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VEGETATION RECOVERY FOLLOWING PIG REMOVAL IN `OLA`A-KOA RAINFOREST UNIT, HAWAII VOLCANOES NATIONAL PARK

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ABSTRACT

A total of 16, 10 x 10 m plots were established in pig disturbed areas to monitor the vegetation changes following removal of pigs from `Ōla`a-Koa Rain Forest Unit in Hawai`i Volcanoes National Park. Native understory cover increased 48% from 1991 to 1998, largely in the first two years following pig removal from the area. Understory ferns made the largest gains followed by tree ferns and native woody species. A flush of seedlings and saplings of sub-canopy native trees observed after pig removal may potentially increases tree canopy cover in the future. Alien understory vegetation increased 190% throughout the seven year study. Almost all alien plant cover increases resulted from the expansion in cover of three very aggressive species, kāhili ginger (*Hedychium gardnerianum*), Himalayan raspberry (*Rubus ellipiticus*), and palm *grass (Setaria palmaefolia*). These species are able to successfully establish independent of pig activity and are spreading in spite of pig control, not because of it. For other alien species, the greater competition and shade environment created from increased numbers of native trees, tree ferns, and understory plants, along with the lack of physical disturbance by pigs, appear to inhibit their establishment and spread. The presence of Banana poka (*Passiflora mollissima*) was reduced from 81% to 40% in the plots. Several herbaceous weeds, *Cardamine flexuosa*, *Hypericum mutilatum*, *Ludwigia palustris*, that were initially present in a few plots were no longer present by the end of the study period. This study indicates the value of pig control as a first important step in the restoration of native Hawaiian rain forest. Monitoring in future years is needed to more accurately predict trends in native understory and sub-canopy tree species. Follow up alien plant control of the more disruptive species should begin as soon as possible after pig removal while these species densities are still low.

INTRODUCTION

Feral pigs (*Sus scrofa* L.) are a major modifier of native Hawaiian plant communities and ecosystems. Through trampling, rooting and feeding, pigs have selectively depleted native plant species, and promoted the dispersal and establishment of weedy plants throughout native plant communities in the Hawaiian Islands (Spatz and Mueller-Dombois 1975, Stone 1985, Aplet *et al.* 1991).

Native rain forest communities are especially vulnerable because pig densities are highest here due to the abundance of food and water (Cuddihy and Stone 1990). Cooray and Mueller-Dombois (1981) calculated that up to one-third of the diggable area in a mountain rain forest can be disturbed by pigs during a one year period. The local extinction of many rare endemic plants is attributed to intensive pig activity (Diong 1982, Stone 1985). Animals preferentially browse on native ferns, mints, bryophytes, lobeliads, woody seedlings and knock over and dine on fallen tree fern or hāpu`u (*Cibotium* spp.). The latter forms an important component of forest floors and many native tree species are observed growing on hāpu`u logs. Their destruction may limit recruitment of native tree species. In addition, increased light penetration to the forest floor caused by the opening of the hāpu`u canopy favors the establishment of light limited banana poka (*Passiflora mollisima*) and other alien plant species over native rain forest species that are more shade adapted (Burton 1981, La Rosa 1992). Pigs digging for earthworms, rhizomes and tubers increase the rate of leaf litter decomposition. This alteration leads to increased nutrient availability that, in turn, further facilitates alien plant invasions to the area (Vitousek *et al.* 1987, Stone *et al.* 1992). Foraging pigs also disseminate non-native seeds. The dispersal and establishment of some of the most disruptive rainforest weeds, including banana poka, and strawberry guava, (*Psidium cattleianum*) are associated with pig activity (Diong 1982, Smith 1985, Cuddihy and Stone 1990, LaRosa 1992). Concurrent with changes to the vegetation, soil fauna are also affected (Stone and Taylor 1984). A study of the distribution of *Collembola* along a temporal gradient found that species diversity was highest in the oldest of three pig exclosure sites (Foote, 1995). The local extinction of two endemic species of *Drosophila* is attributed to the destruction of their native host plants by pigs in a rain forest site (Foote and Carson 1995). In contrast, increased frequencies of cosmopolitan species of *Drosophila* are associated with invasion by non-native plants to an area.

Domestic pigs of Asian ancestry were first introduced to Hawai`i by Polynesians who used them as an important source of food (Diong 1982, Tomich 1986). These pigs were much smaller with longer snouts than today's feral pigs, and were confined to human settlements (Citation?). Those that managed to escape were captured for major feasts. In 1778, Captain Cook introduced European pigs to the Islands. These more recent arrivals eventually interbred with and replaced the older Polynesian stock. European pigs were more venturesome and able to establish wild populations far removed from human settlements. Their ability to subsist in remote forests was enhanced by their large size which enabled them to knock over and dine on large hāpu`u logs, and subsequent introductions of earthworms, strawberry guava and other plants that produced edible fruits to the Islands. Feral pigs are currently present on Ni`ihau, Kaua`i, O'ahu, Moloka`i, Maui and Hawai`i. The latter island has the largest, most widely distributed populations (Cuddihy and Stone 1990).

Prior to their management, feral pigs inhabited approximately 263 km^2 in Hawai`i Volcanoes National Park, HAVO (Katahira *et al.* 1993). They were found in nearly every plant community from 0-2,300 m elevation, including submontane woodlands, rain forests, dry forests, and montane parklands. The first fenced pig exclosure was constructed in Kīpuka Puaulu in 1968 (Morris CITATION?). In the 1980's, additional fences were built to create 11 pig management units enclosing 6,500 hectacres of pig habitat in the Park. Besides the initial costs of fence building and pig removal, approximately $100,000 involving 600 worker days are required annually to maintain exclosure fences and remove pigs that stray into the Park's protected units (Hoshide *pers. comm.*).

The goals of managers are to protect native ecosystems from further disruption by alien species and restore native biodiversity. To determine whether these goals are being met requires an assessment of the ability of native plant communities to recover following pig removal in natural areas. The concerns are twofold. Is pig removal sufficient to allow native forest recovery and is further action required by managers? Several studies conducted within the Park have shown that the degree of deterioration and recovery of an area depend on both the duration, and intensity of the disturbance, the presence of disruptive alien plants, and the available supply of native plant propagules for revegetation (Spatz and Mueller-Dombois 1975, Loope and Scowcroft 1985, Stone *et al.*1992, Tunison *et al.* 1994). A five year study examining vegetation changes in pig exclosures in Nāpau rain forest showed that native plant recovery can be quite dramatic in the absence of aggressive alien weeds (Katahira 1980). Whereas in areas with a high abundance of alien weeds that have prolific seed production, and seed dissemination and seedling success is not dependent on pig activityt, pig removal may not prevent the spread of alien weeds such as faya tree (*Myrica faya*) and kāhili ginger (*Hedychium gardnerianum*) (Stone *et al.* 1992).

This report documents the vegetation recovery occurring in pig disturbed sites following the removal of pigs from `Ōla`a-Koa Rain Forest Unit (Figure 1). The unit is the largest of the rain forest exclosures, and encompasses a 1,000 year old tree fern dominated rain forest that contains a kipuka of the only mixed koa/`ōhi`a rain forest in HAVO, 3 endangered plant species, and 12 additional rare plants. The information provided from the study will allow managers to assess the capacity for native plants to recover and determine whether further management is required after pig control.

STUDY SITE

The `Ōla`a-Koa Rain Forest Unit encloses a 3,200 m x 3,200 m area that lies within Hawai`i Volcanoes National Park on the east slope of Mauna Loa between 1,100-1,200 m elevation (Figure 1). The area is classified as an `Ōhi`a/Hāpu'u (*Metrosideros polymorpha/Cibotium glaucum*) Tree Fern Montane Wet Forest (Wagner *et al.* 1990) with no pronounced dry season and a precipitation range exceeding 2,500 mm/yr. The mean air temperature is 12-20(C. The soil is an inceptisol formed of layers of ash and cinder up to 1.5 m deep on a 4,000 year old lava base (Lockwood and Lipman 1987).

The community is characterized by displacement dieback of `ōhi`a in which cohorts of older trees senesce synchronously and are not replaced by a new cohort of younger trees. Several factors that trigger stand decline include the simplified structure of the cohort, edaphically extreme habitats with poor soil drainage, and physiological shocks that include, non-catastrophic perturbations such as excessive rainfall and drought (Mueller-Dombois 1994). In `Ōla`a, remaining trees form a thinly scattered emergent canopy (Mueller-Dombois 1985). Below this, kāwa`u (*Ilex anomala*), `ōlapa (*Cheirodendron trigynum*), olomea (*Perrottetia sandwicensis*), pilo (*Coprosma* spp.) and other native trees are openly distributed. The largest contributor to the overstory is tree fern (*Cibotium* spp.) which forms a continuous lower canopy. The most abundant species is *Cibotium glaucum* but *C. chamissoi* and *C. menziesii* are also present. Understory vegetation is dominated by native ferns of which the most abundant species are hōʻiʻo (*Diplazium sandwichianum*), and hōʻiʻo kula (*Pneumatopteris sandwicensis*). The primary alien plants present are himalayan raspberry, banana poka, kāhili ginger, and palm grass.

In 1989, a 1,000 ha fenced exclosure unit was constructed and pig control efforts were begun in the unit immediately following fence completion. Remnant densities remained at the initiation of the study in 1991. The last pig was removed from the unit in the summer of 1994.

METHODS

The design of this study was based on a previous 1985 study conducted by Anderson and Higashino (unpublished) in the nearby ʻŌlaʻa-Puʻu Rain Forest Unit. This study differs in that it focuses on the vegetation recovery in recently disturbed areas. At one time or another, probably every area in the unit had experienced some degree of pig activity. Thus the vegetation reflects a mosaic of different stages of plant communities in recovery. To minimize this kind of variation, only recently disturbed pig sites were selected. Native rain forest habitat outside the unit was much weedier than in the unit and prevented managers from establishing comparable untreated control plots in which pig activity was allowed to continue.

