Caespitose Hemicryptophytes** | | |
| | *Heteropogon contortus* | A, B, D |
| I | *Hyparrhenia rufa* | A, D |
| I | *Andropogon virginicus* | A, B, C, D |
| I | *Andropogon glomeratus* | A, B, D |
| I | *Tricholaena repens* | A, B, C, D |
| **Reptant Hemicryptophytes** | | |
| I | *Desmodium triflorum* | A, D |
| I | *Chrysopogon aciculatus* | A, B, D |
| **Caespitose Geophytes** | | |
| N | *Doryopteris sp.* | B, C, D |
| N | *Pellea ternifolia* | D |
| I | *Nephrolepis multiflora* | A, B, C, D |
| I | *Spathoglottis plicata* | A, D |
| I | *Arundina bambusaefolia* | A, B, C |
| **Reptant Geophytes** | | |
| N | *Pleopeltis thunbergiana* | D |
| I | *Phymatosorus scolopendria* | A, C, D |
| **Therophytes** | | |
| I | *Oxalis corniculata* | C, D |
| N | *Ipomoea congesta* | A, B |
| I | *Ageratum conyzoides* | A, D |
| I | *Emilia sonchifolia* | A, B, C, D |
| I | *Conyza canadensis* | A, B, D |

Table 2. (Cont'd)

| Origin | Species by Life-Form | Spectra |
|---|---|---|
| **Therophytes** | | |
| I | *Bidens pilosa* | C, D |
| **Herbaceous Lianas** | | |
| I | *Passiflora foetida* | A, C, D |
| **Suffruticose Lianas** | | |
| N | *Cocculus ferrandianus* | A, D |
| I | *Passiflora edulis* | D |
| **Fruticose Lianas** | | |
| I | *Abrus precatorius* | A, D |
| N | *Mucuna gigantea* | D |
| **Epiphytes** | | |
| N | *Psilotum nudum* | A, B, C, D |
| N | *Asplenium nidus* | C |
| **Parasites** | | |
| N | *Cassytha filiformis* | A, B, D |

## Table 3.

Locational relationships of woody species with habitat types in the study area. Asterisks (* or **) imply a significant difference inpopulation structure between habitats compared in the matrix. Circle (O) indicate species presence but no difference in population structure, and blank cells imply that species was absent for either one or both habitat types compared.

### Komogorov-Smirnov Two-Sample Test

| Species / Habitat Types | 'a'a vs. chunky pähoehoe | 'a'a vs. *flat* pähoehoe | 'a'a vs. *upheaved* pähoehoe | 'a'a vs. 'a'a | *chunky* pähoehoe vs. flat | upheaved pähoehoe vs. flat | upheaved pähoehoe vs. chunky | open canopy vs. semi-open | Comments |
|---|---|---|---|---|---|---|---|---|---|
| Diospyros *ferrea* | * | * | | | O | | | * | 'a'a & semi-open curves exhibit reverse J-shape. Higher and broader than pähoehoe and open canopy curves. |
| Wikstroemia sandwicansis | O | * | O | O | O | O | O | O | Pähoehoe curve is higher and more continuous than 'a'a. Marginal significance. |
| Aleurites moluccana | | | | ** | | | | | A.M. in mixed forest exhibits poor reproduction and truncated curve when compared with pure groves. Semi-open canopy only. |
| Paidium guajava | O | O | O | | O | O | O | ** | Significantly broader diameter class curve under semi-open canopy. |
| Canthium odoratum | O | O | O | | O | | | O | |
| Dodonaea viscosa | O | O | O | | O | O | O | | Open canopy only. |
| Metrosideros polymorpha | | | | | | | O | | Open canopy only. |
| Lantana camara | O | O | | | O | | | O | |
| Psidium cattlelanum | O | | O | | | | O | O | |
| Schinus terebinthifolius | | | | | O | | O | | Open canopy only. |

O - Found in both habitat types with no significant difference in basal diameter class curves

*p 0.05

**P 0.01

# Appendix A.

Checklist of the vascular plants of the coastal lowland vegetation of the Kalapana Extension, Hawaii Volcanoes National Park.

Nomenclature of flowering plants follows St. John (1973). Names of ferns and fern allies are in accordance with the unpublished check-list of I. E. Lane. Key to symbols before species names: E = Endemic, N = Native, I = Introduced, (A) = Aboriginal introduction.

| Family/Scientific Name | | Common Name |
|---|---|---|
| | **Ferns and Fern Allies** | |
| **Aspleniaceae** | | |
| N | *Asplenium nidus* L. | ʻēkaha, bird's nest |
| **Davalliaceae** | | |
| I | *Nephrolepis multiflora* (Roxb.) Jarrett ex. Morton | swordfern |
| **Polypodiaceae** | | |
| I | *Pellaea ternifolia* (Cav.) Link lauliʻi | cliffbrake,kalamoho |
| I | *Phymatosorus scolopendria* (Burm.) Pic.-Ser. | lawai |
| **Psilotaceae** | | |
| N | *Psilotum nudum* L. (Beauv.) | moa, pipi |
| **Pteridaceae** | | |
| E | *Doryopteris decora* Brack. | waiwa, kumuniu |

**Appendix A. (Cont'd)**

| Family/Scientific Name | Common Name |
|---|---|
| | **Flowering Plants** |
| **Aizoaceae (Carpetweed family)** | |
| N *Sesuvium portulacastrum* (L.) | L. ʻäkulikuli, sea purslane |
| **Anacardiaceae (Mango family)** | |
| I *Schinus terebinthifolius* Raddi. | Christmas berry, Brazilian pepper tree, naniohilo, wileaiki |
| **Araliaceae (Ginseng family)** | |
| E *Reynoldsia hillebrandii* Sherff. | ʻohe |
| **Arecaceae (Palm family)** | |
| I(A) *Cocos nucifera* L | coconut, coco palm, niu |
| **Asteraceae (Sunflower family)** | |
| I *Ageratum conyzoides* L. | ageratum, mailehonohono |
| I *Bidens pilosa* L. | Spanish needle, kï beggar's tick, pilipili |
| I *Conyza canadensis* (L.) Cronq. | Canada fleabane, horseweed, ilioha,laniwela |
| I *Emilia sonchifolia* (L.) | lilac pualele |
| I *Pluchea odorata* (L.) Cass. shrubby fleabane | pluchea, sourbush, |
| **Convolvulaceae (Morning-glory family)** | |
| N *Ipomoea congesta* R.Br. | koaliʻawania, koaliʻawa morning glory |
| **Cyperaceae (Sedge family)** | |
| N *Machaerina angustifolia* (Gaud.) | uki Koyama |
| **Ebenaceae (Ebony family)** | |
| E *Diospyros ferrea* (Willd.) Bakh | lama |
| **Epacridaceae (Epacris family)** | |
| N *Styphelia tameiameiae* (Cham.) F.Muell. | pükiawe, maiele, käwaʻu, aʻaliʻimahu |

**Appendix A. (Cont'd)**

| Family/Scientific Name | Common Name |
|---|---|
| **Euphorbiaceae (Spurge family)** | |
| I(A) *Aleurites moluccana* (L.) Willd. | kukui, tutui, candlenut tree |
| **Fabaceae (Pea family)** | |
| I *Abrus precatorius* L. | black-eyed susan, bean vine, pükiawe |
| I *Cassia bicapsularis* L. | kalamona |
| I *Cassia leschenaultiana* DC. | partridge pea, laukähi |
| I *Desmodium triflorum* (L.) DC. | three-flowered beggarweed |
| I *Desmodium uncinatum* (Jacq.) DC. | Spanish clover, chili clover,Hawaiian tick, trefoil |
| E *Erythrina sandwicensis* Deg | wiliwili, Hawaiian erythrina, Haw. coraltree |
| I *Leucaena leucocephala* (Lam.) DeWit | koa haole, ëkoa, false koa, ipilipil, wild rind, lead tree, aroma blanca |
| N *Mucuna gigantea* (Willd.) DC. | kä'e'e, seabean |
| **Lamiaceae (Mint family)** | |
| N *Stenogyne sp.* | mint |
| **Lauraceae (Laurel family)** | |
| N *Cassytha filiformis* L. | kauna'oa |
| **Liliaceae (Lily family)** | |
| I(A) *Cordyline terminalis* (L.) Kunth. | tï, kï |
| **Menispermaceae (Moonseed family)** | |
| E *Cocculus ferrandianus* Gaud. | huehue, hue'ie, 'inalua |
| **Moraceae (Mulberry family)** | |
| I(A) *Artocarpus communis* J.R. & G. Forst. | ulu, breadfruit |
| **Myoporaceae (Naio family)** | |
| E *Myoporum sandwicense* Gray | naio |

| Family/Scientific Name | | Common Name |
|---|---|---|
| **Myrtaceae (Myrtle family)** | | |
| I | *Eugenia cumini* (L.) Druce | java plum, jambolan plum |
| E | *Metrosideros polymorpha* Gaud. | 'ōhi'a-lehua |
| I | *Psidium cattleianum* Sabine | strawberry guava, waiawī'ula'ula |
| I | *Psidium guajava* L. | guava, kuawa |
| **Orchidaceae (Orchid family)** | | |
| I | *Arundina bambusaefolia* (Roxb.) Lindl. | bamboo orchid |
| I | *Spathoglottis plicata* Bl | ground orchid |
| **Oxalidaceae (Wood Sorrel family)** | | |
| I | *Oxalis corniculata* L. | lady's sorrel, wood sorrel,'ihi, ihi'ai, 'ihi'awa |
| **Passifloraceae (Passion Flower family)** | | |
| I | *Passiflora edulis* Sims. | liliko'i |
| I | *Passiflora foetida* L | love-in-a-mist, pohāpohā |
| **Piperaceae (Pepper family)** | | |
| N | *Peperomia sp.* | |
| **Poaceae (Grass family)** | | |
| I | *Andropogon glomeratus* (Walt.) BSP | bush beardgrass |
| I | *Andropogon virginicus* L. | broomsedge, yellow blue stem |
| I | *Chrysopoon aciculatus* (Retz.) Trin | golden beardgrass, pi'ipi'i, pilipili'ula, mānienie'ula |
| N | *Heteropogon contortus* (L.) Beauv. ex. R.& S | pili, piligrass,twisted beardgrass, tanglehead |
| I | *Hyparrhenia rufa* (Nees) Stapf in Spain | thatchinggrass, jaragua |
| I | *Melinis minutiflora* Beauv. | molassesgrass |
| I | *Oplismenus hirtellus* (L.) Beauv. | basketgrass, honohono kukui |

Appendix A. (Cont'd)

**Appendix A. (Cont'd)**

| Family/Scientific Name | Common Name |
|---|---|
| **Poaceae (Grass family) (Cont'd)** | |
| I *Paspalum conjugatum* Berg | Hilo grass, manu'u malihini, ma'uhilo, sour paspalum |
| I *Setaria geniculata* (Poir.) Beauv. | perennial foxtail |
| I *Tricholaena repens* (Willd.) Hitch | natal redtop |
| **Rosaceae (Rose family)** | |
| E *Osteomeles anthyllidifolia* Lindl. | 'ülei, eluehe, Hawaiian hawthorne |
| **Rubiaceae (Cofee family)** | |
| N *Canthium odoratum* | Lam. alahe'e, walahe'e |
| I(A) *Morinda citrifolia* L. | noni, Indian mulberry |
| **Sapindaceae (Soapberry family)** | |
| E *Dodonaea viscosa* Sherff | a'ali'i |
| **Sterculiaceae (Cocoa family)** | |
| N *Waltheria americana* L. | hi'aloa, kanakaloa |
| **Thymeliaceae (Akia family)** | |
| E *Wikstroemia sandwicensis* Meisn. in A.D.C. | 'äkia |
| **Verbenaceae (Verbena family)** | |
| I *Lantana camara* L. | lantana, läkana, mikinoli, hihiu |
| I *Stachytarpheta jamaicensis* (L.) Vahl. | jamaica vervain, öwi |

## Appendix B.

**Numbers of woody individuals by species and height class counted within the coastal woodland of the Kalapana National Park. Belt transect length for the plots is next to the plot number.**

Height classes are < 2m, 2 - 5m, and > 5m.

| | Plot 21, 60m | | |
|---|---|---|---|
| | < 2m | 2-5 | > 5 |
| *Canthium odoratum* | 30 | 30 | 0 |
| *Diosyros ferrea* | 7 | 11 | 0 |
| *Wikstroemia sandwicensis* | 32 | 30 | 0 |
| *Lantana camara* | 32 | 3 | 0 |
| *Psidium guajava* | 22 | 3 | 0 |
| *Osteomeles anthyllidifolia* | 27 | 4 | 0 |
| *Dodonaea viscosa* | 7 | 0 | 0 |
| *Indigofera suffruticosa* | 10 | 0 | 0 |
| *Metrosideros polymorpha* | 0 | 0 | 9 |

| | Plot 22, 60m | | |
|---|---|---|---|
| | < 2m | 2-5 | > 5 |
| *Dodonaea viscosa* | *30* | *0* | |
| *Metrosideros polymorpha* | 2 | 1 | 30 |
| *Styphelia tameiameiae* | 0 | 1 | 30 |
| *Lantana camara* | 2 | 1 | 0 |

| | Plot 23, 50m | | |
|---|---|---|---|
| | < 2m | 2-5 | > 5 |
| *Canthium odoratum* | 31 | 30 | 7 |
| *Diospyros ferrea* | 0 | 2 | 5 |
| *Erythrina sandwichensis* | 0 | 0 | 1 |
| *Indigofera suffruticosa* | 30 | 0 | 0 |
| *Lantana camara* | 31 | 32 | 0 |
| *Psidium guajava* | 6 | 13 | 3 |

Appendix B. (Cont'd)

| | Plot 24, 50m | | |
|---|---|---|---|
| | <2m | 2-5 | >5 |
| *Canthium odoratum* | 30 | 30 | 0 |
| *Diospyros ferrea* | 0 | 5 | 1 |
| *Dodonaea viscosa* | 2 | 0 | 0 |
| *Wikstroemia sandwicensis* | 31 | 30 | 0 |
| *Lantana camara* | 30 | 0 | 0 |
| *Psidium guajava* | 30 | 10 | 0 |
| *Schinus terebinthifolius* | 30 | 30 | 2 |

| | Plot 25, 35m | | |
|---|---|---|---|
| | <2m | 2-5 | >5 |
| *Diospyros ferrea* | 0 | 0 | 2 |
| *Dodonaea viscosa* | 30 | 11 | 0 |
| *Metrosideros polymorpha* | 13 | 30 | 30 |
| *Pluchea odorata* | 3 | 3 | 0 |
| *Psidium cattleianum* | 30 | 12 | |

| | Plot 26, 60m | | |
|---|---|---|---|
| | <2m | 2-5 | >5 |
| *Diospyros ferrea* | 16 | 30 | 30 |
| *Aleurites moluccana* | 0 | 3 | 7 |
| *Cocos nucifera* | 0 | 0 | 1 |
| *Leucaena leucocephala* | 29 | 15 | 10 |
| *Psidium cattleianum* | 30 | 32 | |
| *Psidium guajava* | 30 | 30 | 30 |

| | Plot 27, 30m | | |
|---|---|---|---|
| | <2m | 2-5 | >5 |
| *Canthium odoratum* | 30 | 30 | 30 |
| *Diospyros ferrea* | 29 | 30 | 30 |
| *Wikstroemia sandwicensis* | 8 | 5 | 0 |
| *Aleurites moluccana* | 0 | 4 | 1 |
| *Eugenia cumini* | 0 | 1 | 15 |
| *Psidium cattleianum* | 30 | 30 | 7 |

