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Responses of native and invasive plant species to selective logging in an *Acacia koa-Metrosideros polymorpha* forest in Hawai‘i

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Abstract

Questions: Is the introduced timber species *Fraxinus uhdei* invasive in Hawai‘i? Has logging disturbance facilitated the spread of *Fraxinus* and other alien species?
Location: Windward Mauna Kea, island of Hawai‘i.
Methods: We surveyed 29 plots which were established before selective logging of the native tree *Acacia koa* in 1971 to determine if *Fraxinus* spread beyond the borders of an existing plantation and if other alien species increased. We created gaps in the canopy of the *Fraxinus* plantation and measured seed rain and regeneration, and we sampled foliar and soil nutrients inside and around the plantation.
Results: Basal area of *Fraxinus* increased from 0.7 $m^2.ha^{-1}$ in 1971 to 10.8 $m^2.ha^{-1}$ in 2000. *Fraxinus* was not found in plots that were located more than 500 m from those where it occurred in 1971 except along a road. Basal area of *Acacia koa* decreased after logging but subsequently recovered. Occurrence of the alien vine *Passiflora tarminiana* and alien grass *Ehrharta stipoides* decreased. Seedling regeneration of *Fraxinus* was prolific in gaps but did not occur under the canopy. Basal area of *Fraxinus* did not correlate with soil nutrient concentrations.
Conclusions: *Fraxinus* was able to regenerate following logging more rapidly than native tree species. Basal area growth of *Fraxinus* was great enough to offset a decline in native trees and cause an increase in forest productivity. If the *Fraxinus* plantation is harvested, managers should plan ways of favoring regeneration of the native *Acacia* which is more valuable both for timber and for conservation.

Keywords: *Cibotium;* Disturbance; *Ehrharta stipoides; Fraxinus uhdei; Passiflora tarminiana;* Tropical ash, Tree fern; Tropical island.

Nomenclature: Wagner et al. (1999, 2005) for vascular plants; Palmer (2003) for ferns.

Introduction

The worldwide phenomenon of plant invasions is particularly acute in Hawai‘i. Hawaiian forests evolved from a few chance introductions of species to the most isolated land mass on earth (Carlquist 1980). The resulting native plant communities are relatively low in diversity and are particularly vulnerable to invasion by non-native, human-introduced species (Stone et al. 1992). Hawaii's flowering plant flora today consists of almost as many alien species (47%) as native species (53%) (Wagner et al. 1999). As a result, effective forest management in Hawai‘i requires constant efforts to keep non-native species in check.

Few Hawaiian tree species are commercially valuable; *Acacia koa* Gray is a notable exception (Elevitch et al. 2006). The most common native tree found on all major islands in both wet and mesic forests, *Metrosideros polymorpha* Gaud., is generally unsuited for timber because of its very hard, dense, and unstable wood (Little & Skolmen 1989). To make up for the lack of native timber resources, land managers introduced hundreds of non-native tree species to the Hawaiian islands (Nelson 1965). Some of these species have since proven to be invasive (Stone et al. 1992), and the native *Acacia koa* has increased greatly in value since 1990.

One introduced timber species is *Fraxinus uhdei* (*Oleaceae*) (tropical ash), a deciduous tree native to uplands (800 to 3000 m in elevation) in Mexico and Guatemala (Francis 1990). *Fraxinus uhdei* was introduced to Hawai‘i in the late 1800s and was once considered one of the most promising species for plantation forestry because of its fast initial growth rate (Carlson & Bryan 1963) and high-quality wood (Skolmen 1974). Later, foresters detected some pitfalls such as a tendency toward lodging and poor bole form (Walters & Wick 1973) and very uneven growth rates across sites (Whitesell 1976). *Fraxinus* also has shown a tendency to spread into the native forests where it competes with the highly valuable native *Acacia koa*. Invasion by *Fraxinus* has been observed in the Kamakou Preserve on the island of Moloka‘i (Houck 1987; Tunison 1995), in the Waikamoi Preserve on the island of Maui (Holt 1992), and in the Hōnaunau Forest on the southwestern slopes of Mauna Loa (Ares & Fownes 2001). Naturally regenerating stands of *Fraxinus* also have been found in Hawai‘i Volcanoes National Park (Tunison 1992) and Waiākea Forest Reserve on the island of Hawai‘i, and in the Honouliuli Forest Reserve on the island of O‘ahu (Restom-Gaskill 2004). Smith (1985) included *Fraxinus* in his list of the 87 most invasive plant species in Hawai‘i.