In spring 1991, twenty 10x10 m plots were established in recently disturbed pig sites located in ʻŌlaʻa-Koa Rain Forest Unit (Figure 2) near previously established transects used to monitor alien plant distributions, and pig activity. These transects spanned the enclosure and were placed in a random systematic design at 400 m intervals along the fence line parallel to Wright Road. Plot sites were selected for sampling if they showed recent (2-4 weeks old) severe signs of pig disturbance over a wide area (>10 m^2) as evidenced by damaged hāpuʻu, the absence of understory vegetation and the presence of lots of exposed ground. Small patches of undisturbed ground within a plot were acceptable. Plot location, orientation and corner origin within the pig disturbed site were chosen randomly using a random number tables.

The cover of understory vegetation in each plot was determined along five, 10 m long transects located at 0.6 m, 2.6 m, 4.6 m, 6.6 m and 8.6 m from the corner origin (Figure 3). The vegetation cover in two height strata (<1m; 1<2m) was measured using the point intercept method with slight modifications (Western Region Prescribed and Natural Monitoring Task Force 1992). A 2 m tall, 1/4 inch diameter pole was placed vertically at 20 cm intervals along each transect. All vegetation intercepting the pole within the height strata was recorded at each interval. Within each stratum, species touching the pole multiple times at one interval were only recorded once. Dead vegetation attached to live vegetation was counted as live. If no live vegetation was intercepted then either bryophyte, litter, soil, rock or bare ground was recorded. The presence of each alien species in the plots was recorded.

Frequency, or the presence/absence of alien species was recorded in the plots.

Density of all shrubs, subshrubs and one introduced liana, banana poka, was determined throughout the entire 10 x 10m plot. Plants were measured and grouped into the following basal diameter size classes: <1 cm, 1<5 cm, 5<10 cm. Plants <1 cm were further divided into two height categories (<10 cm and > 10 cm height). Individuals were distinguished as growing epiphytically (including nurse logs) or terrestrially (data not shown).

The number of tree species taller than 10 cm were counted and grouped according to the following basal diameter size classes: <10 cm, 10-20 cm, 20-30 cm, 30-40 cm etc. Trees less than 10 cm basal diameter were subdivided into the following categories: < 1 cm, 1<5 cm and 5<10 cm. Individuals were distinguished as growing epiphytically (including nurse logs) or terrestrially (data not shown).

The number of hāpu`u other than very small seedlings (fronds <10 cm height) was determined in each plot. Individuals were grouped into the following basal diameter size classes: <10 cm, 10<20 cm, 20<30 cm, 30<40 cm. Hāpu`u growing on fallen tree fern boles were counted as separate individuals. Young individuals that lacked a measurable bole were assigned to the smallest basal diameter class. Individuals were distinguished as growing epiphytically (including nurse logs) or terrestrially (data not shown).

Measurements were taken at the beginning of the study period in spring 1991. Vegetative cover, frequency of alien weeds, density of woody species, banana poka, and tree fern smaller than 5 cm basal diameter were re-measured during spring 1993. All measurements were retaken during spring 1998. Changes in vegetation cover and density were analyzed using a Wilcoxon sign-rank test on the differences. Frequency of the more abundant weeds in the plots was analyzed using a chi-square test. Frequency of native species was discarded due to inconsistencies in the data. No adjustments were made for type I errors. Means, standard errors, and probabilities for significance were presented in tables. The population structure of the most abundant tree fern and tree species in 1991 and 1998 were displayed as histograms with the probability for significant differences within each size class displayed in parenthesis.

Four of the plots (plots 9-12) were removed from the analysis when managers began removal of alien plants in a small 500 x 500 m area within the unit in 1992. Missing data from one plot, reduced the number of plots to 15 for analysis of density and population structure of native trees. The number of plots used to analyze changes in cover and frequency remained at 16.

RESULTS

Cover of Understory Vegetation

At the initiation of the study, recently disturbed plots were characterized by a paucity of understory vegetation (23.8% for cover < 1m, and 19.8% for cover 1< 2 m) (Table 1, 2). The exposed forest floor was dominated by litter, followed by non-vascular plants and soil. Alien plants contributed <5% of the total vegetation in the upper understory (1<2 m), and 10% of the total vegetation in the lower understory (< 1m). Native hāpu`u was the largest component of the upper understory (11.4%), followed by native trees (3.5%) and ferns (1.2%). In contrast, native ferns (10.1%) other than hāpu`u were the most abundant component of the lower understory, followed by hāpu`u (7.3%), and native trees (1.7%).

Total vegetation cover increased following pig removal, with the cover of native and alien understory vegetation following two distinct trends. Native vegetation increased between 1991 to 1993 from 21.3% to 36.7% for cover <1m, and from 18.7% to 28.1% for cover 1<2 m, but did not change significantly between 1993 to 1998. In 1998, native vegetation cover was 46.4%, and 27.8% for the lower and upper strata respectively. In contrast, cover of alien plant species continued to increase throughout both sampling periods from 2.4% in 1991 to 7.2% in 1993 and 11.0% in 1998 for cover <1 m in height, and 1.1% in 1989 to 2.2% in 1991 and 3.2% in 1998 for cover 1< 2 m in height. Concurrent with increased vegetation cover, the amount of exposed forest floor was significantly reduced. Hapu`u leaf litter was the primary component of the forest floor, followed by non-vascular plants growing on logs, and soil.

Among native plant groups the most

significant changes were in native trees, tree ferns, and herbaceous ferns. Native tree cover < 1m height increased >2-fold during the first sampling period, and remained greater than at the beginning of the study. These changes were largely due to increases by pilo (Table 3). Cover of hāpu`u 1 < 2 m in height increased significantly the first two years following pig removal, but did not change much thereafter (Table 4). The cover of native fern species <1 m in height doubled by the second year of the study. The largest increases were by hō`i`o, hō`i`o kula, and `akōlea (*Athyrium microphyllum*). Continued increase in native fern cover over subsequent years was largely in the upper understory strata, where hō`i`o increased by over threefold (1.3% in 1993 to 4.6% in 1998 for cover 1<2 m in height). Other native genera, and species that had big cover increases included *Clermontia* spp., *Uncinia uncinata*, and `ala`ala`wainui (*Peperomia* spp.).

In contrast, alien plants continued expanding their abundance in the plots during both sampling periods. Cover of alien plants < 1m height tripled, and cover of alien plants 1< 2m height doubled over the 7 year sampling period. These increases were largely due to kāhili ginger that increased almost 10-fold, palm grass that increased 30-fold, and himalayan raspberry that increased 2-fold.

Presence/absence of alien weeds

Presence of alien species in the plots varied over time and for individual species (Table 5). Cover increase by kāhili ginger is partly due to expansion into formerly unoccupied plots (43.8% in 1991, 81.3% in 1998). Himalayan raspberry, which was present in 81% of the plots at the beginning of the study, is currently in all but one of the plots. While the cover of *Polygonum punctatum* remained unchanged, it continued to expand into new plots and increased it's presence from 25% to 62.5%. Similarly, the presence of palm grass in the plots had increased from 12.5% to 31.3%. In contrast, the presence of banana poka in the plots decreased from 75% to 40%. Herbaceous species, *Cardamine flexuosa, Hypericum mutilum*, and *Ludwigia palustris* that were initially present in a few plots, were no longer present by the end of the study period.

Density of native and alien shrubs, subshrubs and lianas

The most dramatic increases among native shrub densities occurred during the first two years of the study (Table 6). These changes were primarily due to recruitment of `ōhā (*Clermontia* spp.), `ākala (*Rubus hawaiiensis*), and `ōhelo (*Vaccinium* spp.) seedlings in the < 1cm basal diameter but >10 cm height class. Density changes among native shrub seedlings in the larger height, and diameter classes, and among the other species showed few consistent or significant trends over time.

Density of total alien shrubs < 5 cm basal diameter increased (Table 7). These increases were largely due to recruitment of himalayan raspberry and thimbleberry, (*Rubus rosaefolius*). In contrast, banana poka densities decreased over the two sampling periods.

Population distribution of hāpu`u and other tree ferns

The population distribution of hāpu`u changed substantially between 1991 and 1998 (Figure 4). Large increases in the number of *Cibotium glaucum* individuals in the two smaller basal diameter size classes caused the population to shift from one containing relatively few small individuals to one dominated by individuals form the smaller size classes. The shape of the distribution approaches the inverse j-shaped curve that is often associated with self-maintaining populations of tree species (Barbour *et al.* 1980). A similar pattern of increased recruitment among the smaller size classes was found for *Cibotium hawaiiensis*.

Population distribution of native trees

The population distribution of native trees, and of the more abundant native tree species, `ōhi`a, olomea, pilo, and `ōlapa, by basal diameter size classes are presented in Figure 5. Similar to hāpu'u, the seven years following pig removal saw increased recruitment of individuals into the smaller size classes. Pilo, and olomea had the largest increases. These species and `ōlapa owed most of the changes to seedling recruitment (>10 cm in height and < 1 cm basal diameter). Recruitment of `ōhi`a, the dominant emergent tree, did not improve over time. Table 8 shows the distribution of seedlings growing epiphytically and terrestrially. The majority of `ōlapa and `ōhi`a seedlings grew epiphytically, whereas pilo and olomea seedlings were more often found rooted in the soil.

DISCUSSION

Our study indicates the value of pig control as a first important initial step in the restoration of native Hawaiian rain forest. Native understory vegetation recovers rapidly, and sub-canopy tree ferns and native trees begin to regenerate more rapidly. Although native plant recovery and pig control inhibits many alien weeds, it does not stop the spread of several disruptive alien plant species. Other exclosure experiments and research on ecology of species involved allows us to interpret trends from our study, even though we did not have untreated controls still disturbed by feral pigs.