**Appendix B. (Cont'd)**

| | Plot 28, 55m | | |
|---|---|---|---|
| | <2m | 2-5 | >5 |
| *Aleurites moluccana* | 48 | 30 | 30 |
| *Cassia bicapsularis* | 30 | 8 | 0 |
| *Cocos nucifera* | 0 | 1 | 0 |
| *Lantana camara* | 30 | 7 | 0 |

| | Plot 29, 40m | | |
|---|---|---|---|
| | <2m | 2-5 | >5 |
| *Canthium odoratum* | 30 | 29 | 5 |
| *Diospyros ferrea* | 1 | 1 | 29 |
| *Dodonaea viscosa* | 1 | 0 | 0 |
| *Metrosideros polymorpha* | 0 | 0 | 4 |
| *Wikstroemia sandwicensis* | 30 | 30 | 29 |
| *Psidium guajava* | 1 | 4 | 0 |

| | Plot 30, 40m | | |
|---|---|---|---|
| | <2m | 2-5 | >5 |
| *Aleurites moluccana* | 30 | 29 | 14 |
| *Cassia bicapsularis* | 33 | 23 | 0 |
| *Lantana camara* | 28 | 12 | 0 |
| *Pluchea odorata* | 0 | 2 | 0 |

| | Plot 31, 55m | | |
|---|---|---|---|
| | <2m | 2-5 | >5 |
| *Canthium odoratum* | 0 | 0 | 5 |
| *Diospyros ferrea* | 4 | 15 | 4 |
| *Dodonaea viscosa* | 30 | 0 | 0 |
| *Metrosideros polymorpha* | 4 | 10 | 30 |
| *Wikstroemia sandwicensis* | 9 | 2 | 0 |
| *Pluchea odorata* | 1 | 0 | 0 |
| *Psidium cattleianum* | 30 | 18 | 0 |

**Appendix B. (Cont'd)**

| | Plot 33, 120m | | |
|---|---|---|---|
| | < 2m | 2-5 | > 5 |
| *Canthium odoratum* | 6 | 2 | 0 |
| *Diospyros ferrea* | 0 | 2 | 1 |
| *Wikstroemia sandwicensis* | 30 | 30 | 0 |
| *Eugenia cumini* | 0 | 0 | 1 |
| *Indigofera suffruticosa* | 21 | 0 | 0 |
| *Lantana camara* | 30 | 1 | 0 |
| *Pluchea odorata* | 2 | 0 | 0 |
| *Psidium guajava* | 30 | 30 | 0 |
| *Schinus terebinthifolius* | 10 | 0 | 0 |

| | Plot 33, 120m | | |
|---|---|---|---|
| | < 2m | 2-5 | > 5 |
| *Dodonaea viscosa* | 30 | 11 | 0 |
| *Metrosideros polymorpha* | 3 | 8 | 33 |
| *Wikstroemia sandwicensis* | 1 | 0 | 0 |
| *Lantana camara* | 30 | 0 | 0 |
| *Schinus terebinthifolius* | 30 | 0 | 0 |

| | Plot 34, 20m | | |
|---|---|---|---|
| | < 2m | 2-5 | > 5 |
| *Canthium odoratum* | 30 | 32 | 30 |
| *Diospyros ferrea* | 30 | 30 | 13 |
| *Osteomeles anthyllidifolia* | 0 | 8 | 0 |
| *Eugenia cumini* | 0 | 0 | 1 |
| *Lantana camara* | 5 | 1 | 0 |
| *Psidium cattleianum* | 30 | 18 | 0 |
| *Psidium guajava* | 3 | 7 | 11 |

| | Plot 35, 60m | | |
|---|---|---|---|
| | < 2m | 2-5 | > 5 |
| *Canthium odoratum* | 19 | 30 | 30 |
| *Diospyros ferrea* | 0 | 0 | 4 |
| *Aleurites moluccana* | 30 | 30 | 30 |
| *Psidium guajava* | 8 | 22 | 30 |

**Appendix B. (Cont'd)**

| | Plot 36, 35 m | | |
|---|---|---|---|
| | <2m | 2-5 | >5 |
| *Canthium odoratum* | 30 | 30 | 15 |
| *Diospyros ferrea* | 30 | 30 | 30 |
| *Dodonaea viscosa* | 1 | 0 | 0 |
| *Osteomeles anthyllidifolia* | 22 | 2 | 0 |
| *Wikstroemia sandwicensis* | 32 | 7 | 0 |
| *Lantana camara* | 31 | 19 | 0 |
| *Morinda citrifolia* | 0 | 2 | 0 |
| *Psidium guajava* | 13 | 0 | 1 |

| | Plot 37, 45m | | |
|---|---|---|---|
| | <2m | 2-5 | >5 |
| *Canthium odoratum* | 31 | 30 | 0 |
| *Diospyros ferrea* | 0 | 8 | 1 |
| *Osteomeles anthyllidifolia* | 3 | 3 | 0 |
| *Wikstroemia sandwicensis* | 30 | 30 | 0 |
| *Psidium guajava* | 30 | 0 | 0 |

| | Plot 38, 20m | | |
|---|---|---|---|
| | <2m | 2-5 | >5 |
| *Canthium odoratum* | 30 | 31 | 0 |
| *Dodonaea viscosa* | 30 | 18 | 0 |
| *Indigofera suffruticosa* | 0 | 2 | |
| *Lantana camara* | 18 | 7 | 0 |
| *Psidium cattleianum* | 15 | 1 | 0 |
| *Psidium guajava* | 31 | 30 | 0 |

| | Plot 39, 20m | | |
|---|---|---|---|
| | <2m | 2-5 | >5 |
| *Canthium odoratum* | 30 | 30 | 11 |
| *Dodonaea viscosa* | 30 | 30 | 0 |
| *Osteomeles anthyllidifolia* | 1 | 0 | 0 |
| *Indigofera suffruticosa* | 6 | 0 | 0 |
| *Lantana camara* | 30 | 30 | 0 |
| *Psidium cattleianum* | 30 | 3 | 0 |
| *Psidium guajava* | 30 | 31 | 6 |

**Appendix B. (Cont'd)**

| | Plot 40, 55m | | |
|---|---|---|---|
| | <2m | 2-5 | >5 |
| *Canthium odoratum* | 30 | 9 | 0 |
| *Dodonaea viscosa* | 30 | 1 | 0 |
| *Osteomeles anthyllidifolia* | 5 | 2 | 0 |
| *Wikstroemia sandwicesis* | 30 | 30 | 0 |
| *Lantana camara* | 27 | 0 | 0 |
| *Psidium guajava* | 14 | 0 | 0 |
| *Schinus terebinthifolius* | 1 | 0 | 0 |

| | Plot 41, 30m | | |
|---|---|---|---|
| | <2m | 2-5 | >5 |
| *Canthium odoratum* | 30 | 30 | 0 |
| *Diospyros ferrea* | 5 | 10 | 0 |
| *Wikstroemia sandwicensis* | 30 | 30 | 0 |
| *Psidium guajava* | 26 | 6 | 0 |
| *Schinus terebinthifolius* | 30 | 30 | 2 |

## Appendix C.

Plant species located below 2,000 feet elevation in selected Hawaiian dry forest locations. Sources of information for each area are noted before each listing.

| Species | Kalapana[1] | Manuka[2] | Auwahi[3] | Mokuleia[4] |
|---|---|---|---|---|
| Acacia cfr. koaia | | | x | |
| *Acacia koa* | | | | x |
| *Achyranthes splendens* | | | x | |
| *Alyxia olivaeformis* | | | x | x |
| *Antidesma pulvinatum* | x | x | | x |
| *Bobea eliator* | | | | x |
| *Bobea hookeri* | | | | x |
| *Bobea sandwicensis* | | | x | |
| *Canthium odoratum* | x | x | | x |
| *Charpentiera obovata* | | x | | x |
| *Cassia gaudichaudi* | x | | x | |
| *Chenopodium oahuense* | | | x | |
| *Colubrina oppositifolia* | | x | | x |
| *Coprosma sp.* | | x | | |
| *Diospyros ferrea* | x | x | x | |
| *Diospyros hillebrandii* | | | | x |
| *Diospyros sandwicensis* | | | | x |
| *Dodonaea eriocarpa* | | | x | x |
| *Dodonaea sandwicensis* | | | | x |
| *Dodonaea sp.* | | x | | |
| *Dodonaea viscosa* | x | | | |
| *Dracaena aurea* | | | | x |
| *Dubautia linearis* | | | x | |
| *Elaeocarpus bifidus* | | | | x |
| *Erythrina sandwicensis* | x | | x | x |
| *Eugenia reinwardtiana* | | | | x |
| *Eugenia sandwicensis* | | | | x |
| *Euphorbia celastroides* | x | x | x | |
| *Euphorbia hillebrandii* | | | | x |
| *Hedyotis acuminata* | | | | x |
| *Hibiscus tiliaceus* | x | | x | |
| *Metrosideros polymorpha* | x | x | x | x |
| *Mezoneuron kavaiensis* | | | | x |
| *Myoporum sandwicense* | x | x | | x |
| *Myrsine lessertiana* | | x | | x |
| *Myrsine sandwicense* | | x | | |

| Species | Kalapana[1] | Manuka[2] | Auwahi[3] | Mokuleia[4] |
|---|---|---|---|---|
| *Neraudia angulata* | | | | x |
| Nesoluma polynesicum | | | x | |
| *Nothocestrum latifolium* | | | x | |
| *Nototrichium sandwicense* | | | x | |
| *Nototrichium viride* | | | | x |
| *Ochrosia sandwicensis* | | | | x |
| *Osmanthus sandwicensis* | | x | | x |
| *Pelea wawreana* | | | | x |
| *Pipturus albidus* | x | x | | |
| *Pisonia umbellifera* | | | | x |
| *Pittosporum sulcatum* | | | | x |
| *Pittosporum terminalioides* | x | | | |
| *Planchonella spathulata* | | | x | |
| *Pleomele aurea* | x | x | | |
| *Pouteria sandwicensis* | | | | x |
| *Pseudomorus brunoniana* | | | | x |
| *Psychotria hathewayi* | | | | x |
| *Psychotria mariniana* | | | | x |
| *Psychotria sp.* | | x | | |
| *Rauvolfia sandwicensis* | x | | | x |
| *Reynoldsia hillebrandii* | x | x | | |
| *Reynoldsia sandwicensis* | | | | x |
| *Rumex sp.* | | x | | |
| *Sapindus oahuensis* | | | | x |
| *Santalum ellipticum* | | | x | |
| *Santalum freycinetianum* | | | | x |
| *Scaevola coriacea* | | | x | |
| *Scaevola gaudichaudi* | | | x | |
| *Sida fallax* | | | x | x |
| *Sophora chrysophylla* | | | x | |
| *Strongylodon lucidus* | | | | x |
| *Styphelia tameiameiae* | x | x | | x |
| *Tetraplasandra kaalae* | | | | x |
| *Vaccinium reticulatum* | | x | | |
| *Wikstroemia oahuensis* | | | | x |
| *Wikstroemia sandwicensis* | x | x | | |
| *Wikstroemia sp.* | | | x | |
| *Xylosma hawaiiensis* | | | | x |
| *Xylosma hillebrandii* | x | x | | |

[1] Data from Warshauer (1974), Warshauer & Jacobi (1973)
[2] Data from Yoshinaga and Higashino (pers. comm.)
[3] Data from Holt (pers. comm.), Medeiros, Loope and Holt (1984, unpub.ms.)
[4] Data from Wirawan (1972)

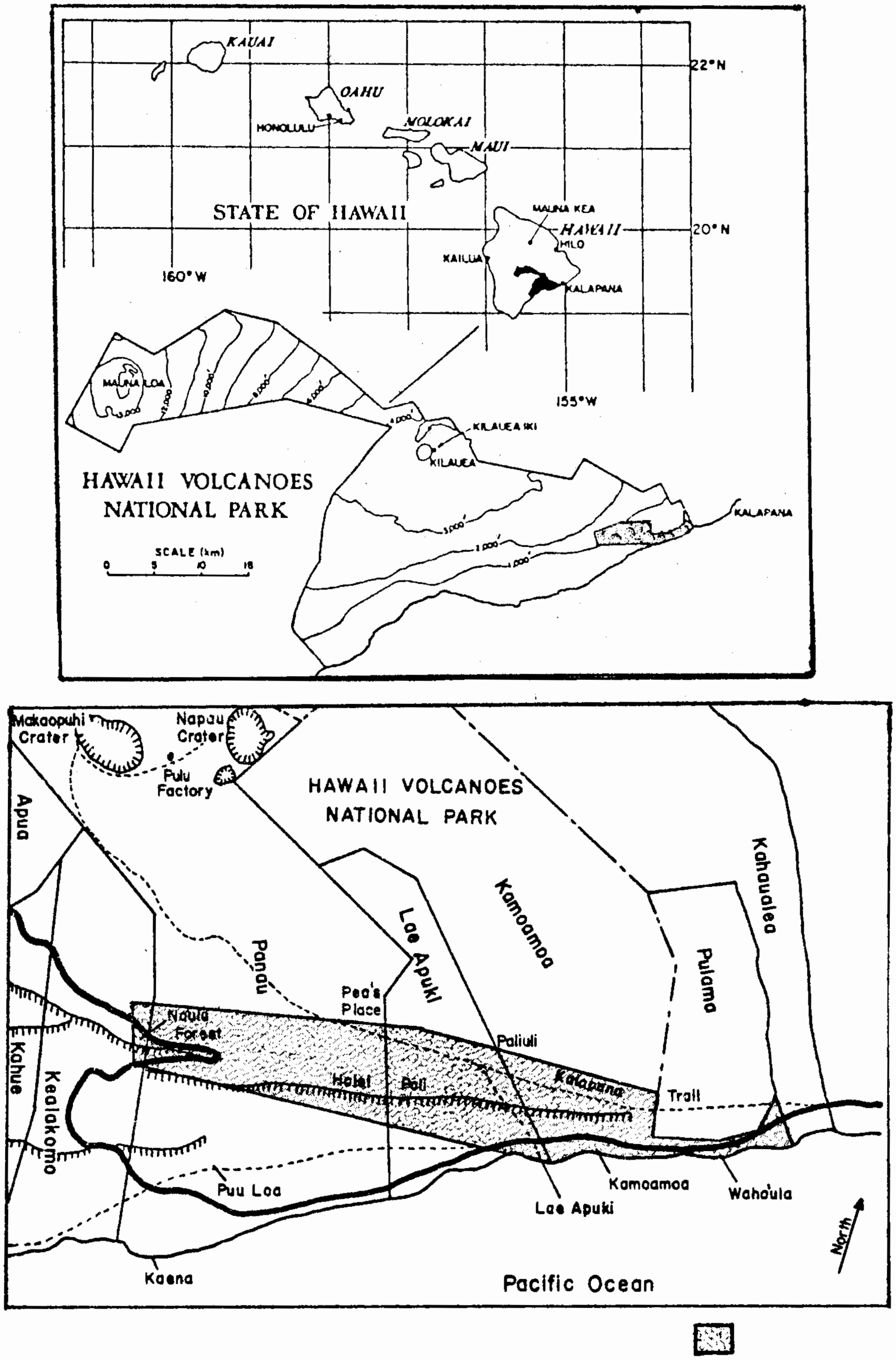
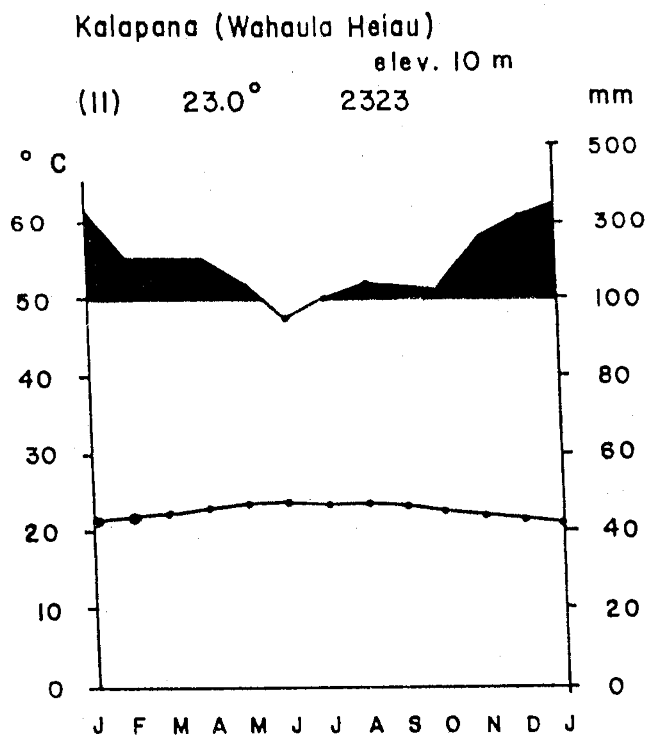



Figure 1. Map of the study area located in the southeast portion of Hawaii Volcanoes National Park, Island of Hawaii. Boundaries in the lower figure outline ahupua'a (Hawaiian land divisions).