Other widespread invaders of the Hawaiian forest include *Passiflora tarminiana* Coppens & Barney (syn. *Passiflora mollissima* (Kunth) L. H. Bailey [misapplied]), a vine originally introduced into Hawai‘i from the Andean highlands for ornamental purposes and for its edible fruit (LaRosa 1992). It has widely naturalized and because it can form dense mats covering tree crowns it has been considered one of the major threats to the Hawaiian forest (Cuddihy & Stone 1990). *Ehrharta stipoides* is a shade-tolerant alien grass that can form dense stands in the understory of native forests and inhibit regeneration of native species (Denslow et al. 2006).

We studied how an established *Fraxinus* plantation and other alien plant species were affecting an adjacent native Hawaiian forest that had been selectively logged for *Acacia* in the early 1970s. We hypothesized that (1) *Fraxinus* was spreading into the native forest from the original plantation into forest gaps created by logging and natural processes (2) *Fraxinus* was out-competing the native tree species and suppressing both native and alien forest understory vegetation, and (3) the spread of *Fraxinus* was related to soil nitrogen, as *Fraxinus* has been shown to be N-limited in Hawai‘i uplands (Ares & Fownes 2001). We further hypothesized that (4) the disturbance created by logging facilitated invasion by *Passiflora* and *Ehrharta*.

Methods

Study site

The study area was in the Laupāhoehoe section of the Hilo Forest Reserve, located on the windward slope of Mauna Kea, on the island of Hawai‘i (19°55' N, 155°19' W), at elevations of 1430 to 1620 m (Fig. 1). Average annual rainfall is ca. 3000 mm (Giambelluca et al. 1986), annual average minimum temperature is 13 °C, and annual average maximum temperature is 21 °C (Anon. 2006; Juvik & Juvik 1998). Soils are classed as Acrudoxic Hydrudands (USDA classification), which are highly weathered forest soils developed in volcanic ash under conditions of high, year-round rainfall. These soils have high water retention capacity, low bulk density, are very strongly acid, and have high cation leaching (Anon. 2001). Local volcanic ash deposits are 3000 to 10 000 years old on the surface overlaying ‘a‘ā (blocky) lava (Wolfe & Morris 1996). Mueller-Dombois & Fosberg (1998) class the forest type as upper montane rain forest. The native forest overstory is composed primarily of large trees of *Metrosideros polymorpha* and *Acacia koa*. *Metrosideros* is a slow-growing, long-lived species, and in this forest it is the dominant canopy species that maintains itself by regenerating in gaps and disturbances, often on fallen logs (Friday & Herbert 2006; Scowcroft & Nelson 1976). *Acacia koa* is a light-demanding, early successional species, which persists in the canopy of mature forests but does not regenerate under the forest canopy (Elevitch et al. 2006; Whitesell 1990). The understory is most commonly dominated by the native tree species *Cheirodendron trigynum*, *Myrsine lessertiana*, and *Ilex anomala* (Cuddihy et al. 1982). The native raspberry *Rubus hawaiiensis* and the alien blackberry *Rubus argutus* are common in the shrub layer, as are tree ferns of the genus *Cibotium*. Forest groundcover is composed largely of native ferns in the genera *Diplazium*, *Dryopteris*, *Microlepia*, *Athyrium*, *Nothoperanema*, and *Asplenium* and the alien grass *Ehrharta stipoides* and alien broadleaf *Polygonum glabrum* (Cuddihy et al. 1982).