Native vegetation recovered rapidly, as evidenced by the expansion in cover of understory ferns, herbs, and tree ferns in recently dug sites following pig removal from the unit. Understory species that made the largest gains were terrestrially rooted rather than rooted epiphytically on live stems and nurse logs. Plants rooted in the soil are the most vulnerable to pig activity, and can be expected to benefit the most from ending pig disturbance. The species with the most notable recovery included hō`i`o, hō`i`o kula, `akōlea, and more recently `ala `ala wainui. Increases in native herbaceous and fern abundance occured early on with most of the increase in crown cover occurring in the first two years following pig removal. Hō`i`o, continued to expand vertically in the plots as evidenced by increased crown cover in the 1-2 m height strata. Other species may have continued their growth by increasing density and height, parameters that were not detected with our sampling method.

Similar recovery of native vegetation has been documented in previous exclosure studies in the Park's Nāpau and Thurston Rain Forests. Dramatic recovery of `ama`u fern (*Sadleria pallida*), hāpu`u, and `ohā (*Clermontia parviflora*) occurred 4.5 years following construction of fenced exclosures in Nāpau (Katahira 1980). More modest increases in native understory were detected in Thurston Rain Forest following 13 years of pig exclusion (Higashino and Stone 1982, Stone *et al.* 1992).

While the amount of exposed forest floor was significantly reduced, decrease in the amount of exposed soil was not significant in this study. Hāpu`u leaf litter is the primary component of the forest floor and its abundance and consequently the proportion of exposed soil is seasonally dependent in the area. An earlier study conducted in an `ōhi`a dominated rainforest found the amount of exposed roots and soil was much greater immediately outside the Nāpau pig exclosure (Higashino and Stone1982).

The flush of seedlings and saplings of sub-canopy native trees observed after pig removal may potentially increase tree canopy cover in the future. There was a general pattern of increased recruitment of young sub-canopy native trees. This recovery was most evident among species such as `olomea and pilo whose seedlings were often rooted in the soil and consequently had been most vulnerable to past pig activity. Monitoring in future years is needed to more accurately predict trends in sub-canopy trees by tracking the success of seedlings and saplings in growing through the tree fern canopy. A fairly consistent pattern of recruitment among some native shrub species suggests the recovery of a native shrub understory in a pig-free rain forest. Densities in the smallest size class (<10 cm height) were more likely to reflect seasonal variation in rainfall rather than release from pigs. Nevertheless, we detected a steady progression of small seedlings into larger seedlings in `ākala, ‘ōhelo, and `ohā, a pattern of recruitment boding well for recovery of these species. `Ohā is particularly vulnerable to pig activity and serves as an important host to some endangered endemic species of *Drosophila* (Foote ad Carson1995).

Cover of the most abundant tree fern species, hāpu`u, increased rapidly following pig disturbance and removal. At the beginning of the study, young hāpu`u were considerably impacted by pig disturbance as evidenced by the population distribution in 1991. This distribution did not have the inverse j-shape characteristic to self-maintaining populations. Instead, there were fewer individuals in the smallest size class. Numbers in this size class increased 3-fold in the plots following pig removal from the area. This recovery of hāpu`u is essential to the maintenance of the rainforest ecosystem. In rain forest undergoing displacement dieback of `ōhi`a, tree ferns are a major contributor to the biomass in the community, and play an important role in nutrient cycling, tree seedling establishment and understory microclimate (Burton 1981, Burton and Mueller-Dombois 1984, Aplet *et al.* 1994). Nearly all `ōlapa, `ōhi`a and `ōhā seedling establishment was epiphytic on tree fern logs in this study.

The recovery of tree fern following pig removal may reinforce the current trend of displacement dieback of `ōhi`a in `Ōla`a. Germination, and seedling survival of `ōhi`a is dramatically inhibited by tree fern canopy closure where light levels are reduced to <5% full irradiance (Burton and Mueller-Dombois 1984, Drake 1993), and this may account for the low recruitment observed in these study plots.

Continued recovery of native vegetation should reduce factors that promote the presence of most weeds. Greater competition from understory plants and greater shade created by increased native cover, along with lack of physical disturbance, may eventually inhibit the establishment and spread of weedy species. Many weeds depend on canopy gaps for establishment despite the presence of a prolific seedbank and seed fall to the area (Burtom 1981, Drake 1998). The importance of tree fern cover suppressing weed species has been documented in `Ōla`a (Burton 1981) where hāpu`u fronds were removed from experimental plots and subsequent recruitment of native and alien species were monitored. In plots where 100% of the canopy was removed, the cover of weed species exploded from almost 0% to 19%, and only 4 of the 30 species that established were native, `ōhi`a, mamaki (*Pipturus albidus*), Hawaiian pokeweed (*Phytolacca sandwicensis*), and `ena`ena (*Gnaphalieum sanwicensium*).

Increased native canopy cover and cessation of soil disturbance may limit expansion and contribute to the decline of some of the herbaceous and woody weed species described in this and previous studies (Aplet *et al.* 1991, Stone *et al.* 1992, Pratt citation). The decline of banana poka from the plots is particularly important. Banana poka, radically alters native plant communities by stunting, damaging and strangling native trees when forming a thick mat over secondary forest (Smith 1985). This species decline after pig control is attributed to light limitations created by increased canopy closure of hāpu`u and native trees. Young seedlings are shade intolerant, and the effects on seedling recruitment are evident in its reduced presence from nearly all to half the plots (La Rosa 1984). These findings are similar to observations made from a nearby pig exclosure unit that included paired treated and untreated areas disturbed by pigs (Pratt *pers. comm*). Very little strawberry guava was present in the study site, although it is abundant and forms almost monotypic stands immediately outside the unit. It reproduces both sexually and by vegetative cloning (Huennecke and Vitousek 1990). Pigs and birds that feed on the pulpy fruit are the primary dispersal agents for propagules, and strawberry guava's continued low abundance in the unit maybe partly due to the cessation of pig activity.

Despite reduction in cover of some species, total alien weed expansion in the plots dramatically increased following pig removal. While native understory cover increased 48% from 1991 to 1998 largely in the first two years, alien understory vegetation increased 190% throughout the seven years study.

Almost all increases in alien plant cover resulted from the invasion and expansion in cover of just three very aggressive species, kāhili ginger, Himalayan raspberry, and palm grass. Other exotic species (*Ehrharta stipoides* and *Polygonum punctatum*) experienced relatively modest increases either by increasing abundance in plots where they were previously established or invading new plots.

The continued spread of these alien species may be occurring in spite of pig control, not because of it. However, the design of this study did not address the mechanisms for invasive species success, and very little information exists on the factors that allow successful invasion by weeds. Successful weeds may have substantial soil seed banks, which are able to germinate in the absence of continued soil disturbance, and seed dissemination by birds and wind from nearby unmanaged forest may account for invasions into new areas despite pig removal from the unit. Kāhili ginger appears to be highly tolerant of shade and seedling recruitment occurs in disturbed or undisturbed soil (Authors *pers. obs.*). Its low abundance in nearby exclosures and bright fleshy fruit suggests that birds are responsible for its dispersal into the unit despite pig control. However, no insights are available from comparative pig disturbed and pig free sites. Similarly, very little information exists on palm grass invasion in Hawaiian rain forest. Small seed size, that allows for wind dispersal, and possible shade tolerance are probable reasons for its spread and establishment into new sites. Himalayan raspberry becomes established best in disturbed areas and expands most rapidly in light gaps (Stratton 1996). However, the species continued to expand its presence in the plots despite cessation of pig disturbance and closing of the canopy.

Vegetation changes in the study plots represent an early stage of native plant recovery following pig disturbance. The majority of the vegetation in `Ōla`a-Koa Rain Forest unit represents a mosaic of different stages of recovery from repeated episodes of pig disturbance. The lack of untreated controls, which continue to be disturbed by pigs, make it difficult to draw a tight cause and effect relationship between pig removal and vegetation changes. However, our results can be interpreted in light of similar patterns in recovery of native vegetation and continued spread of alien plants found in other exclosure studies (Katahira 1980, Higashino and Stone 1982, Loope and Scowcroft 1985, Stone *et al.* 1992) and in our study site (La Rosa 1992, Stratton 1996).

The extent of pig impacts to the area may be inferred to some degree by the amount of recovery observed among native plants in the plots. Native forest biomass is dramatically reduced. Herbaceous plants, woody seedlings and young hāpu`u are most vulnerable to pig damage and the diversity of native woody species is subsequently decreased. The full extent to which pig activity reduces species richness is difficult to evaluate because knowledge of species presence prior to pig disturbance is lacking. Inferences made from this study are conservative and its probable that some plants were permanently extirpated from the area by pigs.

We expect the extent of native rain forest habitat recovery to be highly dependent on the degree of degradation prior to pig removal. An inverse relationship exists between degree of weediness and potential for recovery (Stone *et al.* 1992). Its possible that extremely disturbed areas that have a high abundance of alien plants may be beyond the point of recovery.

RECOMMENDATIONS

Follow up alien plant control is needed in `Ōla`a-Koa Rain Forest Unit. Pig control resulted in a flush of native plant recovery, and many herbaceous alien plants were suppressed. However, the most disruptive alien plant species such as kāhili ginger, Himalayan raspberry, and palm grass continued to expand and need to be controlled. Control efforts should begin as soon as possible after pig control is effective because these species are very aggressive and found now at very low densities in many areas. Efforts should include research on potential biological controls as well as refining current manual and herbicide techniques.