A.




B.

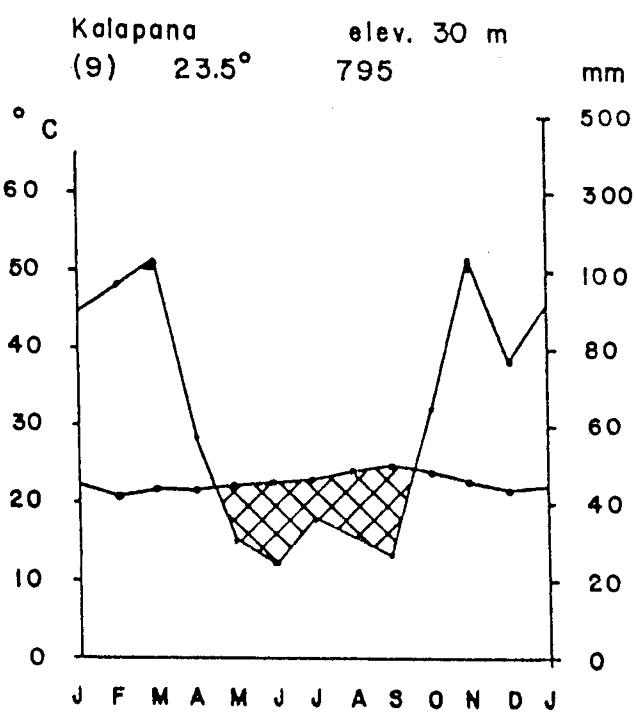



Figure 2. Climate diagrams for two stations in the Kalapana Extension Hawaii Volcanoes National Park. A is located in the eastern study area at Waha'ula. B is just west of Lae Apuki.

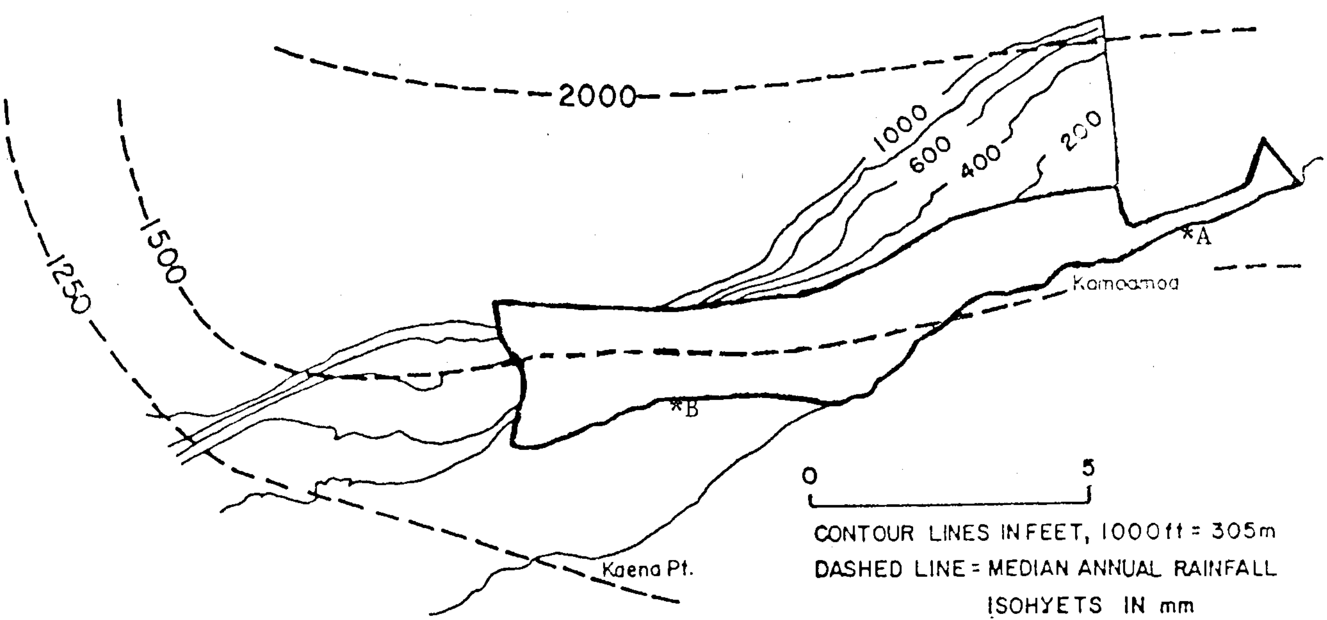



Figure 3. Rainfall map for the Kalapana Extension of Hawaii Volcanoes National Park. Asterisk (*) marks the location of climatic stations A and B.

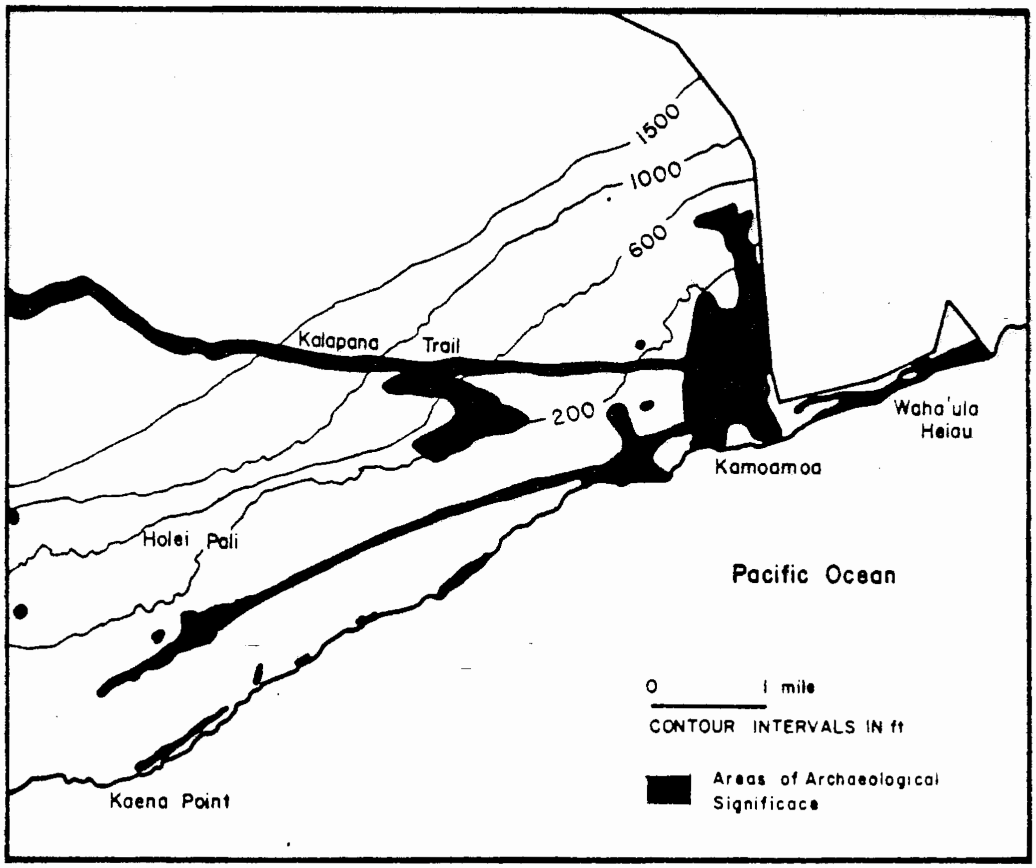



Figure 4. Map of the southeastern lowland of Hawaii Volcanoes National Park showing areas of archaeological significance shaded in black (from Ladd 1974). These areas include former agricultural sites.

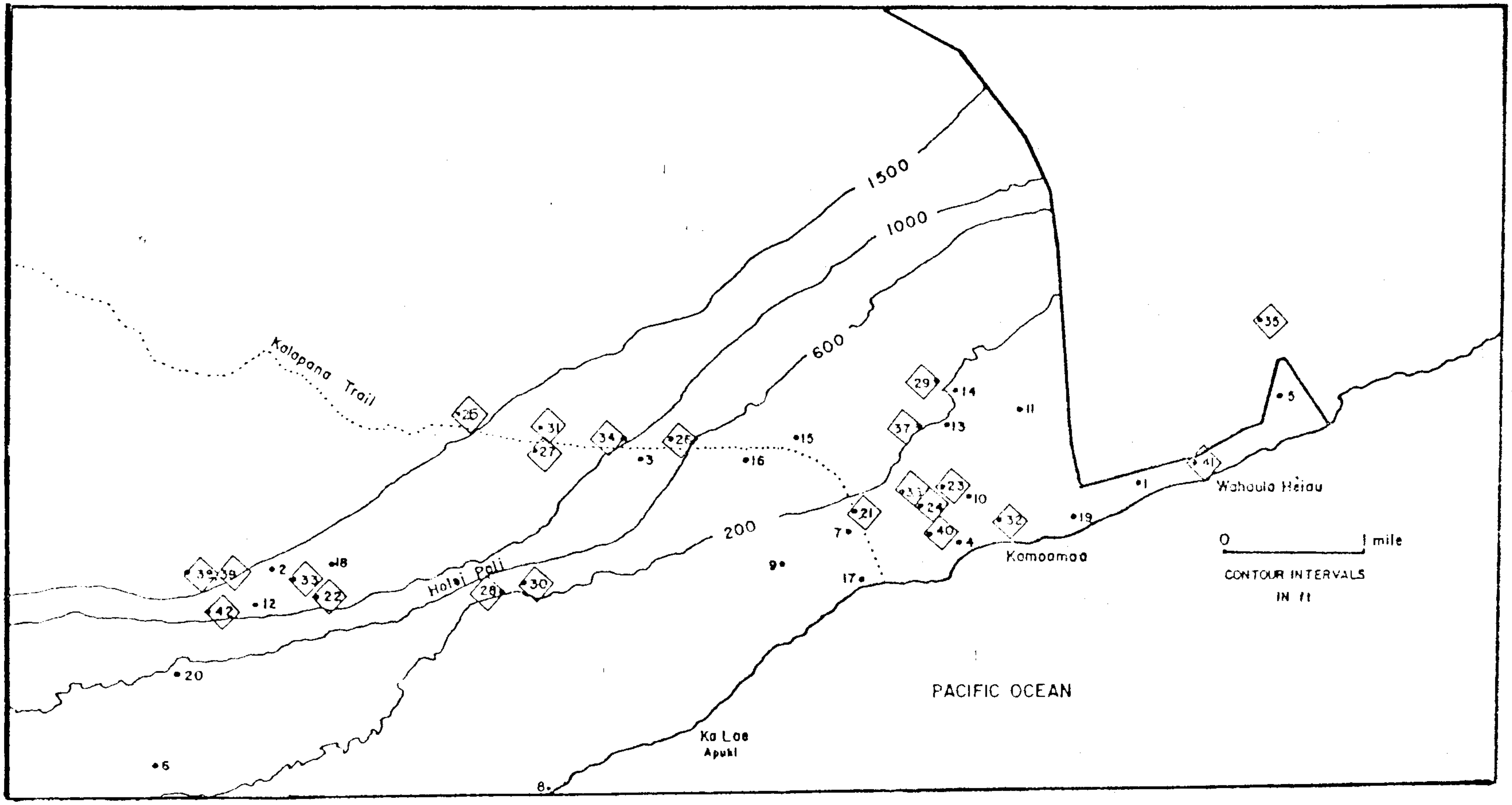



Figure 5. Distribution of the 42 relevès studied in the coastal woodland of the Kalapana Extension, Hawaii Volcanoes National Park. Forest relevès are represented by numbers within diamonds, scrub relevès are not enclosed.

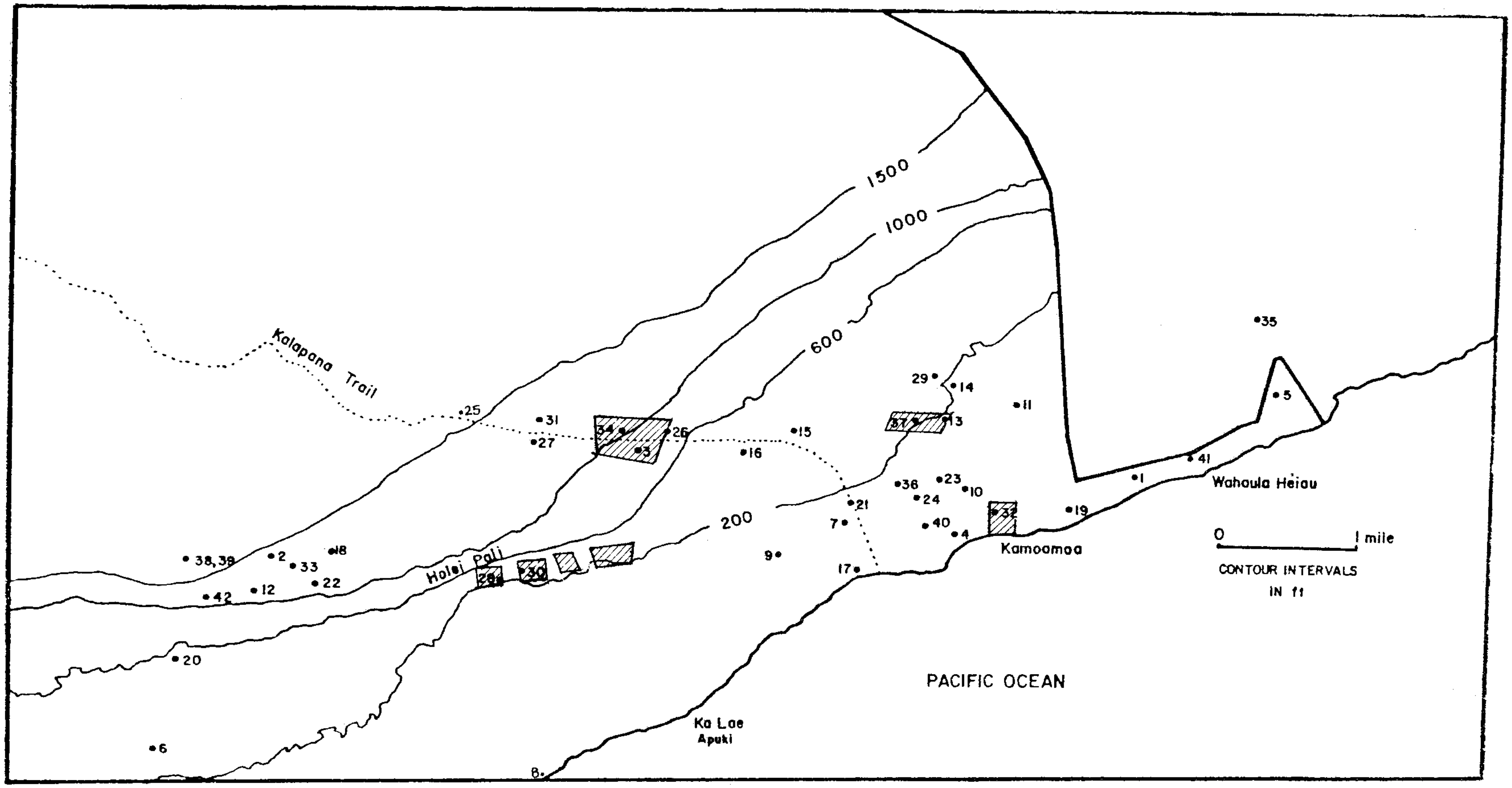



Figure 6. Distribution of the seven aerial photoplots (represented by lined blocks) in the non-littoral coastal vegetation of the Kalapana Extension, Hawaii Volcanoes National Park.