Approximately half of the plots are located in management blocks that were targeted for alien plant removal beginning in Fall 1998, and the remaining plots are in areas that will be treated over the next two years. These plots will continue to be monitored. This will help interpret initial positive results including seedling and sapling flushes of sub-canopy native trees, native shrubs, and tree ferns in the presence and absence of alien weed control.

The distribution and abundance of the worst weeds are being mapped to determine their current status throughout all the `Ōla`a Rain Forest Units. More studies are needed to understand the physiological requirements and ecological significance of palm grass, strawberry guava and kāhili ginger. Future monitoring of plant recovery after pig control should be designed to include pre-treatment status of vegetation prior to pig removal and untreated controls which pigs continue to disturb. The latter is critically important, and would directly address questions about the relationship of pig disturbance and weed invasions not answerable by the design available to the current study.

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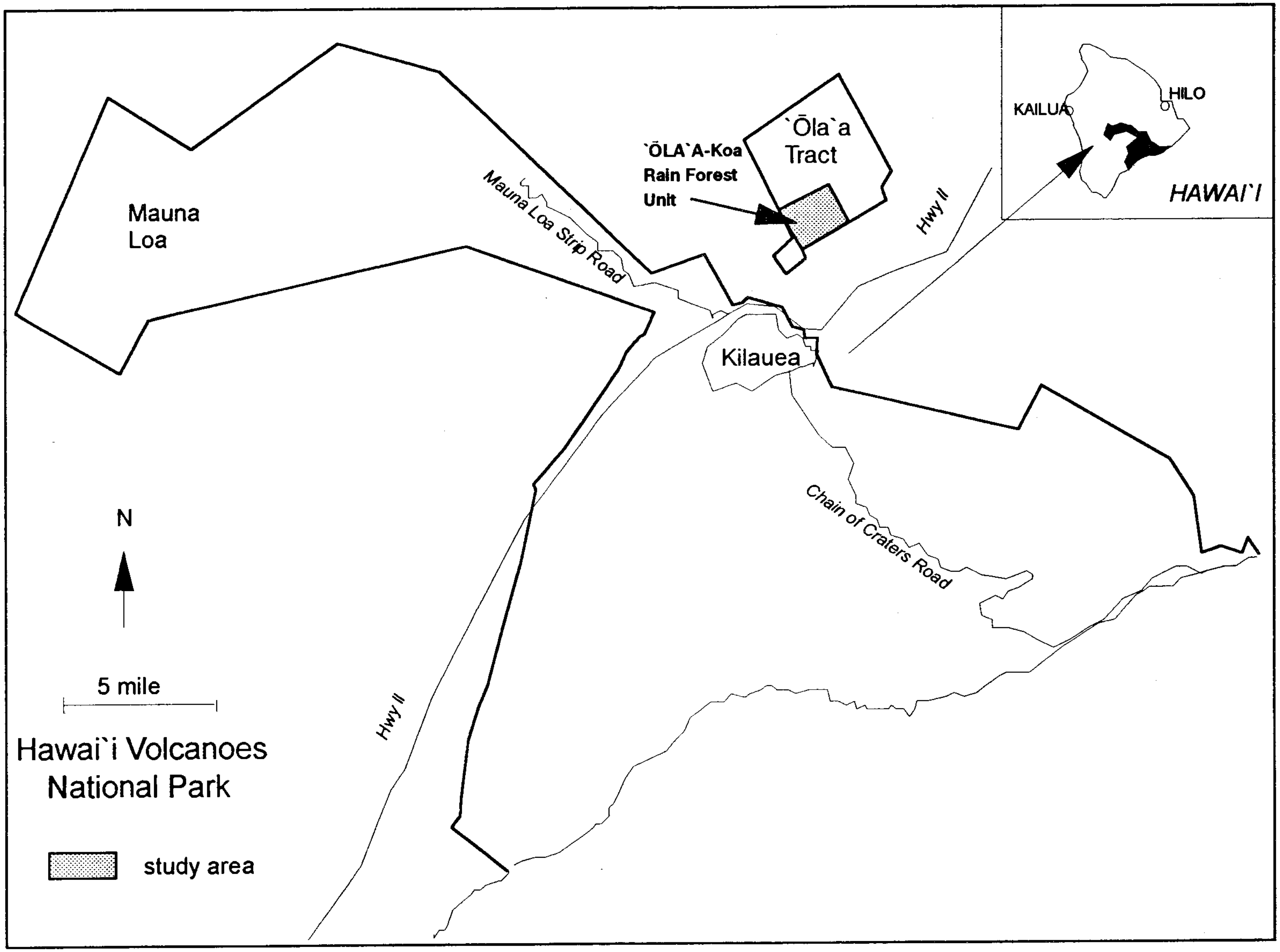

Figure 1. Location of study area, `Ōla`a-Koa Rain Forest Unit, Hawai`i Volcanoes National Park.

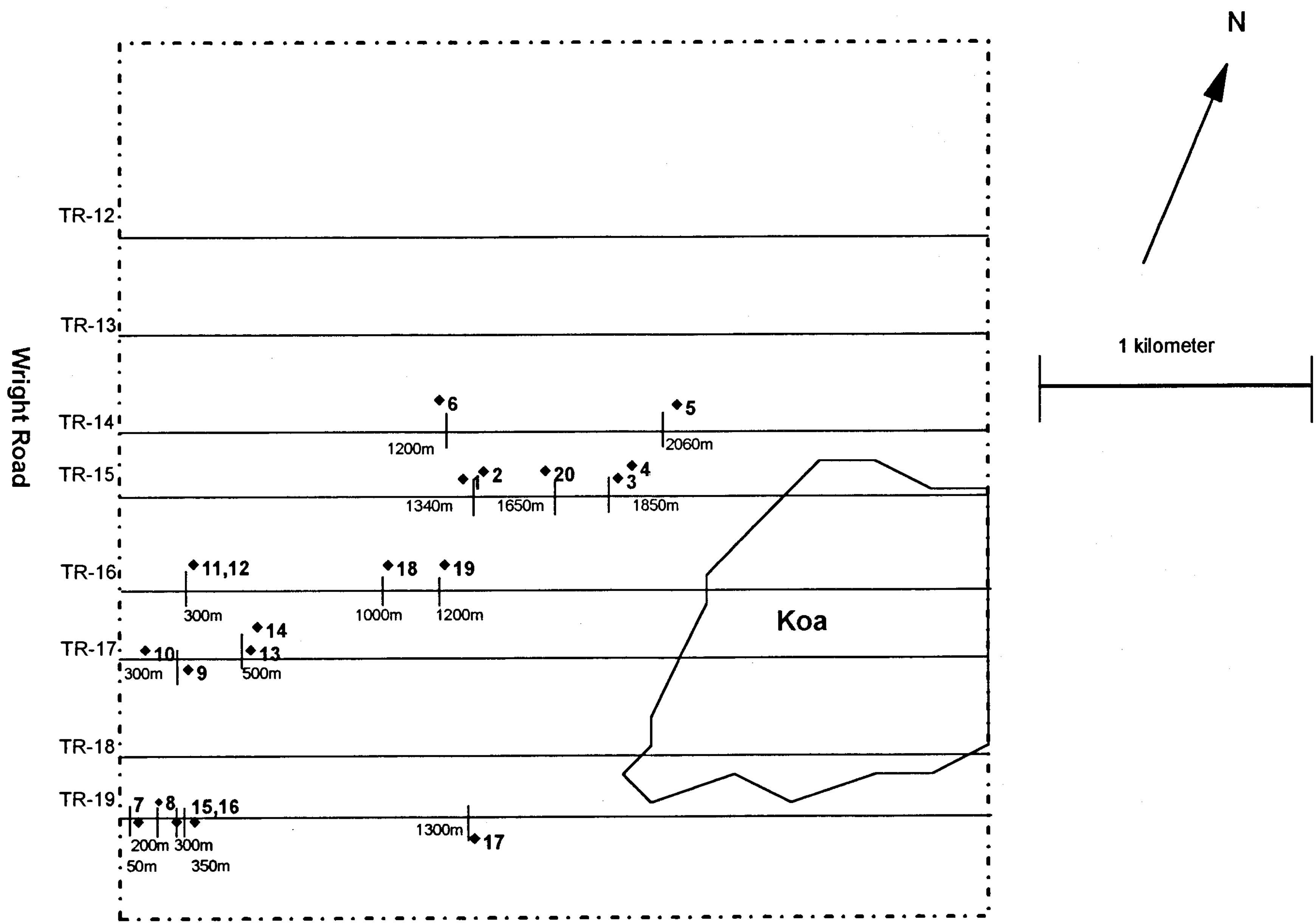

Figure 2. Location of 10x10 m plots in study area, `Ōla`a-Koa Rain Forest Unit, Hawai`i Volcanoes National Park.

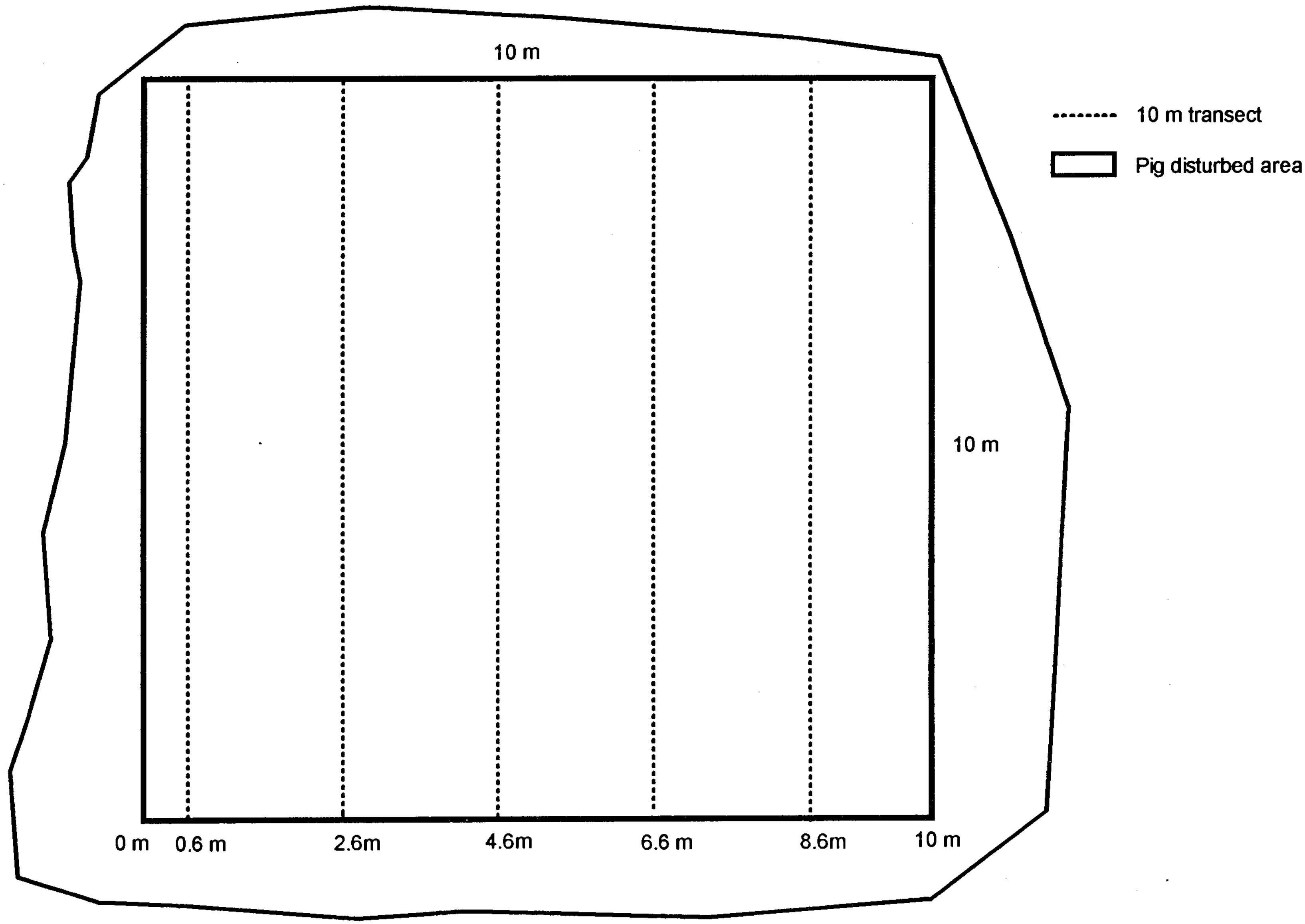

Figure 3. 10x10 m study plot, \`Ōla\`a-Koa Rain Forest Unit, Hawai\`i Volcanoes National Park. Five 10 m transects were established at, 0.6, 2.6, 4.6, 6.6, and 8.6 m from zero point.

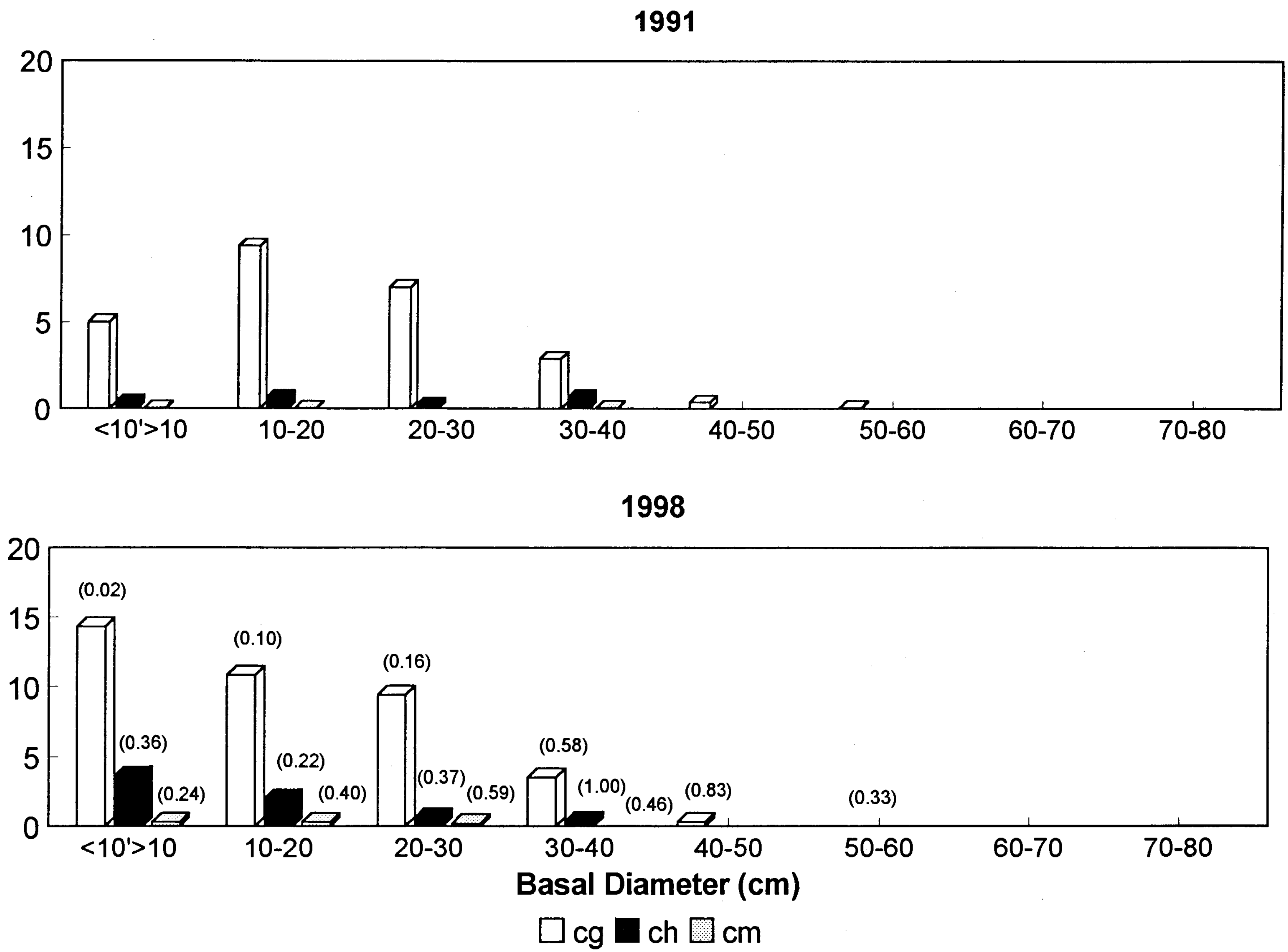

Figure 4. Average number of tree ferns in 10x10 m plots: cg = *Cibotium glaucum*, ch = *C. hawaiiensis*, cm = *C. menziesii*. P values are given in parenthesis.

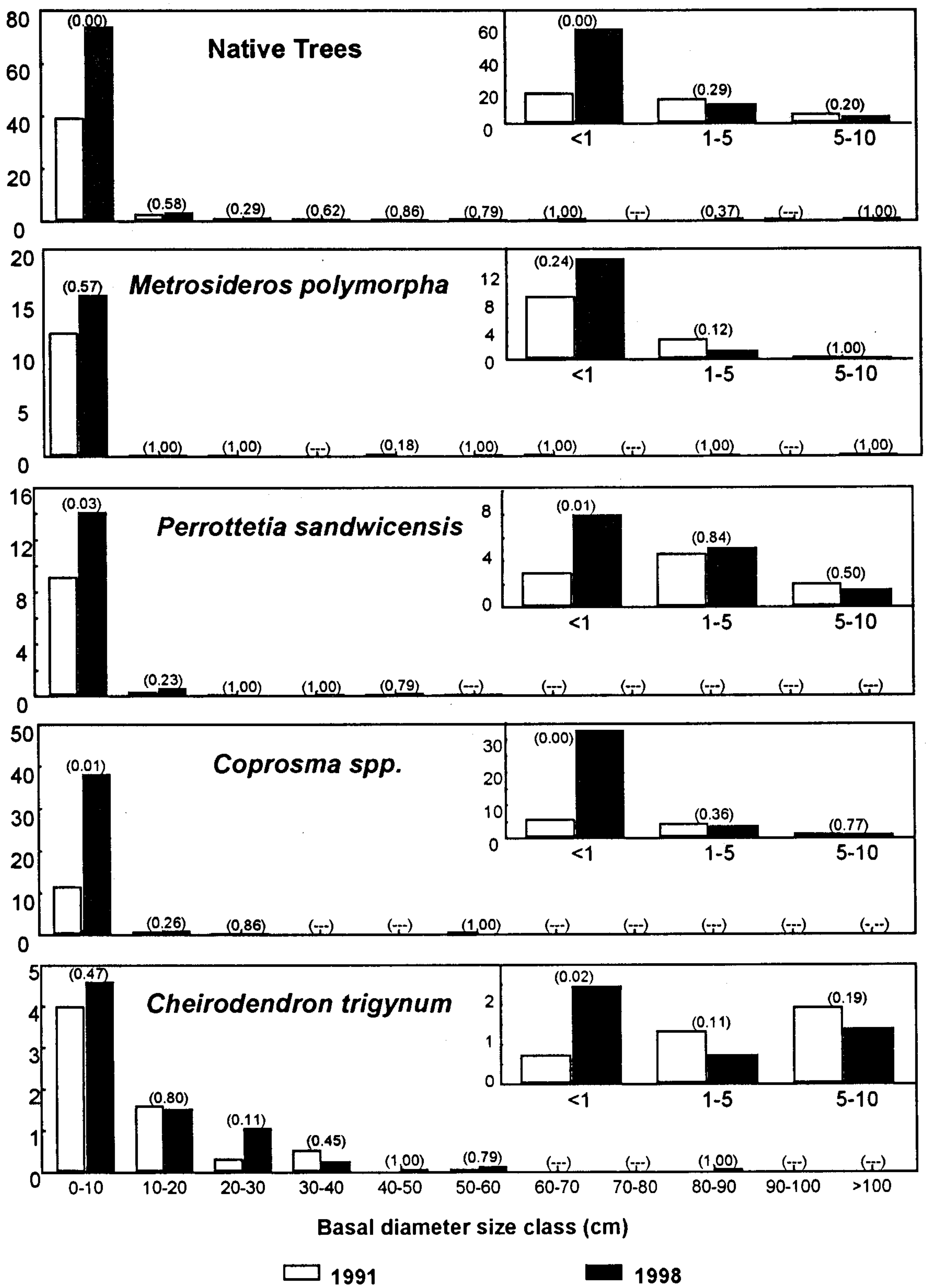

Figure 5. Average number of individual native trees in 10x10 m plots. P values are given in parenthesis.