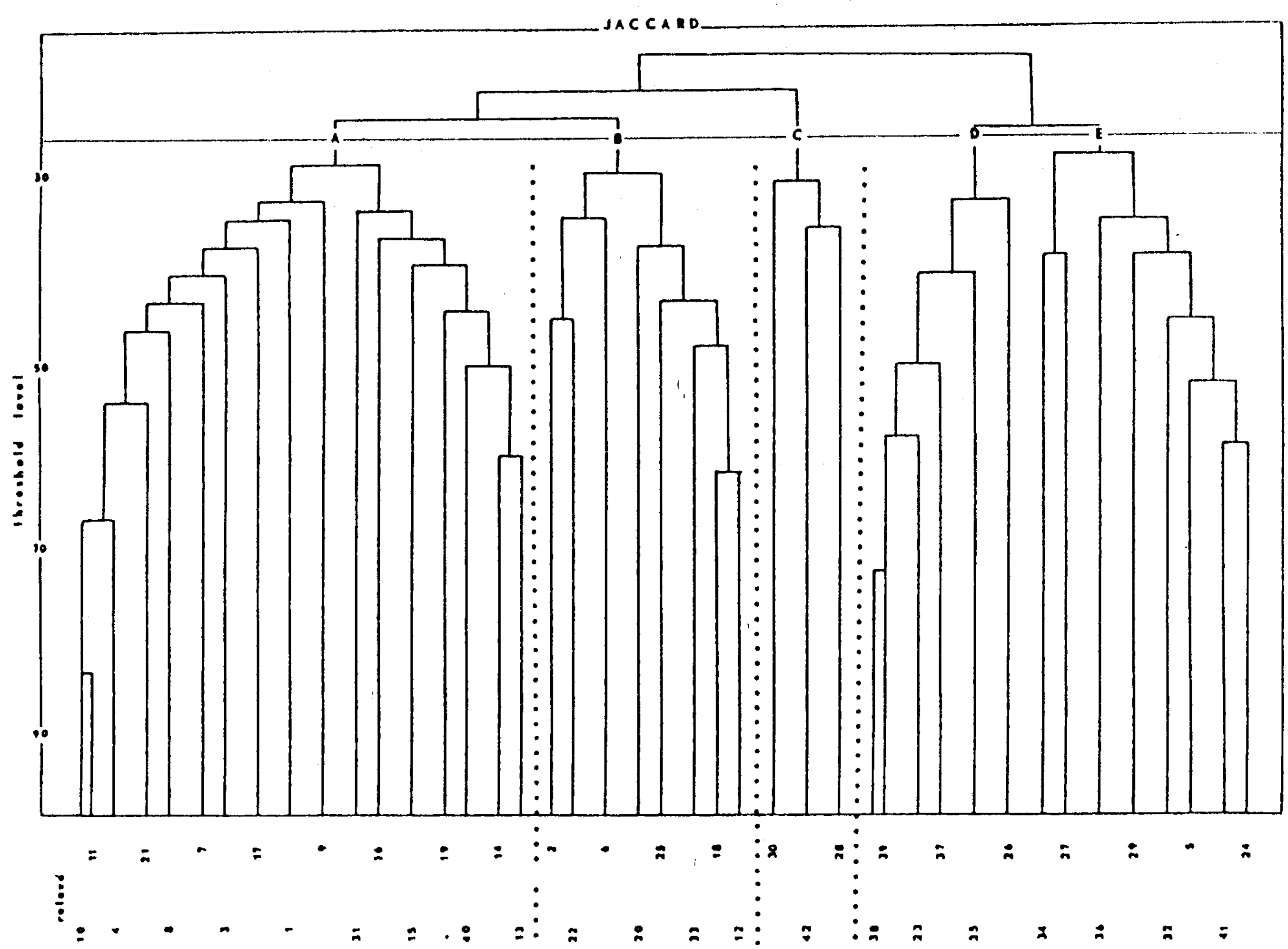



Figure 7. The dendrograph according to Jaccard's method.

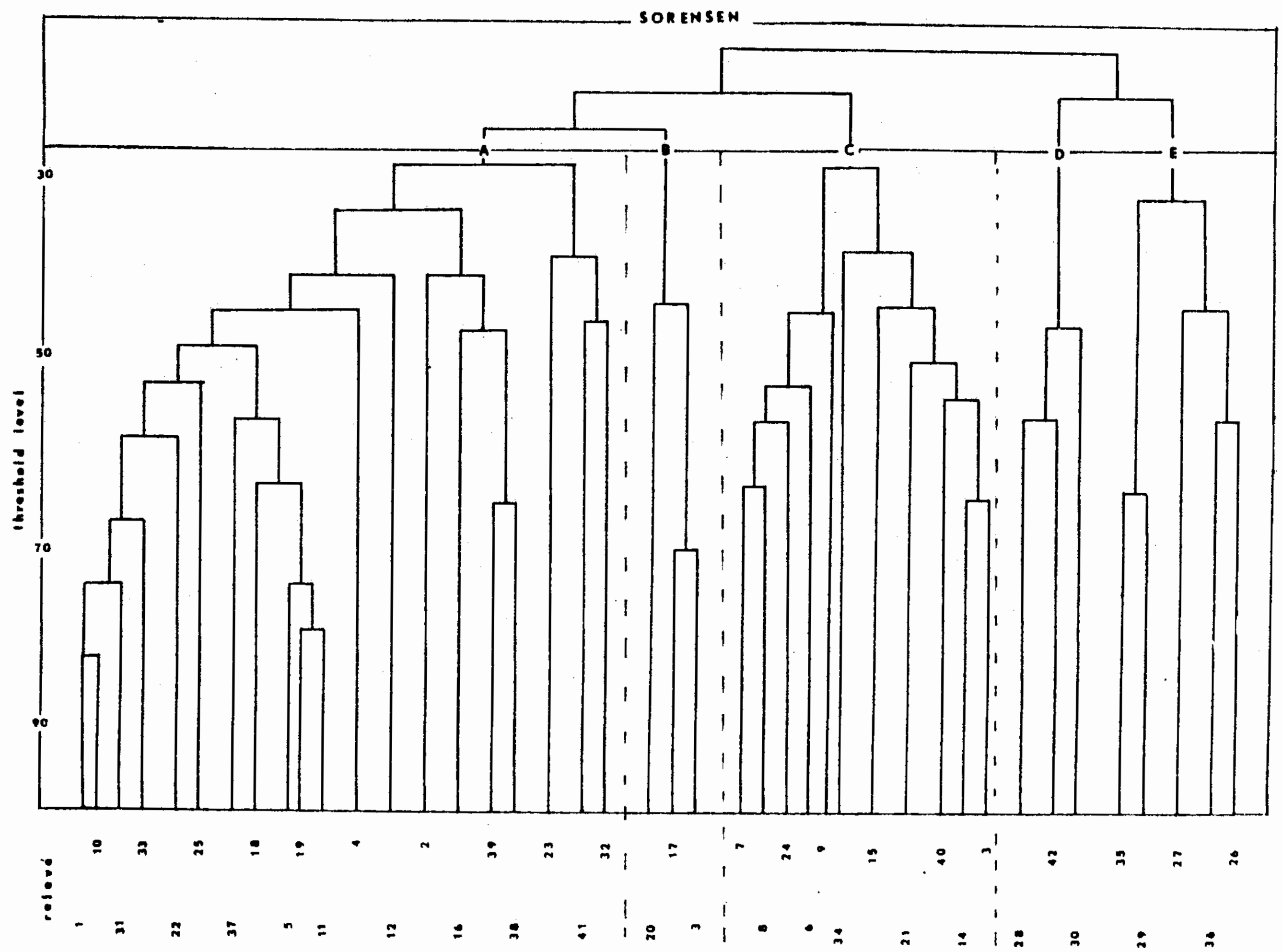



Figure 8. The dendrograph according to Motyka's quantitative modification of Sorenson's method.

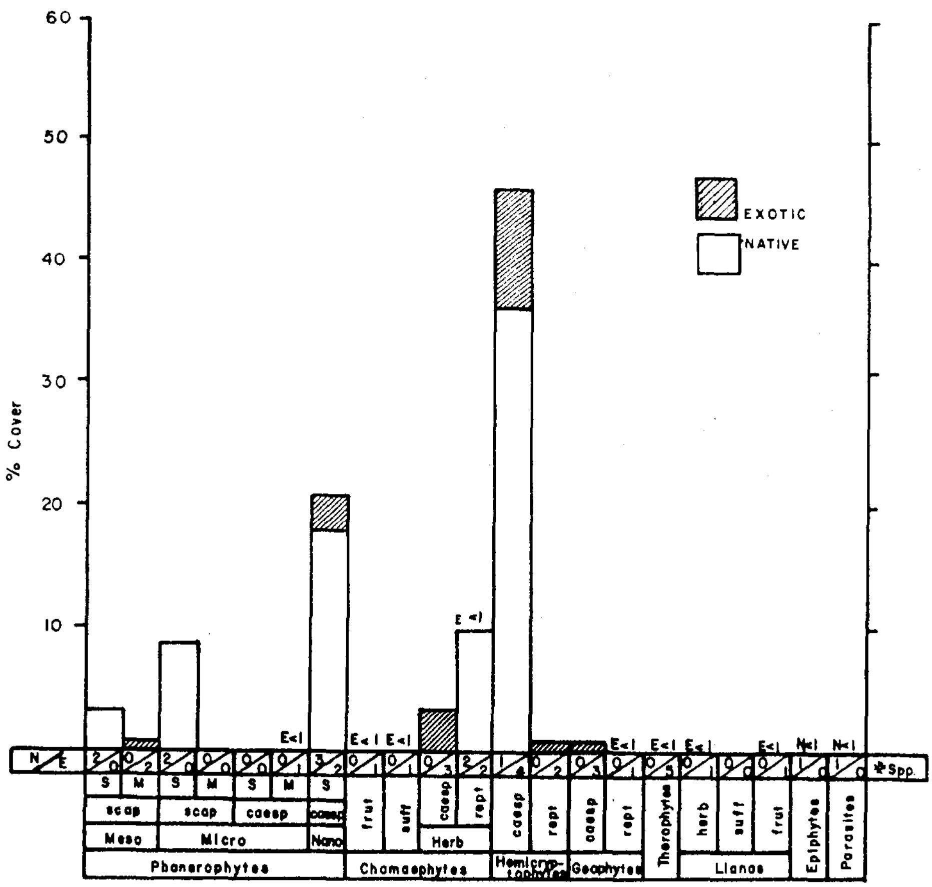



Figure 9. Life-form spectrum of scrub dominated by native species in the coastal woodland of the Kalapana Extension, Hawaii Volcanoes National Park. N = native, E = exotic, S = sclerophyllous, M = malacophyllous, scap = scapose, caesp = caespitose, frut = fruticose, suff = suffruticose, rept-reptant, herb = herbaceous, meso = mesophanerophyte, micro = microphanerophyte, nano = nanophanerophyte. For further explanation of these terms see page 11.

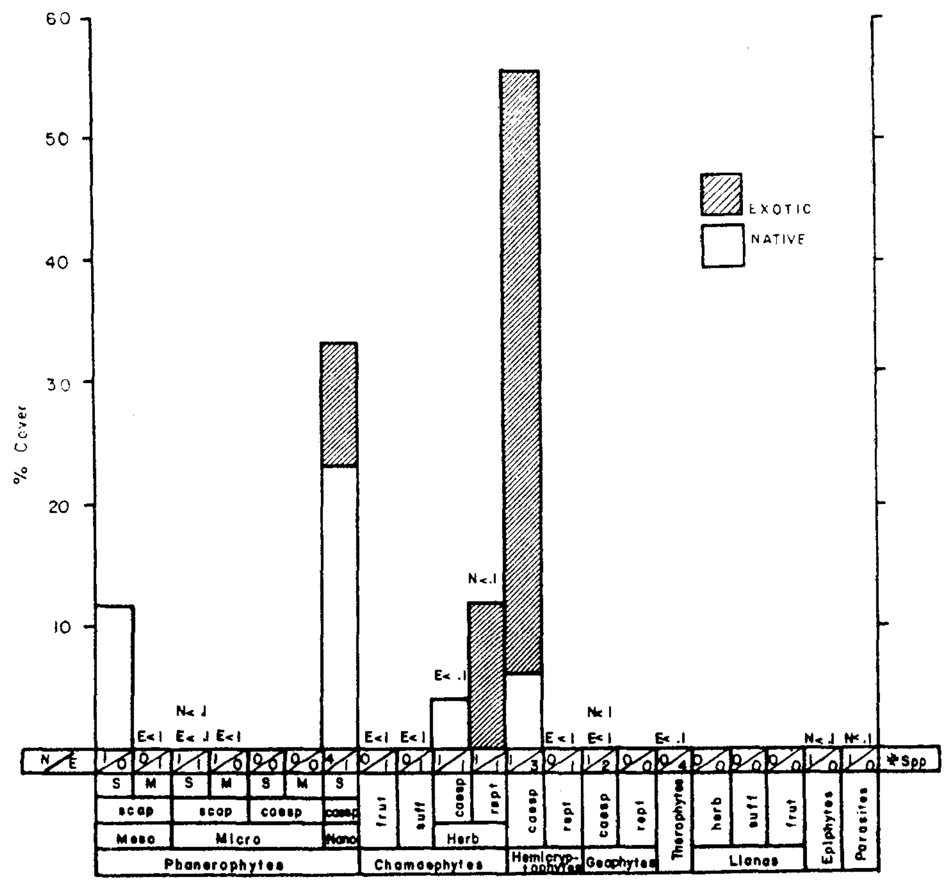



Figure 10. Life-form spectrum of scrub dominated by introduced species in the coastal woodland of the Kalapana Extension, Hawaii Volcanoes National Park. N = native, E = exotic, S = sclerophyllous, M = malacophyllous, scap = scapose, caesp = caespitose, frut = fruticose, suff = suffruticose, rept = reptant, herb = herbaceous, meso = mesophanerophyte, micro = microphanerophyte, nano = nanophanerophyte.

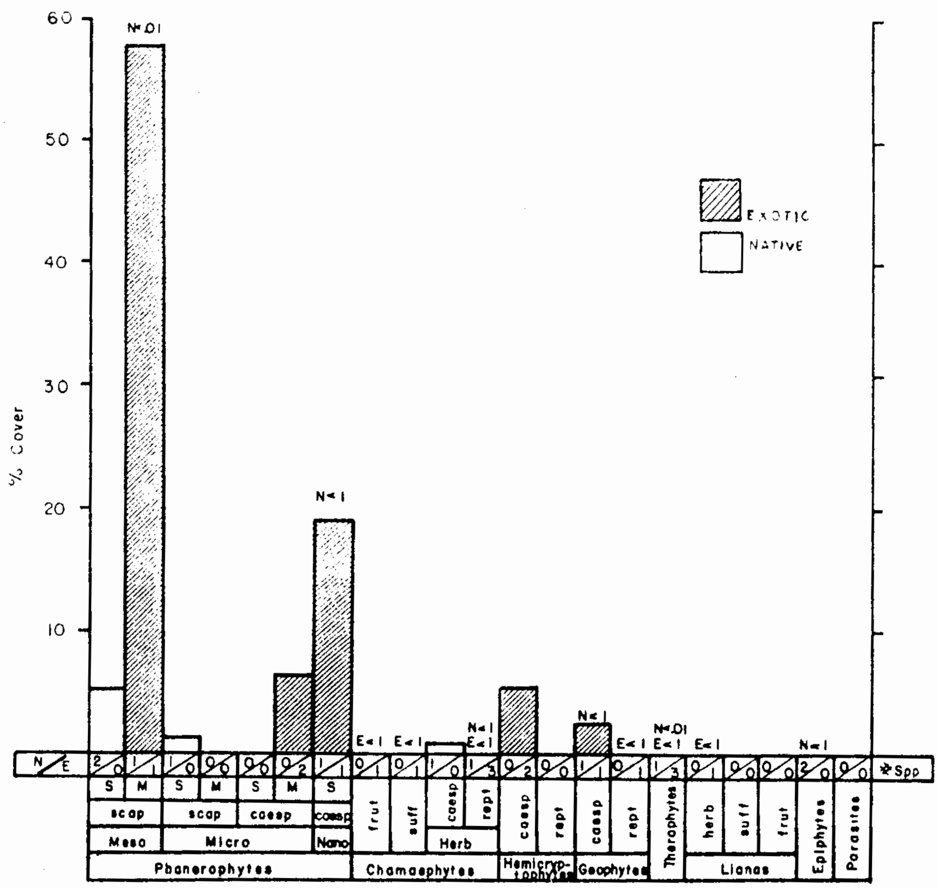



Figure 11. Life-form spectrum of *Aleurites moluccana* (kukui) groves in the coastal woodland of the Kalapana Extension, Hawaii Volcanoes National Park. N = native, E = exotic, S = sclerophyllous, M = malacophyllous, scap = scapose, caesp = caespitose, frut = fruticose, suff = suffruticose, rept = reptant, herb = herbaceous, meso = mesophanerophyte, micro = microphanerophyte, nano = nanophanerophyte.