Table 1. Change in absolute percent cover of vegetation by plant categories <1 m height in 16, 10x10 m plots `Ōla`a-Koa Rain Forest Unit, HAVO.

	1990 <1m mean	se	1993 <1m mean	se	1998 <1m mean	se	P values 1991-1993	P values 1993-1998	P values 1991-1998
Native Trees	1.7	0.3	4.0	0.9	2.8	0.5	0.02	0.21	0.05
Native Tree Ferns	8.3	1.1	9.7	1.2	9.4	1.0	0.35	0.90	0.41
Native Shrubs	0.4	0.1	0.9	0.4	1.1	0.4	0.16	0.66	0.18
Native Ferns	10.1	1.5	20.2	2.9	20.2	2.7	0.00	0.88	0.00
Native Herbs/Vines/Sedges	0.8	0.3	1.8	0.6	1.8	0.4	0.03	0.46	0.01
Total Native Vegetation	21.3	1.8	36.7	2.9	35.4	2.8	0.00	0.70	0.00
Alien Shrubs	1.0	0.4	1.6	0.5	2.3	0.7	0.14	0.19	0.04
Alien Ferns	0.1	0.1	0.0	0.0	0.1	0.1	0.37	---	0.37
Alien Herbs/Vines/Sedges	1.2	0.4	2.9	0.7	4.7	1.4	0.10	0.42	0.10
Alien Grasses	1.8	1.8	2.7	1.3	3.9	2.1	0.10	0.42	0.10
Total Alien Vegetation	2.4	0.8	7.2	1.9	11.0	2.5	0.01	0.03	0.00
Total Vegetation	23.8	1.9	44.0	3.2	46.4	3.1	0.01	0.26	0.01

Table 2. Changes in absolute percent cover of vegetation by plant categories 1-2 m height in 16, 10x10 m plots in `Ōla`a-Koa Rain Forest Unit, HAVO.

	1991 1-2m mean	se	1993 1-2m mean	se	1998 1-2m mean	se	P values 1991-1993	P values 1993-1998	P values 1991-1998
Native Trees	3.5	0.7	4.8	1.0	3.1	0.7	0.06	0.10	0.78
Native Tree Ferns	13.0	0.7	20.6	1.1	18.6	1.7	0.00	0.12	0.03
Native Shrubs	1.0	0.4	1.2	0.5	1.1	0.4	0.72	0.94	0.78
Native Ferns	1.2	0.2	1.6	0.6	5.0	1.4	0.92	0.01	0.00
Native Herbs/Vines/Sedges	0.0	0.0	0.1	0.1	0.0	0.0	1.00	1.00	1.00
Total Native Vegetation	18.7	2.3	28.1	1.6	27.8	1.6	0.00	0.96	0.00
Alien Shrubs	0.9	0.5	1.6	1.0	1.5	0.5	0.21	0.88	0.24
Alien Ferns	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
Alien Herbs/Vines/Sedges	0.2	0.1	0.6	0.3	1.0	0.4	0.45	0.34	0.45
Alien Grasses	0.0	0.0	0.0	0.0	0.8	0.5	1.00	0.18	0.18
Total Alien Vegetation	1.1	0.5	2.2	1.0	3.2	0.8	0.10	0.11	0.01
Total Vegetation	19.8	2.4	30.3	1.7	31.0	1.8	0.00	0.71	0.00

Table 3. Change in absolute cover of plant species <1 m height in 16, 10x10 m plots `Ōla`a-Koa Rain Forest Unit, HAVO.

	1990 <1m mean	se	1993 <1m mean	se	1998 <1m mean	se	P values 1991-1993	P values 1993-1998	P values 1991-1998
Native Trees									
Charpenteria obovata	0.1	0.1	0.0	0.0	0.0	0.0	1.00	1.00	1.00
Cheirodendron trigynum.	0.2	0.1	0.6	0.2	0.3	0.2	0.29	0.13	0.80
Coprosma spp.	0.6	0.2	1.6	0.6	1.2	0.3	0.06	0.91	0.07
Hedyotis terminalis	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
Ilex anamola	0.1	0.1	0.5	0.2	0.1	0.1	0.01	0.03	1.00
Metrosideros polymorpha	0.2	0.1	0.5	0.2	0.4	0.1	0.12	0.55	0.50
Myrsine lessertiana	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
Perrottetia sandwicensis	0.5	0.2	0.8	0.3	0.7	0.2	0.51	0.72	0.82
Subtotal	1.7	0.3	4.0	0.9	2.8	0.5	0.02	0.21	0.05
Native Tree Ferns									
Cibotium chamissoi	0.6	0.3	0.1	0.1	0.9	0.5	0.11	0.13	1.00
Cibotium glaucum	7.3	1.1	9.5	1.2	8.4	1.1	0.20	0.72	0.48
Cibotium menziesii	0.4	0.2	0.1	0.1	0.2	0.1	0.21	0.61	0.50
Sadleria cyathoides	0.0	0.0	0.0	0.0	0.0	0.0	---	1.00	1.00
Sadleria pallida	0.1	0.1	0.0	0.0	0.0	0.0	1.00	1.00	---
Total	8.3	1.1	9.7	1.2	9.4	1.0	0.35	0.90	0.41
Native Shrubs									
Broussasia arguta	0.2	0.1	0.2	0.2	0.1	0.1	0.59	0.37	0.37
Clermontia spp.	0.0	0.0	0.1	0.1	0.6	0.2	0.37	0.21	0.06
Cyrtandra spp.	0.0	0.0	0.0	0.0	0.1	0.1	1.00	0.36	0.18
Pipturus albidus	0.0	0.0	0.0	0.0	0.0	0.0	1.00	1.00	---
Rubus hawaiiensis	0.2	0.1	0.5	0.3	0.4	0.3	0.46	0.46	0.59
Vaccinium calycinum	0.0	0.0	0.1	0.0	0.1	0.1	0.79	0.28	0.53

Total	0.4	0.1	0.9	0.4	1.1	0.4	0.16	0.66	0.18
Alien Shrubs									
Rubus ellipticus	1.0	0.4	1.4	0.5	1.9	0.6	0.22	0.29	0.08
Rubus rosaefolius	0.1	0.1	0.2	0.2	0.4	0.3	0.18	0.20	0.18
Total	1.0	0.4	1.6	0.5	2.3	0.7	0.14	0.19	0.04
Native Ferns									
Asplenium spp.	1.2	0.3	1.2	0.2	1.4	0.2	1.00	0.24	0.46
Athyrium microphyllum	0.2	0.1	0.7	0.3	0.6	0.2	0.04	0.96	0.10
Diplazium sandichianum	5.8	0.9	13.6	2.0	13.0	2.4	0.00	0.64	0.01
Dryopteris spp.	0.3	0.2	0.2	0.1	0.6	0.2	1.00	0.18	0.06
Elaphoglossum hirtum	0.1	0.0	0.0	0.0	0.1	0.1	0.37	0.37	0.86
Grammitis spp.	0.0	0.0	0.0	0.0	0.1	0.1	---	1.00	1.00
Microlepia strigosa	0.7	0.3	1.4	0.9	1.0	0.4	0.80	0.40	0.89
Nephrolepis cordifolia	0.1	0.1	0.2	0.1	0.4	0.3	1.00	0.79	0.42
Pneumopteris sandwicensis	1.7	1.0	2.9	1.2	2.5	1.0	0.14	0.42	0.10
Polypodium pellucidum	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
Pseudogopteris	0.0	0.0	0.0	0.0	0.1	0.1	---	1.00	1.00
Psilotum spp.	0.0	0.0	0.1	0.1	0.0	0.0	0.79	0.79	1.00
Pteris excelsia	0.1	0.1	0.0	0.0	0.0	0.0	1.00	---	1.00
Sphenomeris chinensis	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
Hymenoptera Family	0.1	0.1	0.0	0.0	0.6	0.2	1.00	0.02	0.01
Subtotal	10.1	1.5	20.2	2.9	20.2	2.7	0.00	0.88	0.00
Alien Ferns									
Athyriopsis japonica	0.0	0.0	0.0	0.0	0.1	0.1	---	---	---
Cristella cyanoides	0.1	0.1	0.0	0.0	0.0	0.0	0.37	---	0.37
Subtotal	0.1	0.1	0.0	0.0	0.1	0.1	0.37	---	0.37
Native Herbs/Vines/Sedges									
Alyxia olivaeformis	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
Astelia menzeisii	0.0	0.0	0.0	0.0	0.0	0.0	1.00	---	1.00

Freycinatia arborea	0.1	0.1	0.0	0.0	0.0	0.0	1.00	1.00	1.00
Peperomia spp. (Tall one)	0.2	0.1	0.2	0.1	0.5	0.2	1.00	0.03	0.04
Stenogyne calyminthoides	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
Uncinia uncinata	0.6	0.2	1.6	0.5	1.3	0.4	0.00	0.79	0.02
Subtotal	0.8	0.3	1.8	0.6	1.8	0.4	0.03	0.46	0.01
Alien Herbs/Vines/Sedges									
Ageratina riparia	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
Anenome hupuensis	0.0	0.0	0.1	0.1	0.0	0.0	1.00	1.00	1.00
Cardamine flexuosa	0.1	0.1	0.2	0.2	0.0	0.0	0.58	0.18	1.00
Cuphea carthogenesis	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
Cyprus halpans	0.2	0.1	0.0	0.0	0.8	0.8	1.00	1.00	1.00
Drymaria cordata	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
Erechtites valerinafolia	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
Hedychium gardnerianum	0.3	0.2	0.8	0.4	3.4	1.1	0.01	0.01	0.06
Hypericum mutilatum	0.1	0.1	0.0	0.0	0.0	0.0	1.00	---	1.00
Juncus effusus	0.0	0.0	0.2	0.2	0.0	0.0	1.00	1.00	---
Ludwigia	0.1	0.1	0.0	0.0	0.0	0.0	1.00	---	1.00
Passiflora mollissma	0.0	0.0	0.6	0.4	0.1	0.1	0.18	0.10	1.00
Phaius tankervillae	0.0	0.0	0.0	0.0	0.0	0.0	---	1.00	1.00
Polygonum punctatum	0.5	0.3	1.0	0.5	0.4	0.3	0.01	0.10	0.89
Solanum nigrescens	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
Subtotal	1.2	0.4	2.9	0.7	4.7	1.4	0.10	0.42	0.10
Alien Grasses									
Ehrharta stipoides	0.0	0.0	1.2	0.8	0.7	0.7	0.37	0.37	1.00
Holcus lanatus	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
Setaria palmaefolia	0.1	0.1	1.5	0.9	3.2	1.9	0.18	0.10	0.10
Subtotal	1.8	1.8	2.7	1.3	3.9	2.1	0.10	0.42	0.10

Mosses, Lichens, Liverworts	7.5	1.1	12.1	1.3	8.4	0.7	na	na	na
Litter	64.6	2.5	41.0	2.0	47.2	2.5	na	na	na
Soil	4.3	0.8	3.2	0.5	2.0	0.5	na	na	na
Rock	0.0	0.0	0.0	0.0	0.0	0.0	na	na	na
Total Native Vegetation	21.3	1.8	36.7	2.9	35.4	2.8	0.00	0.70	0.00
Total Alien Vegetation	2.4	0.8	7.2	1.9	11.0	2.5	0.01	0.03	0.00
Total Vegetation	23.8	1.9	44.0	3.2	46.4	3.1	0.01	0.26	0.01

Table 4. Changes in absolute percent cover of plant species 1-2 m height in 16, 10x10 m plots in `Ōla`a-Koa Rain Forest Unit, HAVO.

	1991 1-2m		1993 1-2m		1998 1-2m		P values		
	mean	se	mean	se	mean	se	1991-1993	1993-1998	1991-1998
Native Trees									
Charpenteria obovata	0.1	0.1	0.0	0.0	0.0	0.0	---	---	---
Cheirodendron trigynum.	0.5	0.2	1.1	0.6	0.7	0.3	0.04	0.26	0.33
Coprosma spp.	0.8	0.4	1.1	0.3	0.7	0.2	0.41	0.29	0.80
Hedyotis terminalis	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
Ilex anamola	0.1	0.1	0.4	0.2	0.1	0.1	0.35	0.20	0.86
Metrosideros polymorpha	0.4	0.2	0.4	0.2	0.3	0.1	0.78	0.80	0.50
Myrsine lessertiana	0.0	0.0	0.0	0.0	0.1	0.1	---	1.00	1.00
Perrottetia sandwicensis	1.6	0.5	1.8	0.5	1.3	0.5	0.42	0.12	0.56
Subtotal	3.5	0.7	4.8	1.0	3.1	0.7	0.06	0.10	0.78
Native Tree Ferns									
Cibotium chamissoi	0.8	0.4	0.6	0.4	1.4	0.6	0.59	0.08	0.33
Cibotium glaucum	11.4	1.7	19.5	1.2	16.8	1.8	0.00	0.05	0.02
Cibotium menziesii	0.8	0.4	0.5	0.3	0.4	0.3	0.68	0.53	0.60
Sadleria cyathoides	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
Sadleria pallida	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
Total	13.0	0.7	20.6	1.1	18.6	1.7	0.00	0.12	0.03
Native Shrubs									
Broussasia arguta	0.2	0.1	0.0	0.0	0.1	0.1	0.37	0.37	0.37
Clermontia spp.	0.0	0.0	0.0	0.0	0.3	0.2	1.00	0.18	0.27
Cyrtandra spp.	0.0	0.0	0.0	0.0	0.0	0.0	1.00	1.00	1.00
Pipturus albidus	0.1	0.1	0.0	0.0	0.2	0.1	1.00	0.42	0.59
Rubus hawaiiensis	0.6	0.3	1.1	0.5	0.5	0.3	0.16	0.11	1.00
Vaccinium calycinum	0.2	0.1	0.0	0.0	0.1	0.1	0.59	1.00	0.79
Total	1.0	0.4	1.2	0.5	1.1	0.4	0.72	0.94	0.78

Alien Shrubs									
Rubus ellipticus	0.9	0.5	1.6	1.0	1.5	0.5	0.28	0.81	0.24
Rubus rosaefolius	0.0	0.0	0.0	0.0	0.0	0.0	1.00	---	1.00
Total	0.9	0.5	1.6	1.0	1.5	0.5	0.21	0.88	0.24
Native Ferns									
Asplenium spp.	0.3	0.1	0.0	0.0	0.3	0.1	0.21	0.09	1.00
Athyrium microphyllum	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
Diplazium sandichianum	0.7	0.3	1.3	0.6	4.6	1.4	0.76	0.00	0.01
Dryopteris spp.	0.0	0.0	0.0	0.0	0.2	0.2	---	1.00	1.00
Elaphoglossum hirtum	0.0	0.0	0.1	0.1	0.0	0.0	1.00	1.00	1.00
Grammitis spp.	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
Microlepia strigosa	0.0	0.0	0.0	0.0	0.1	0.1	1.00	1.00	---
Nephrolepis cordifolia	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
Pneumopteris sandwicensis	0.1	0.1	0.1	0.1	0.0	0.0	1.00	1.00	0.37
Polypodium pellucidum	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
Pseudogopteris	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
Psilotum spp.	0.0	0.0	0.0	0.0	0.1	0.1	1.00	1.00	1.00
Pteris excelsia	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
Sphenomeris chinensis	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
Hymenoptera Family	0.1	0.1	0.0	0.0	0.0	0.0	1.00	1.00	---
Subtotal	1.2	0.2	1.6	0.6	5.0	1.4	0.92	0.01	0.00
Alien Ferns									
Athyriopsis japonica	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
Cristella cyanoides	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
Subtotal	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
Native Herbs/Vines/Sedges									
Alyxia olivaeformis	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
Astelia menzeisii	0.0	0.0	0.0	0.0	0.0	0.0	---	1.00	1.00
Freycinatia arborea	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
Peperomia spp. (Tall one)	0.0	0.0	0.1	0.1	0.0	0.0	1.00	---	---

Stenogyne calyminthoides	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
Uncinia uncinata	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
Subtotal	0.0	0.0	0.1	0.1	0.0	0.0	1.00	1.00	1.00
Alien Herbs/Vines/Sedges									
Ageratina riparia	0.0	0.0	0.0	0.0	0.0	0.0	1.00	---	---
Anenome hupuensis	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
Cardamine flexuosa	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
Cuphea carthogenesis	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
Cyprus halpans	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
Drymaria cordata	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
Erechtites valerinafolia	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
Hedychium gardnerianum	0.1	0.1	0.2	0.1	0.9	0.4	0.37	0.04	0.04
Hypericum mu	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
Juncus effusus	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
Ludwigia	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
Passiflora mollissma	0.2	0.2	0.4	0.3	0.1	0.1	0.79	0.83	0.42
Phaius tankervillae	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
Polygonum punctatum	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
Solanum nigrescens	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
Subtotal	0.2	0.1	0.6	0.3	1.0	0.4	0.45	0.34	0.45
Alien Grasses									
Ehrharta stipoides	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
Holcus lanatus	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
Setaria palmaefolia	0.0	0.0	0.0	0.0	0.8	0.5	1.00	0.18	0.18
Subtotal	0.0	0.0	0.0	0.0	0.8	0.5	1.00	0.18	0.18
Total Native Vegetation	18.7	2.3	28.1	1.6	27.8	1.6	0.00	0.96	0.00
Total Alien Vegetation	1.1	0.5	2.2	1.0	3.2	0.8	0.10	0.11	0.01
Total Vegetation	19.8	2.4	30.3	1.7	31.0	1.8	0.00	0.71	0.00

Table 5. Frequency of alien plant species in 16, 10x10 m plots, `Ōla`a-Koa Rain Forest Unit, HAVO.