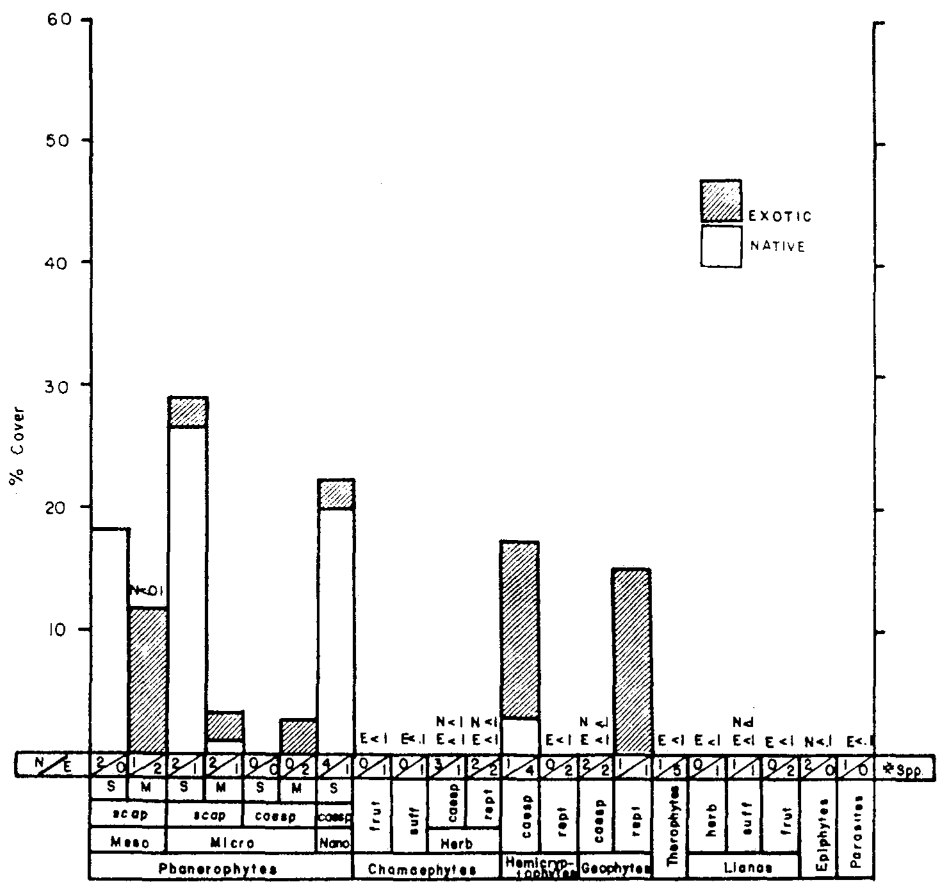



Figure 12. Life-form spectrum of the native forest with non-native groundcover in the coastal woodland of the Kalapana Extension, Hawaii Volcanoes National Park. N = native, E = exotic, S = sclerophyllous, M = malacophyllous, scap = scapose, caesp = caespitose, frut = fruticose, suff = suffruticose, rept = reptant, herb = herbaceous, meso = mesophanerophyte, micro = microphanerophyte, nano = nanophanerophyte.

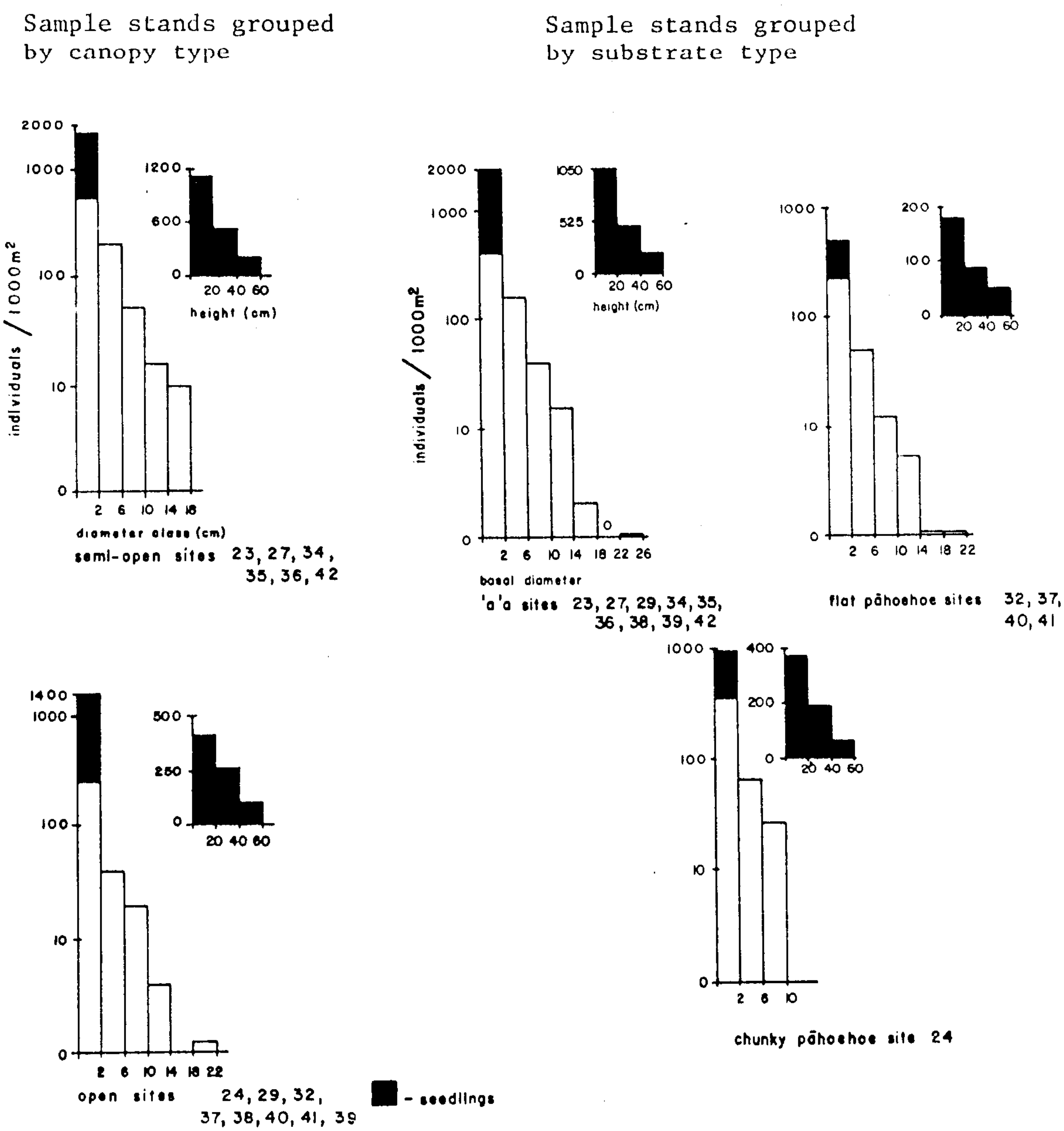



Figure 13. Structural analysis histograms for *Canthium odoratum* (alahe'e) in the coastal woodland of the Kalapana Extension, Hawaii Volcanoes National Park. The smaller histograms show in detail the shaded block. These represent seedlings. The seedling histograms are not all the same scale.

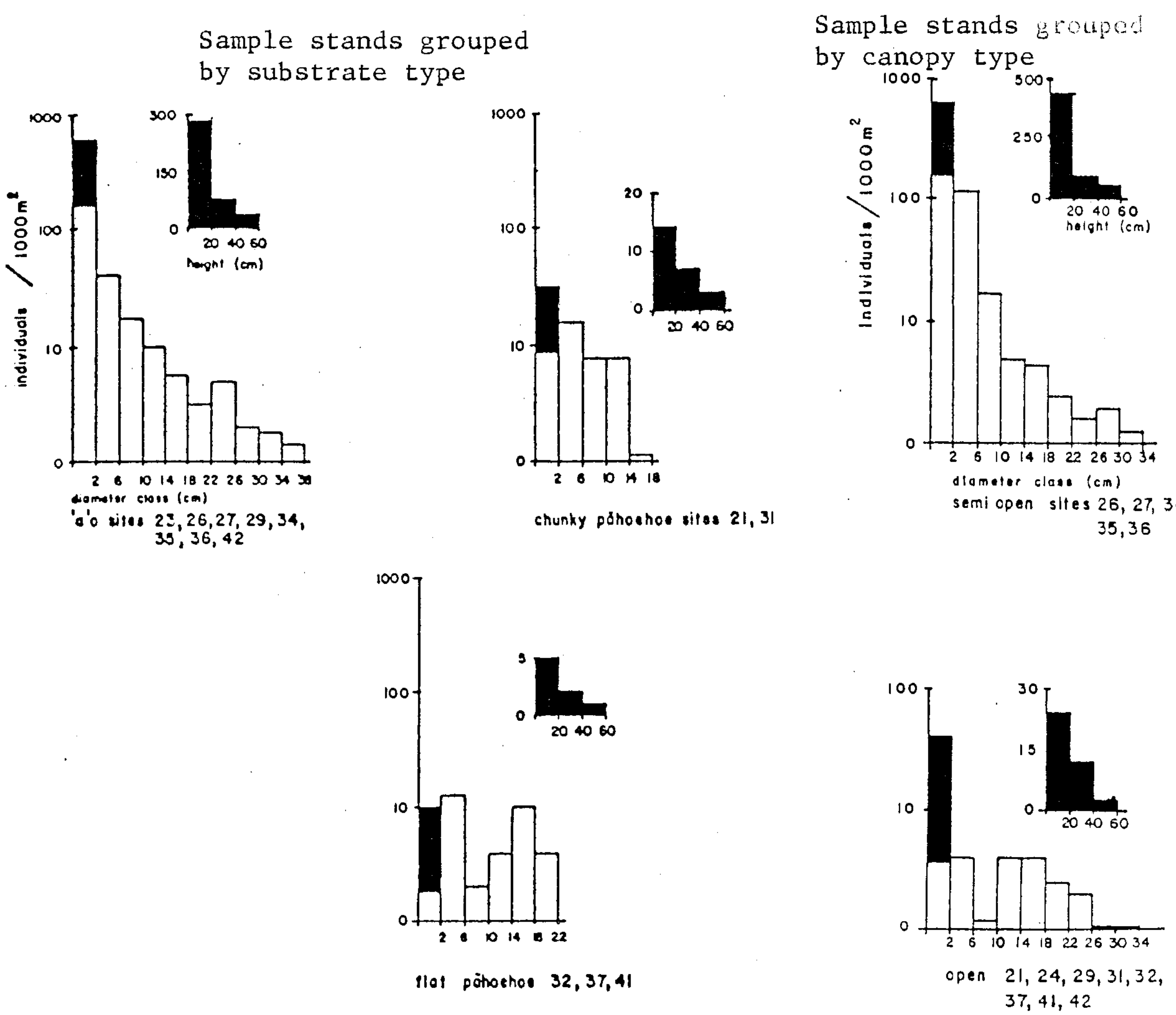



Figure 14. Structural histograms for *Diospyros ferrea* (lama) in the coastal woodland of the Kalapana Extension, Hawaii Volcanoes National Park grouped by canopy and substrate type in logarithmic scale. The smaller histograms show in detail the shaded block. These represent seedlings. The seedling histograms are not all the same scale.

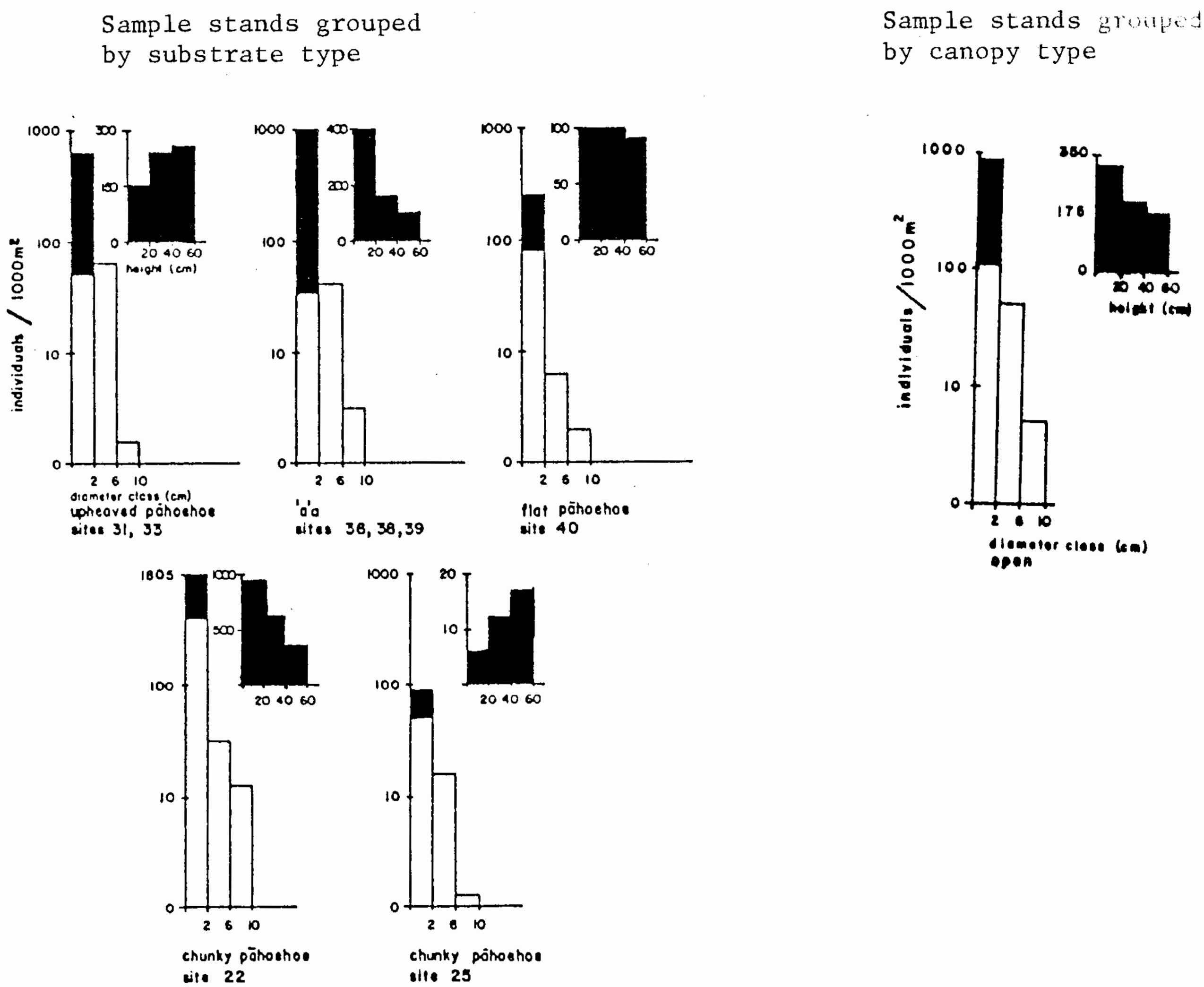



Figure 15. Structural histograms for *Dodonaea viscosa* (a'ali'i) in the coastal woodland of the Kalapana Extension, Hawaii Volcanoes National Park grouped by canopy and substrate type in logarithmic scale. The smaller histograms show in detail the shaded block. These represent seedlings. The seedling histograms are not all the same scale.