Species	% Frequency 1991	1993	1998	P value
Alien Shrubs				
Rubus argutus	12.5	12.5	0.0	0.82
Rubus ellipticus	81.3	81.3	93.8	0.67
Rubus rosaefolius	12.5	12.5	18.8	0.99
Alien Ferns				
Athyriopsis japonica	12.5	12.5	25.0	0.94
Cristella cyaneoides	6.3	6.3	0.0	0.96
Alien herbs/sedges/vines				
Ageratina riparia	0.0	6.3	12.5	0.83
Anenome hepehensis	6.3	6.3	6.3	1.00
Cardamine flexuosa	6.3	12.5	0.0	0.83
Cuphea carthagenesis	0.0	0.0	6.3	0.84
Cyperus halpans	6.3	0.0	6.3	0.96
Drymaria spp.	0.0	6.3	0.0	0.84
Erechtites valaerianifolia	0.0	0.0	6.3	0.84
Hedychium gardnerianum	43.8	31.3	81.3	0.12
Hypericum mutilatum	6.3	0.0	0.0	0.84
Juncus effusus	0.0	6.3	0.0	0.84
Ludwigia palustris.	6.3	0.0	0.0	0.84
Passiflora mollissima	75.0	81.3	40.0	0.16
Phaius tankervillae	0.0	0.0	6.3	0.84
Polygonum punctatum	25.0	50.0	62.5	0.45
Alien Grasses				
Ehrharta stipoides	6.3	12.5	6.3	0.99
Holcus lanatus	0.0	0.0	6.3	0.84
Setaria palmaefolia	12.5	18.8	31.3	0.88

Table 6. Average number of native shrub and subshrub species in 15, 10x10 m plots, \`Ōla\`a-Koa Rain Forest Unit, HAVO.

		1991		1993		1998		P values		
		Mean	SE	Mean	SE	Mean	SE	1991-1993	1993-1998	1991-1998
Broussasia arguta										
<1 cm dbh	<10 cm hgt	0.0	0.0	0.0	0.0	0.0	0.0	----	----	----
	>10 cm hgt	0.2	0.1	0.8	0.3	0.5	0.3	0.10	0.36	1.00
1-5 cm dbh		0.8	0.3	0.4	0.3	0.6	0.4	0.18	0.37	1.00
>5 cm dbh		0.1	0.1			0.1	0.1			----
Clermontia spp.										
<1 cm dbh	<10 cm hgt	0.9	0.3	0.3	0.1	1.5	0.6	0.22	0.18	0.86
	>10 cm hgt	1.0	0.4	3.3	0.7	2.4	0.5	0.04	0.62	0.13
1-5 cm dbh		1.3	0.4	0.4	0.2	1.2	0.4	0.03	0.06	0.53
>5 cm dbh		0.0	0.0			0.1	0.1			1.00
Cyanea pilosa										
<1 cm dbh	<10 cm hgt	0.2	0.2	0.0	0.0	0.0	0.0	1.00	----	1.00
	>10 cm hgt	0.0	0.0	0.0	0.0	0.0	0.0	1.00	----	1.00
1-5 cm dbh		0.0	0.0	0.0	0.0	0.0	0.0	1.00	----	1.00
>5 cm dbh		0.0	0.0			0.0	0.0			----
Cyrtandra spp.										
<1 cm dbh	<10 cm hgt	0.2	0.2	0.0	0.0	0.2	0.1	1.00	0.37	1.00
	>10 cm hgt	0.2	0.1	0.1	0.1	0.3	0.2	1.00	0.37	0.59
1-5 cm dbh		0.1	0.1	0.2	0.1	0.4	0.2	1.00	1.00	1.00
>5 cm dbh		0.0	0.0			0.0	0.0			----
Freycinatia arborea										
<1 cm dbh	<10 cm hgt	0.0	0.0	0.0	0.0	0.0	0.0	----	----	----
	>10 cm hgt	0.1	0.1	0.0	0.0	0.0	0.0	----	----	----
1-5 cm dbh		0.0	0.0	0.0	0.0	0.0	0.0	----	----	----
>5 cm dbh		0.0	0.0			0.0	0.0	----	----	----
Pipturus albidus										
<1 cm dbh	<10 cm hgt	0.0	0.0	0.4	0.3	0.0	0.0	1.00	1.00	----
	>10 cm hgt	0.0	0.0	0.4	0.3	0.1	0.1	1.00	0.79	0.37
1-5 cm dbh		0.0	0.0	0.3	0.1	0.5	0.2	0.10	0.46	0.18
>5 cm dbh		0.0	0.0			0.1	0.1			1.00
Rubus hawaiiensis										
<1 cm dbh	<10 cm hgt	0.7	0.3	0.3	0.1	0.3	0.2	0.58	1.00	00.46
	>10 cm hgt	0.4	0.1	1.3	0.5	1.0	0.4	0.08	0.80	0.04
1-5 cm dbh		0.8	0.4	0.4	0.2	0.5	0.2	0.23	0.86	0.46
>5 cm dbh		0.1	0.1			0.1	0.1			1.00

Touchardia spp.										
<1 cm dbh	<10 cm hgt	0.0	0.0	0.0	0.0	0.0	0.0	----	----	----
	>10 cm hgt	0.0	0.0	0.0	0.0	0.0	0.0	----	----	----
1-5 cm dbh		0.1	0.1	0.0	0.0	0.0	0.0	----	----	----
>5 cm dbh		0.0	0.0			0.0	0.0			----
Vaccinium calycinum										
<1 cm dbh	<10 cm hgt	0.5	0.3	0.2	0.1	2.2	1.1	0.086	0.18	0.45
	>10 cm hgt	0.7	0.4	3.0	1.0	5.4	2.0	0.02	0.24	0.01
1-5 cm dbh		0.0	0.0	0.0	0.0	0.3	0.2	----	1.00	1.00
>5 cm dbh		0.0	0.0			0.0	0.0			----
Total Native Shrubs										
<1 cm dbh	<10 cm hgt	2.4	0.6	1.1	0.4	4.1	1.2	0.05	0.13	0.80
	>10 cm hgt	2.8	0.6	8.7	1.6	9.6	2.4	0.00	1.00	0.00
1-5 cm dbh		3.5	0.7	1.5	0.4	3.0	0.8	0.04	0.05	0.21
>5 cm dbh		0.1	0.1			0.3	0.1			0.59

Table 7. Average number of alien woody plant species in 15, 10x10 m plots, `Ōla`a-Koa Rain Forest Unit, HAVO.

		1991		1993		1998		P values		
		Mean	SE	Mean	SE	Mean	SE	1991-1993	1993-1998	1991-1998
Alien Shrubs										
Budleja asiatica										
<1 cm dbh	<10 cm hgt	0.0	0.0	0.0	0.0	0.0	0.0	----	----	----
	>10 cm hgt	0.0	0.0	0.1	0.1	0.0	0.0	----	----	----
1-5 cm dbh		0.2	0.2	0.3	0.3	0.0	0.0	1.00	----	1.00
>5 cm dbh		0.0	0.0			0.0	0.0			----
Rubus argutus										
<1 cm dbh	<10 cm hgt	0.1	0.1	0.0	0.0	0.3	0.2	1.00	----	1.00
	>10 cm hgt	0.0	0.0	0.0	0.0	0.2	0.2	0.37	----	0.37
1-5 cm dbh		0.0	0.0	0.0	0.0	0.0	0.0	1.00	----	1.00
>5 cm dbh		0.0	0.0			0.0	0.0			----
Rubus ellipticus										
<1 cm dbh	<10 cm hgt	1.5	0.7	8.4	2.9	3.6	1.1	0.03	0.17	0.72
	>10 cm hgt	0.9	0.2	11.4	4.0	9.2	2.3	0.01	0.72	0.00
1-5 cm dbh		1.1	0.6	0.9	0.6	2.6	0.9	0.12	0.17	1.00
>5 cm dbh		0.1	0.1			0.3	0.2			0.59
Rubus rosaefolius										
<1 cm dbh	<10 cm hgt	0.2	0.2	0.5	0.3	0.5	0.4	0.37	0.79	1.00
	>10 cm hgt	0.6	0.5	2.7	1.5	2.4	1.2	0.10	0.86	0.18
1-5 cm dbh		1.1	0.9	0.0	0.0	0.0	0.0	0.37	----	0.37
>5 cm dbh		0.0	0.0			0.0	0.0			----
Total Alien Shrubs										
<1 cm dbh	<10 cm hgt	1.8	0.7	8.8	3.0	4.4	1.2	0.03	0.13	0.91
	>10 cm hgt	1.6	0.6	14.3	4.4	12.1	2.6	0.00	0.76	0.00
1-5 cm dbh		2.4	1.2	1.1	0.6	2.6	0.9	0.06	0.06	0.81
>5 cm dbh		0.1	0.1			0.3	0.2			0.59
Alien Vines										
Passiflora mollissima										
<1 cm dbh	<10 cm hgt	7.3	3.6	0.6	0.3	0.2	0.1	0.06	0.09	0.04
	>10 cm hgt	20.7	13.8	1.8	0.6	0.5	0.2	0.58	0.04	0.01
1-5 cm dbh		1.0	0.7	0.3	0.3	0.0	0.0	0.30	1.00	0.18
>5 cm dbh		0.0	0.0			0.0	0.0			----

Table 8. Average number of epiphytic and terrestrial native woody seedlings (< 1 cm basal diameter) in 15, 10x10 m plots, \`Ōla\`a-Koa Rain Forest Unit, HAVO (1998).

	Epiphytic		Terrestrial		P values
Species	Mean	SE	Mean	SE	
Cheirodendron trigynum	25.6	13.5	0.7	0.4	0.00
Clermontia spp.	3.3	0.8	0.2	0.1	0.00
Coprosma spp.	13.8	4.3	33.6	10.1	0.07
Metrosideros polymorpha	40.3	16.7	0.1	0.1	0.00
Perrottetia sandwicensis	6.4	3.8	7.8	2.0	0.13