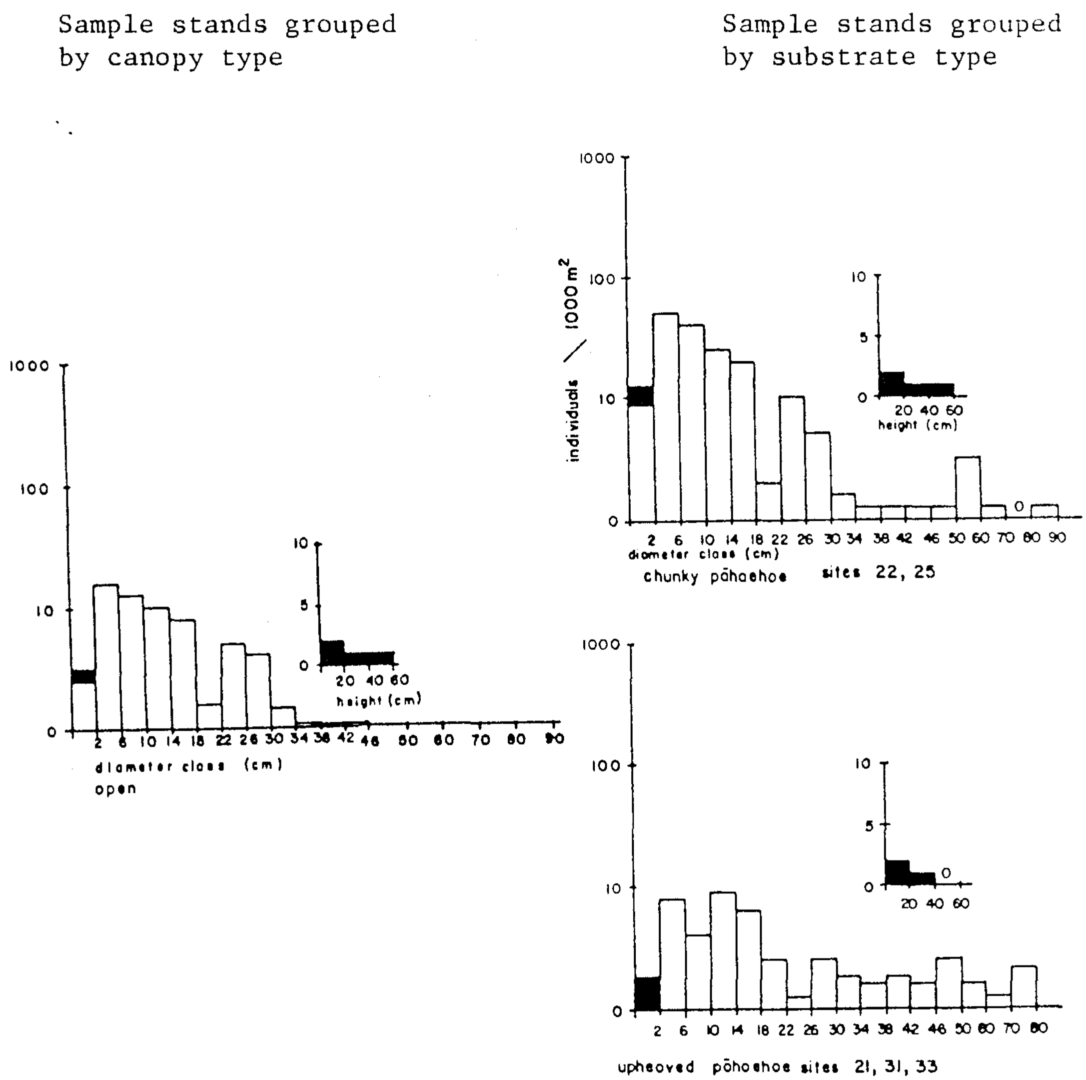



Figure 16. Structural histograms for *Metrosideros polymorpha* ('ohi'a) in the coastal woodland of the Kalapana Extension, Hawai'i Volcanoes National Park grouped by canopy and substrate type in logarithmic scale. The smaller histograms show in detail the shaded block. These represent seedlings. The seedling histograms are not all the same scale.

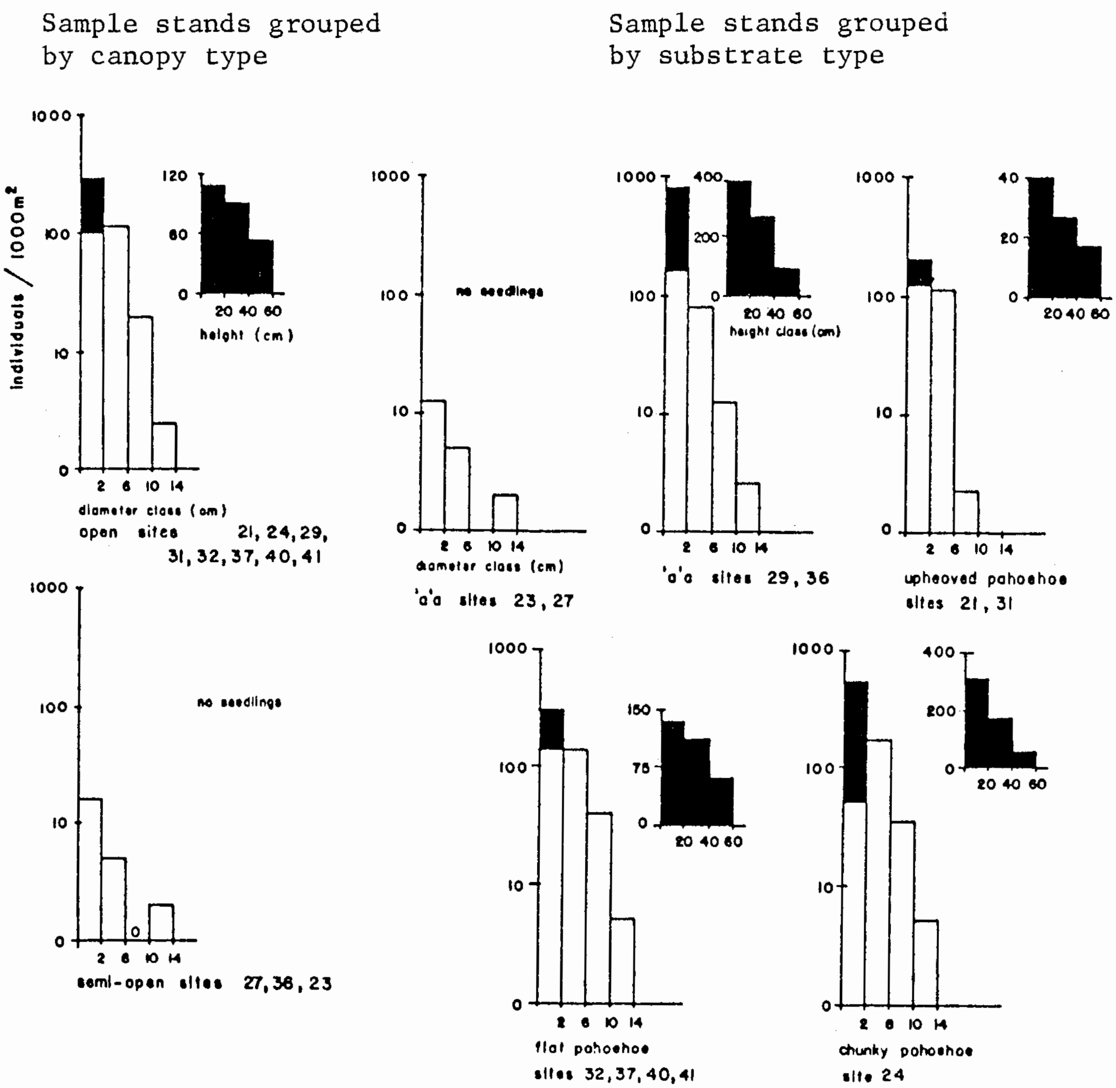



Figure 17. Structural histograms for *Wikstroemia sandwicensis* ('akia)in the coastal woodland of the Kalapana Extension, Hawaii Volcanoes National Park grouped by canopy and substrate type in logarithmic scale. The smaller histograms show in detail the shaded block. These represent seedlings. The seedling histograms are not all the same scale.

Sample stands grouped by canopy type

Sample stands grouped by substrate type

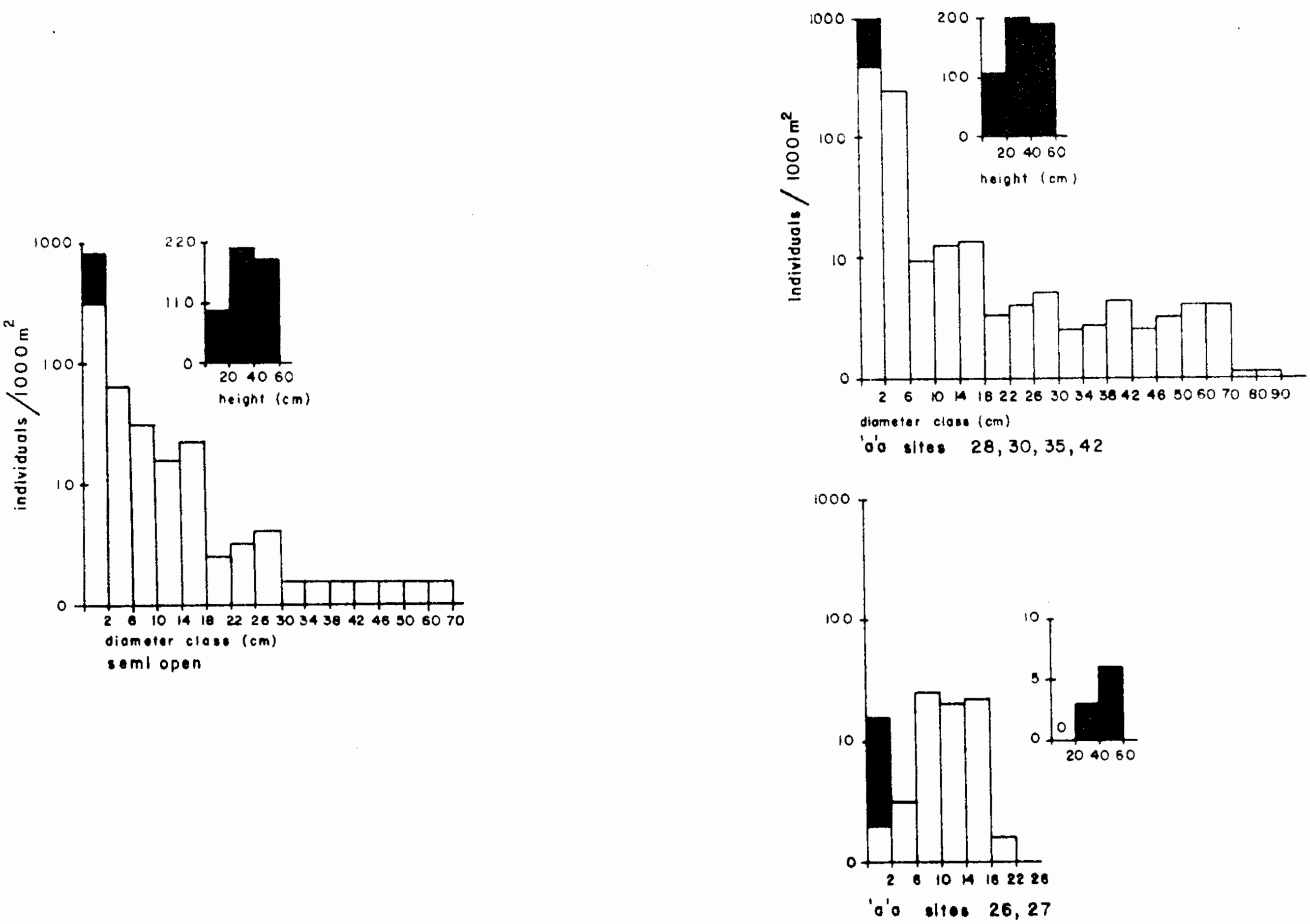



Figure 18. Structural histograms for *Aleurites moluccana* (kukui) in the coastal woodland of the Kalapana Extension, Hawaii Volcanoes National Park grouped by canopy and substrate type in logarithmic scale. The smaller histograms show in detail the shaded block. These are seedlings. The seedling histograms are not all the same scale.

Sample stands grouped by canopy type

Sample stands grouped by substrate type

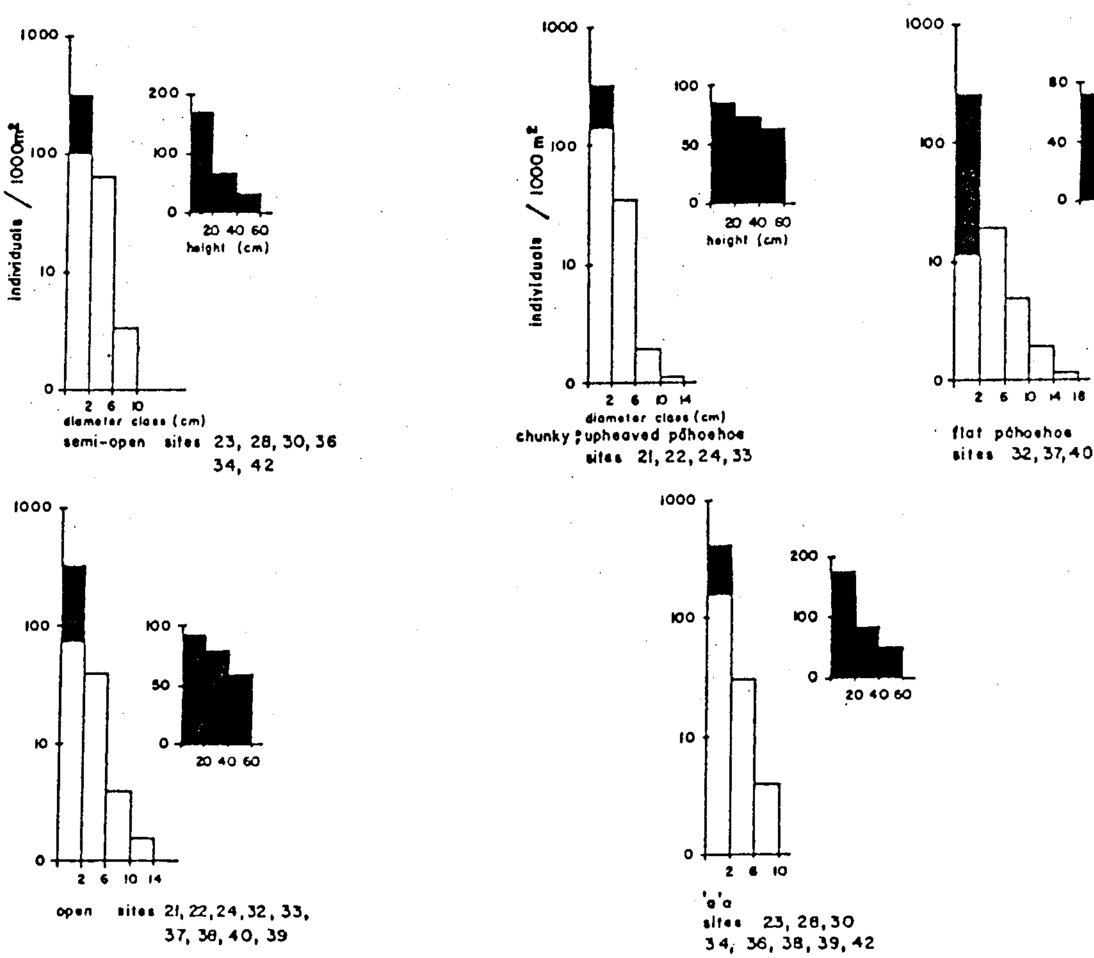



Figure 19. Structural histograms for *Lantana camara (lantana)* in the coastal woodland of the Kalapana Extension, Hawaii Volcanoes National Park grouped by canopy and substrate type in logarithmic scale. The smaller histograms show in detail the shaded block. These represent seedlings. The seedling istograms are not all the same scale.

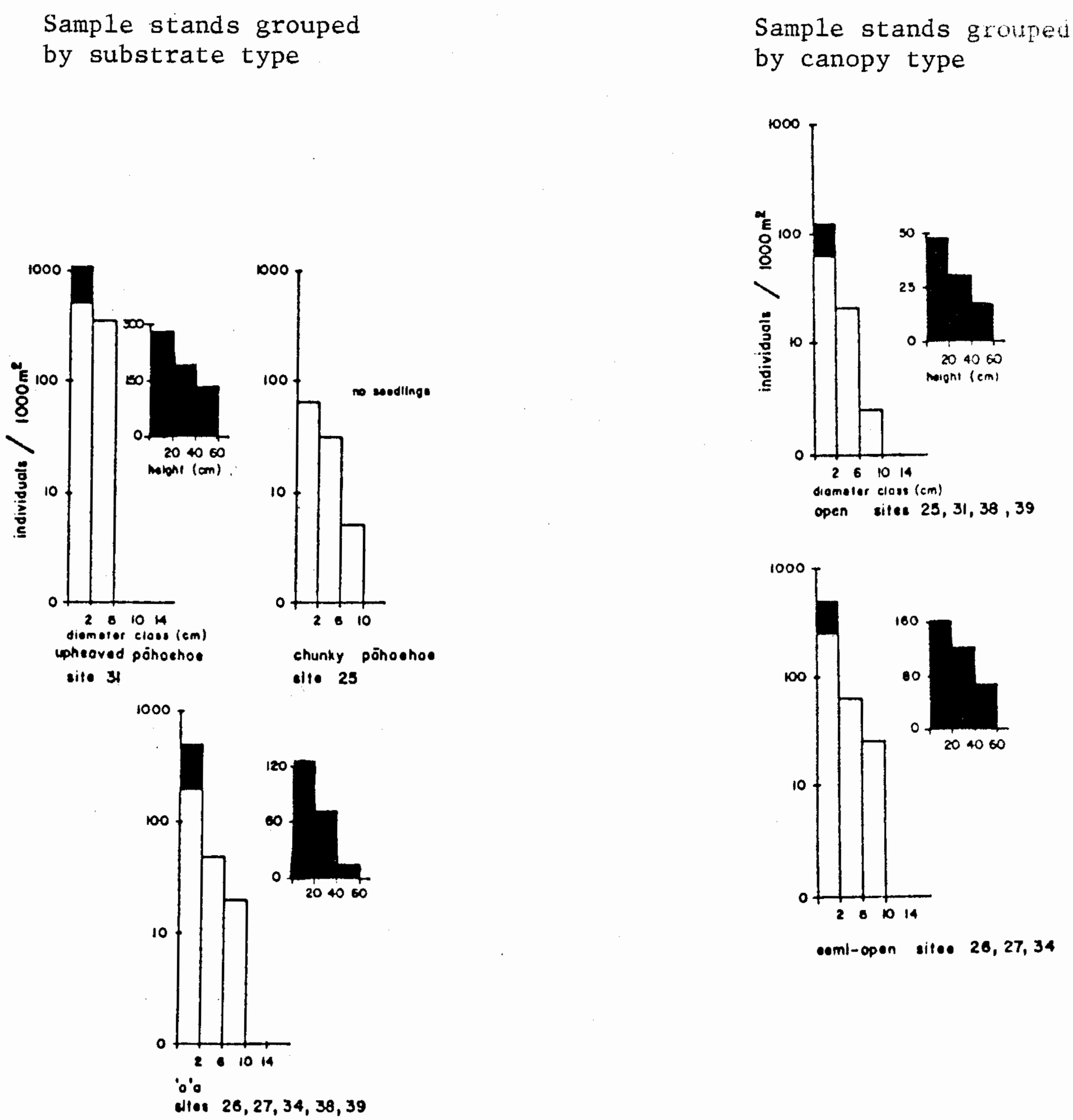



Figure 20. Structural histograms for *Psidium cattleianum* (strawberry guava) in the coastal woodland of the Kalapana Extension, Hawai'i Volcanoes National Park grouped by canopy and substrate type in logarithmic scale. The smaller histograms show in detail the shaded block. These represent seedlings. The seedling histograms are not all the same scale.

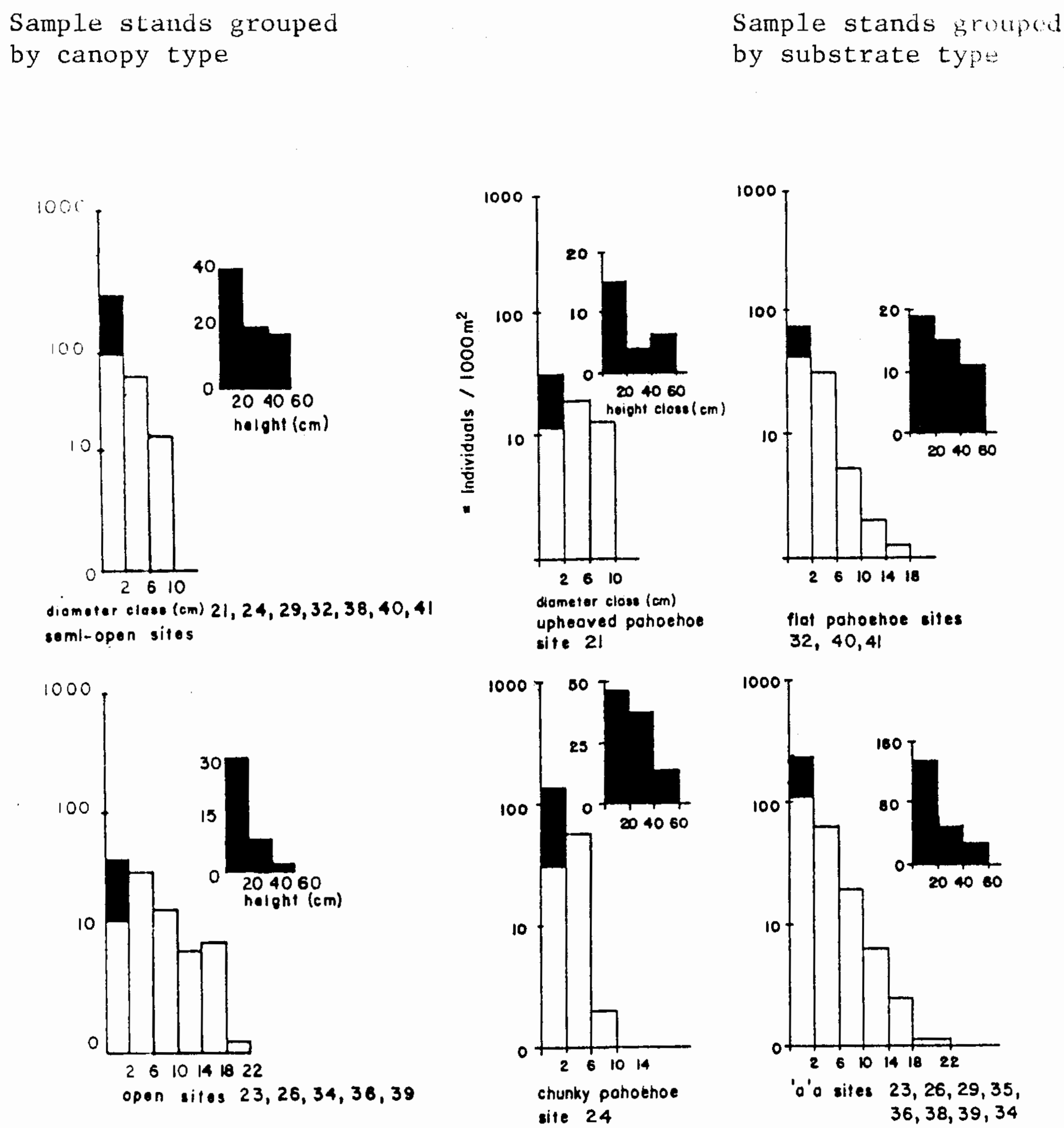



Figure 21. Structural histograms for *Psidium guajava* (guava) in the coastal woodland of the Kalapana Extension, Hawaii Volcanoes National Park grouped by canopy and substrate type in logarithmic scale. The smaller histograms show in detail the shaded block. These represent seedlings. The seedling histograms are not all the same scale.

Sample stands grouped by canopy type

Sample stands grouped by substrate type

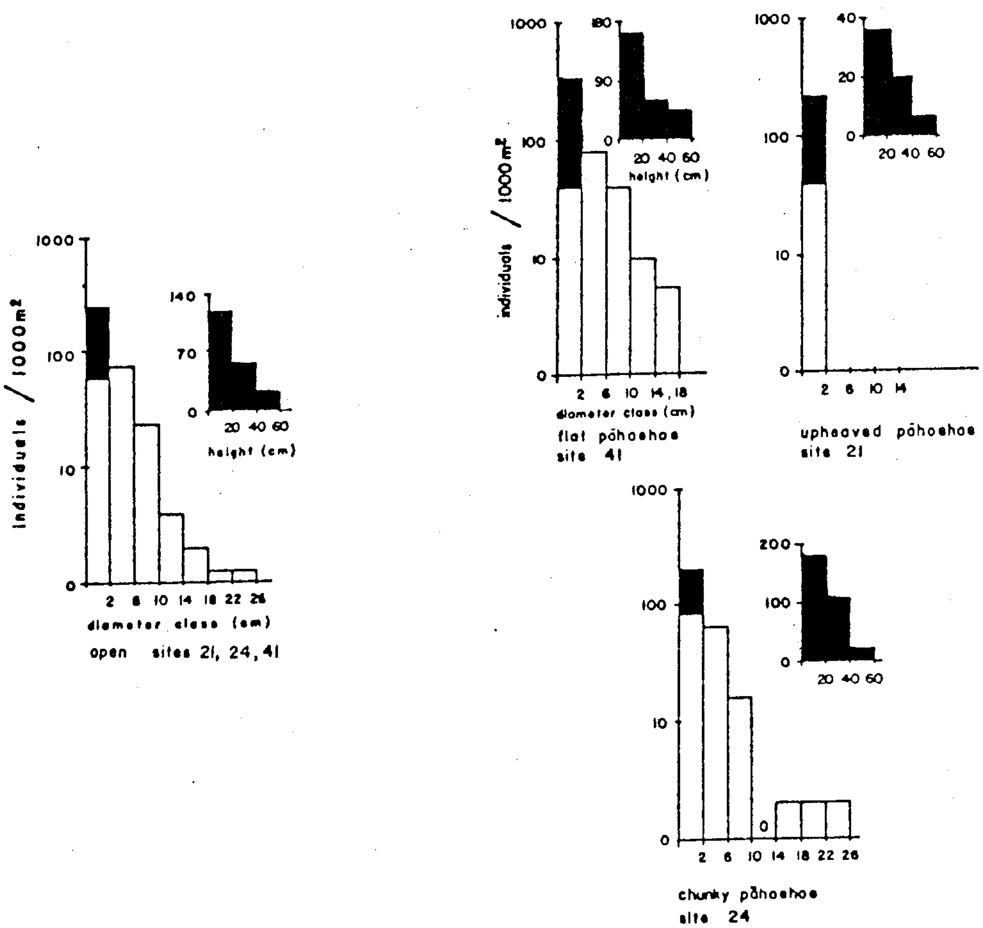



Figure 22. Structural histograms for *Schinus terebenthifolius* (Christmas berry) in the coastal woodland of the Kalapana Extension, Hawaii Volcanoes National Park grouped by canopy and substrate type in logarithmic scale. The smaller histograms show in detail the shaded block. These represent seedlings. The seedling histograms are not all the same scale.

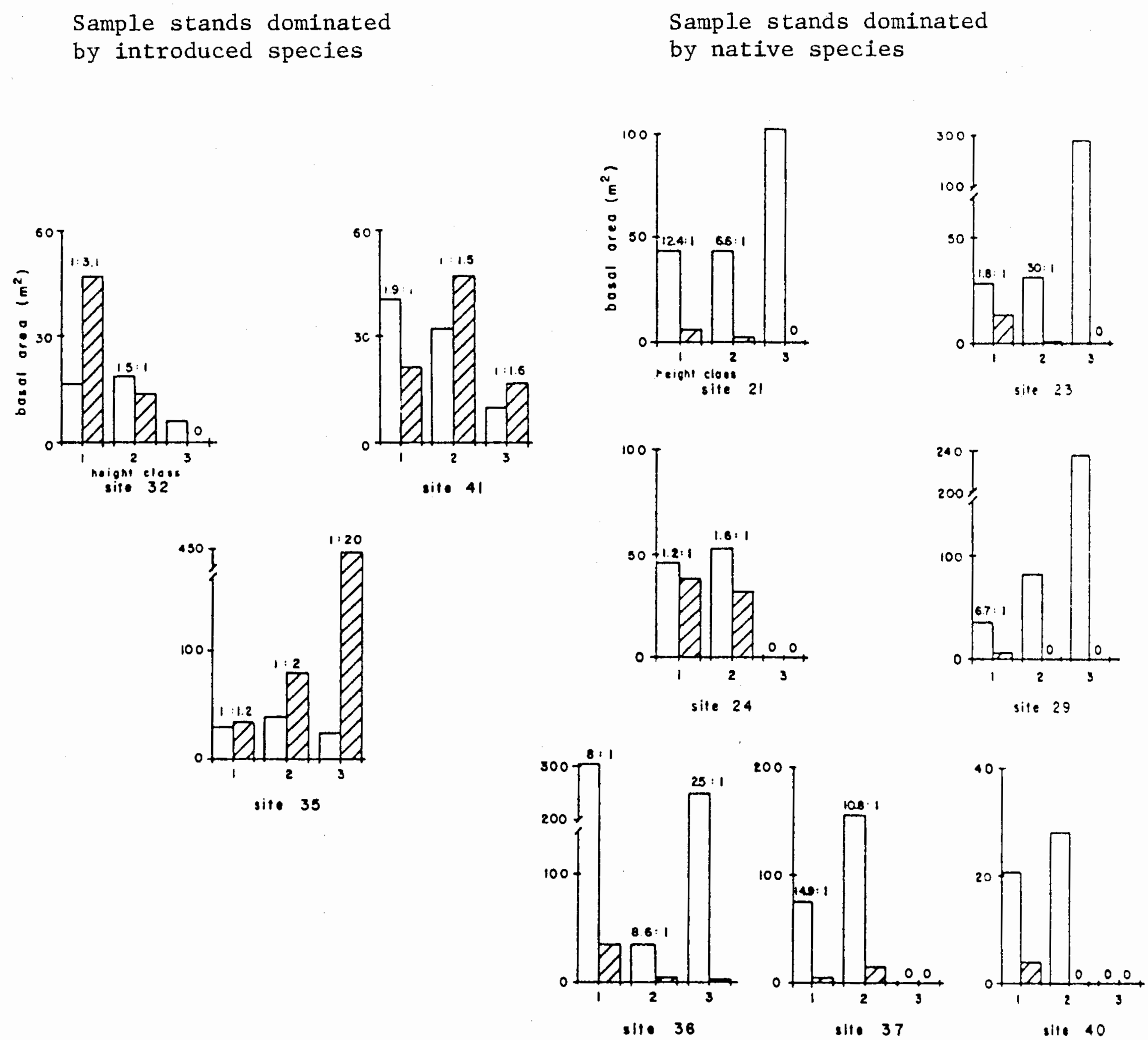



Figure 23. Proportions of native and introduced woody species in different height classes in sample stands of the lowland mixed native/introduced community type in the coastal woodland of the Kalapana Extension, Hawaii Volcanoes National Park. Native = unstriped, introduced = striped bars. To save space, bar graphs are not all to the same scale. Height classes are as follows: 1 = less than 2m tall, 2 = 2 to 5m tall, 3 = greater than 5m tall.

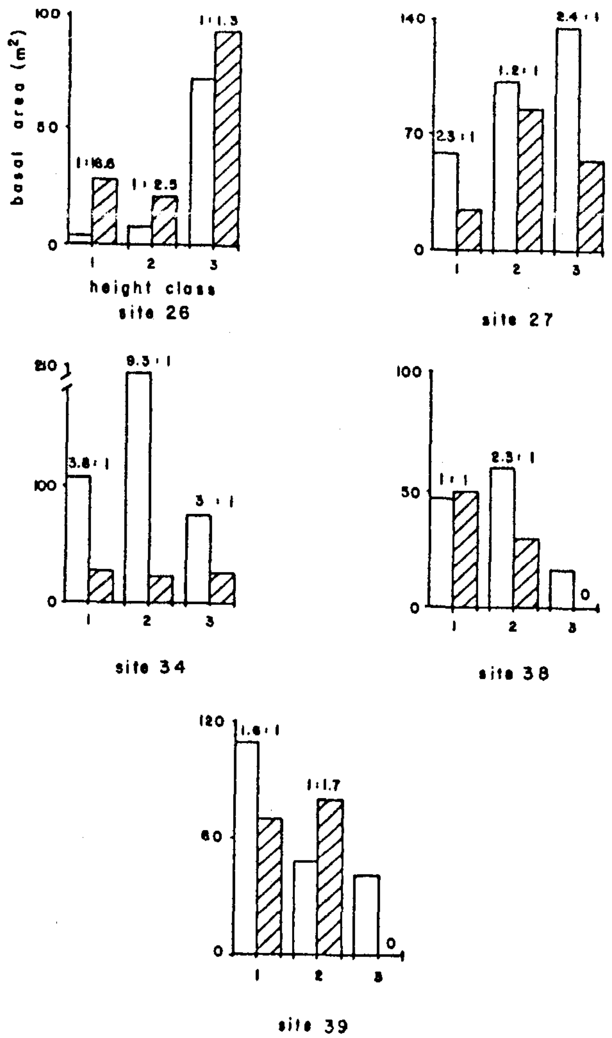



Figure 24. Proportions of native and introduced woody species in different height classes in sample stands of the upland mixed native/introduced community type in the coastal woodland of the Kalapana Extension, Hawaii Volcanoes National Park. Native = unstriped, introduced = striped bars. To save space, the bar graphs are not all to the same scale. Height classes are as follows: 1 = less than 2m tall, 2 = 2 to 5m tall, 3 = greater than 5m tall.

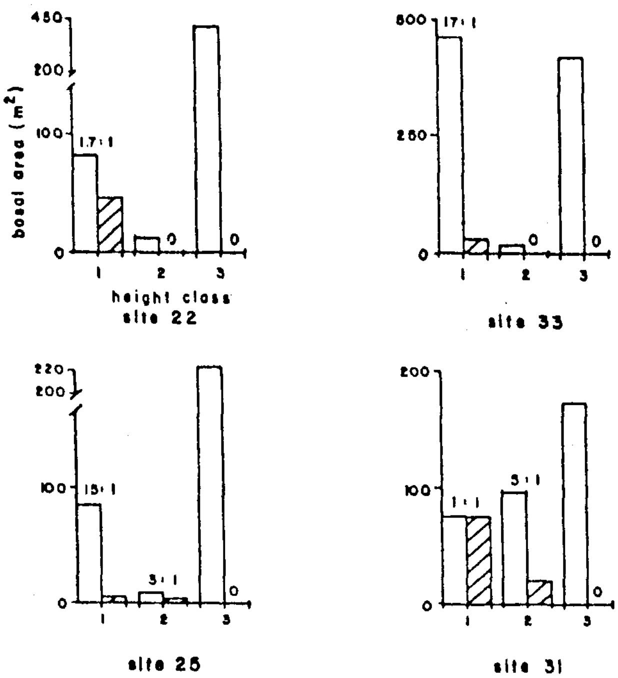



Figure 25. Proportions of native and introduced woody species in different height classes in sample stands of the upland native forest community type in the coastal woodland of the Kalapana Extension, Hawaii Volcanoes National Park. unstriped, introduced = striped bars. To save space, bar graphs are not all to the same scale. Height classes are as follows: 1 = less than 2m tall, 2 = 2 to 5m tall, 3 = greater than 5m tall.

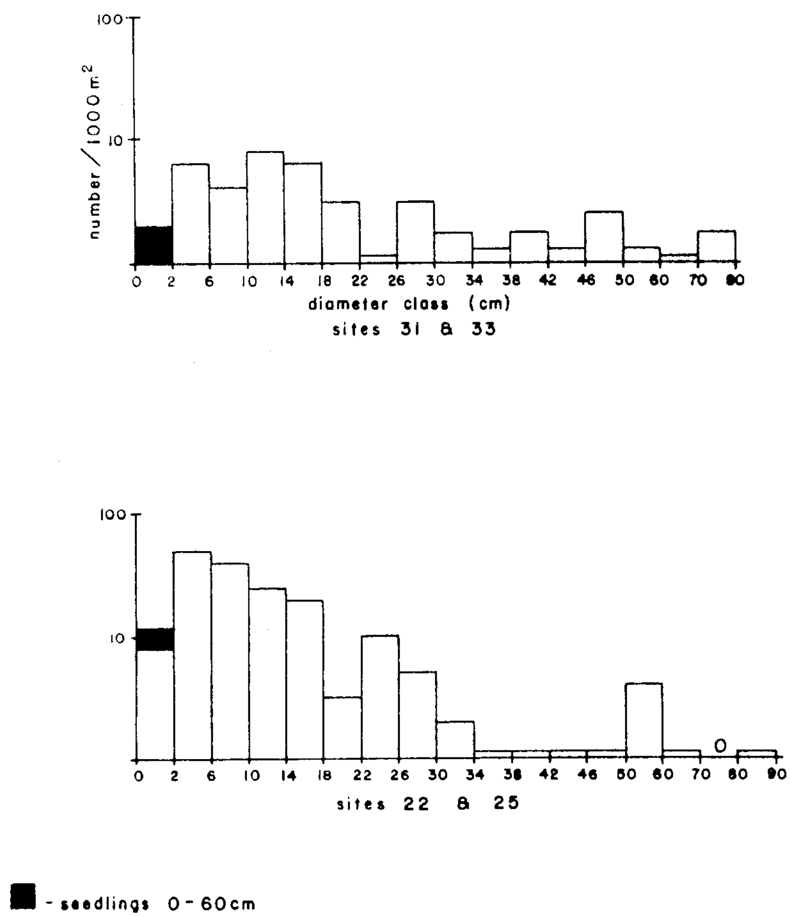



Figure 26. Structural histograms for *Metrosideros polymorpha* ('ohi'a) from the coastal woodland of the Kalapana Extension, Hawaii Volcanoes National Park demonstrating more than one mode.

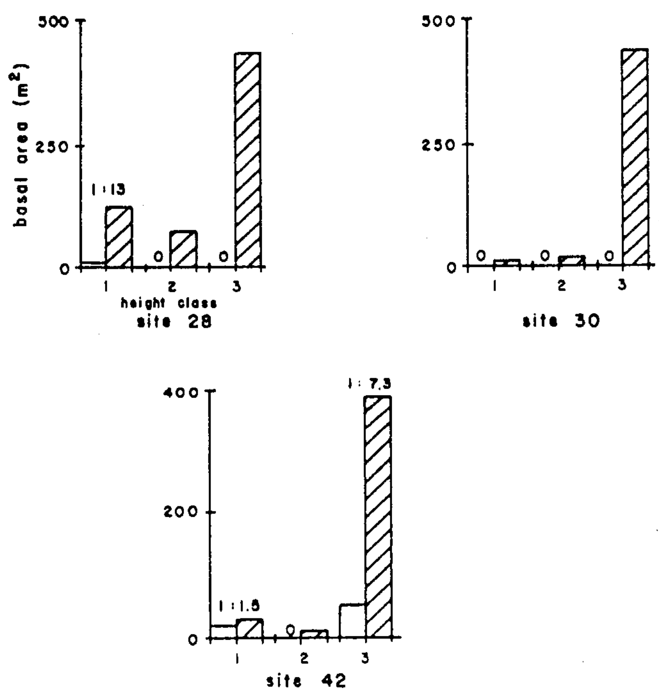



Figure 27. Proportions of native and introduced woody species in different height classes in sample stands of the *Aleurites moluccana* (kukui) community type in the coastal woodland of the Kalapana Extension, Hawaii Volcanoes National Park. Native = unstriped, introduced = striped bars. To save space, bar graphs are not all to the same scale. Height classes are as follows: 1 = less than 2m tall, 2 = 2 to 5m tall, 3 = greater than 5m tall.

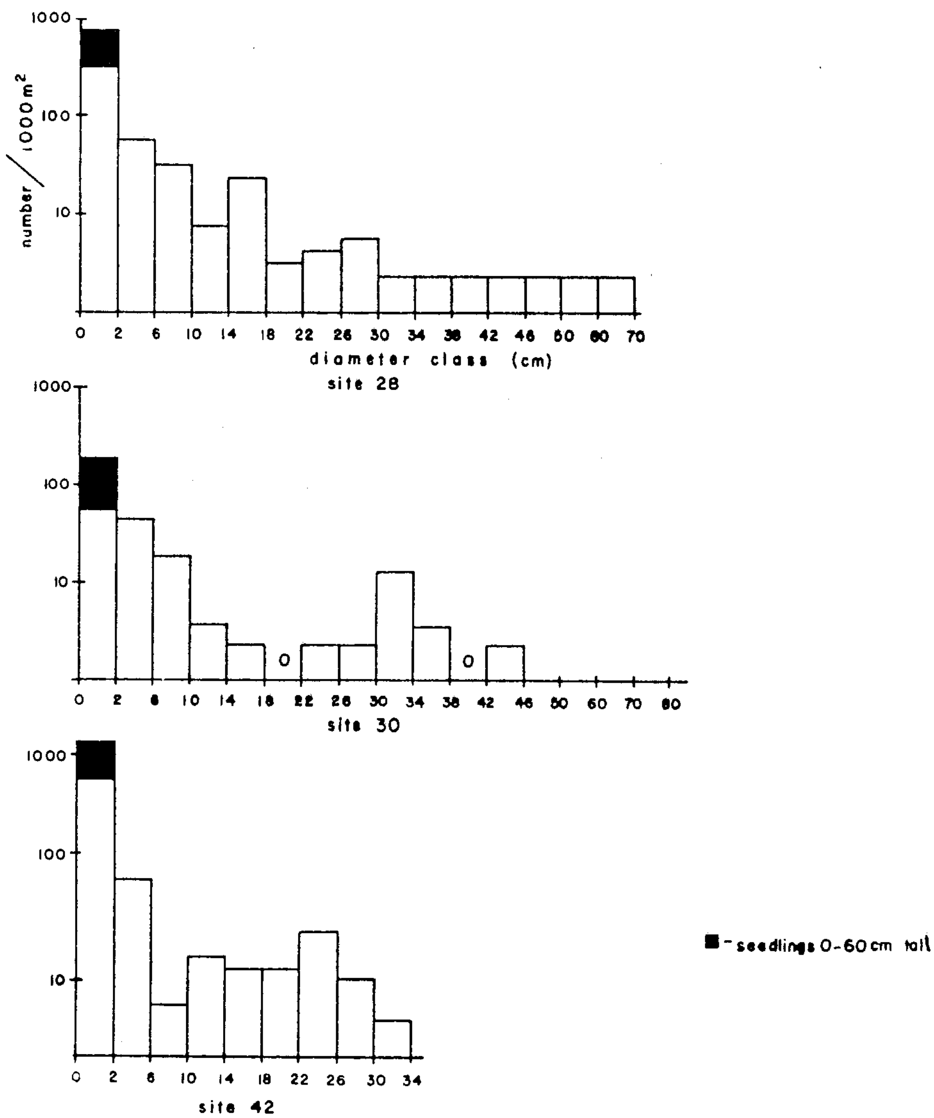



Figure 28. Structural histograms for *Aleurites moluccana* from the coastal woodland of the Kalapana Extension, Hawaii Volcanoes National Park demonstrating more than one mode.

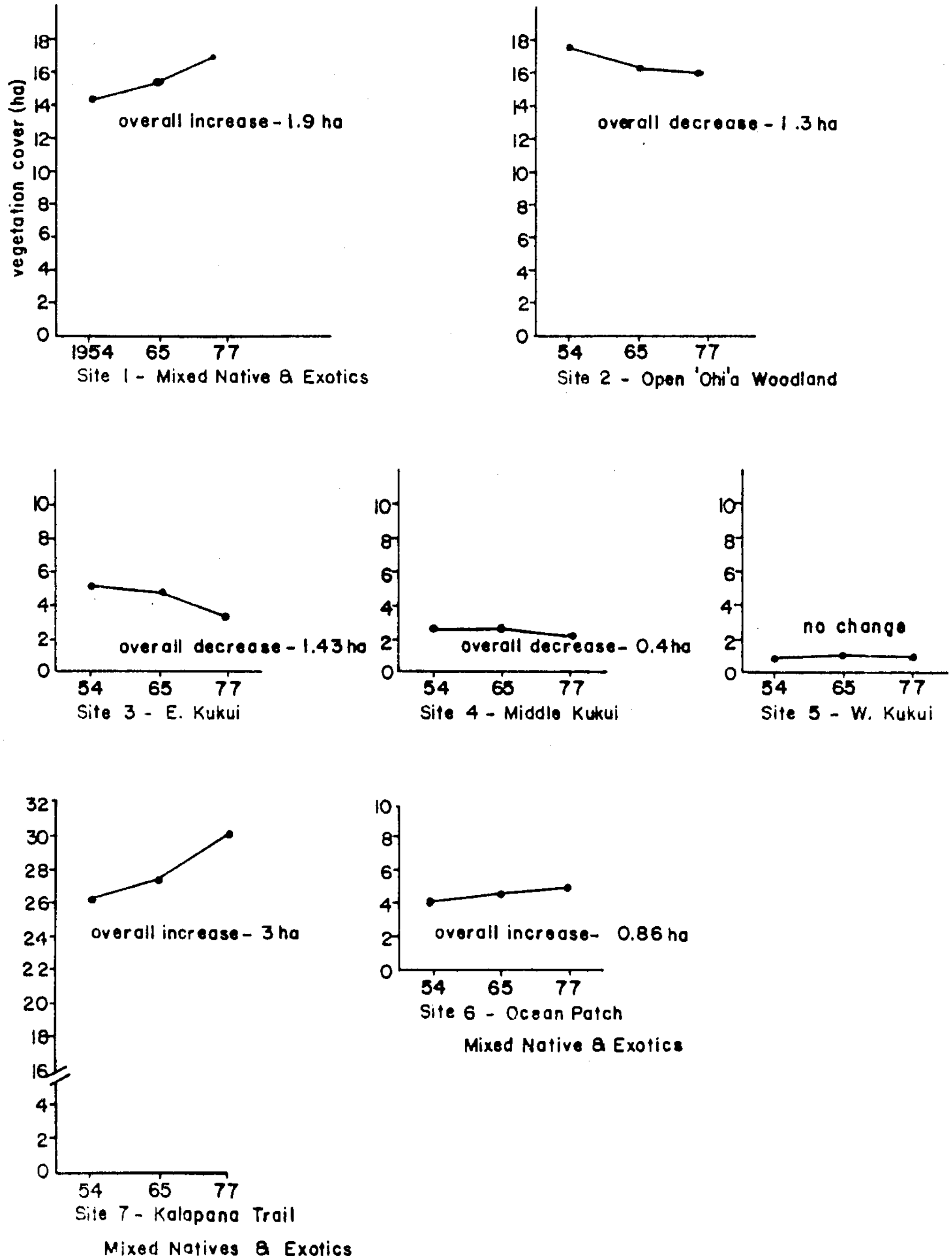



Figure 29. Changes in vegetation cover for seven aerial photoplots of the coastal vegetation of the Kalapana Extension, Hawaii Volcanoes National Park using aerial photographs for the period 1954 to 1977 ("site" = "photoplot" in text).

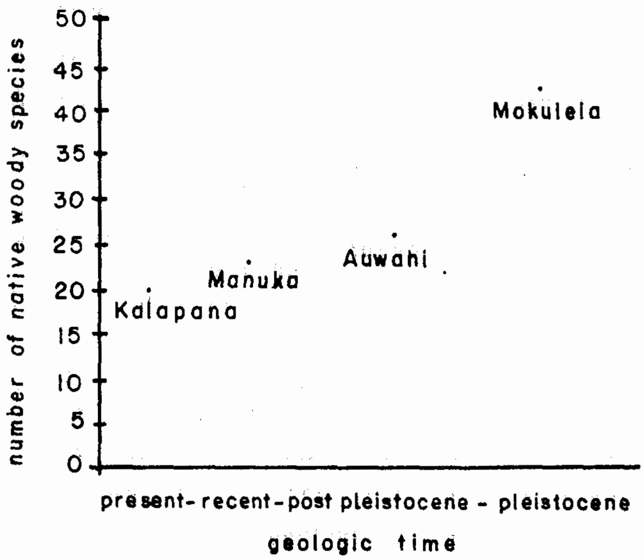



Figure 30. Numbers of native woody species by approximate substrate age for selected dry forest areas in Hawai'i under 2,000 feet elevation. Data for Kalapana from Warshauer and Jacobi (1973). Data for Manuka from Yoshinaga and Higashino (pers. comm.) Data fro Aubvahi from Holt (pers. comm.) and Loope and Medeiros (1984). Data for Mokuleia from Wirawan (1972).