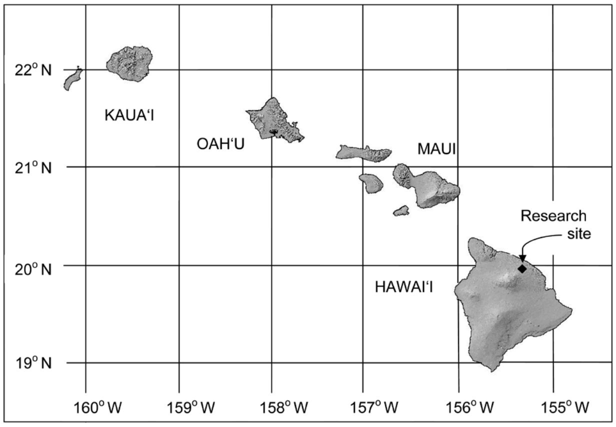

Fig. 1. Location of research site on the windward slope of Mauna Kea, Island of Hawai‘i.

Until the 1930s, cattle were driven between pastures to the north and south of the forest along a trail that runs along the elevational contour through the center of the forest. In an effort to protect the watershed and create an eventual source of local timber, a 25-ha *Fraxinus uhdei* plantation was established along the cattle drive trail in 1935. Trees were planted in rows or small blocks into disturbed areas in the existing forest where there were gaps in the canopy. There is no regular perimeter to the plantation.

The native forest above and below the plantation was selectively logged for *Acacia* from 1971 to 1973. An access road was constructed up from the main highway along the coast to the forest to allow for removal of logs. Where feasible, an area 40 to 50 m on either side of the road was soil scarified with a bulldozer to regenerate *Acacia*. Individual large trees were marked and felled with chainsaws, and the gaps where these trees were removed were also scarified. Skid trails were constructed throughout the forest to access the merchantable trees and remove the logs, which were skidded out with a bulldozer. Of the ground surface in the forest 41% was disturbed by the logging activities, and natural *Acacia* regeneration from buried seed banks was prolific in these areas (Scowcroft & Nelson 1976).

Experimental design

In 1971, after most of the road was surveyed but before the start of logging, permanent plots were set up in the forest to monitor the regeneration and growth of native forest trees, particularly *Acacia koa*, and to monitor invasion of alien pest species, particularly *Passiflora tarminiana* (Scowcroft & Nelson 1976). The rectangular 200-ha timber sale area was sampled using a stratified block design. First the area was divided into three equal blocks from lower to upper elevations. Each block was further divided into two strata: the road corridor and the rest of the forest. Four plots per road stratum and eight plots per forest stratum were randomly established within each block as follows. Starting points for five transects per block were randomly located along a fence line to the north of the study area, and straight-line transects were projected at right angles to the fence line and approximately along the elevational contour. Each transect was divided into as many contiguous plot segments (40.2 m long) as transect length allowed, and segments lying completely within a given block and stratum were identified. Segments for each set of five transects were consecutively numbered and eight segments within the forest stratum and four within the road stratum were randomly selected. In 1971 30 0.04-ha plots (40.2 m × 10.1 m) were established, and six additional plots were added in 1973 after the last portion of the access road was surveyed (Scowcroft & Nelson 1976).

The plots were organized into a nested design to separately sample overstory trees and tree ferns, intermediate layer trees, and understory plants. All trees greater than 12.7 cm diameter at breast height (DBH) and all tree ferns were measured in a rectangular main plot of 0.04 ha; all trees reaching a height of 60 cm were measured on two randomly chosen 0.004-ha sub-plots within the main plot, and all seedlings and herbaceous plants were tallied in 66 0.36-m^2 microplots along one edge of the main plot. Species and DBH were recorded for trees in the main and subplots; basal diameters of tree fern trunks were recorded in main plots. All plant species present were recorded in each of the 66 microplots regardless of size. Trees in the main plots were marked, numbered, and located with reference to the plot corner. Plots were re-surveyed in 1973 and 1976. In 2000, we re-inventoried 32 of the 36 plots in the block containing the access road, covering an area of 100 ha including both plantation and native forest (Fig. 2). We were unable to locate four plots, probably because there were no trees left alive from the time of the original survey. Because three of the 32 plots that we found were not established until 1973, we excluded them from our time sequence analyses.

Experimental gap creation in 2000

To test the hypothesis that *Fraxinus* regenerates better in forest canopy gaps than in shaded understory areas, we created two separate gaps in the *Fraxinus* plantation in 2000 by felling two large *Fraxinus* trees at each location. One gap measured ca. 12 m in diameter; the other was ca. 7 m in diameter. The forest canopy surrounding the gap was ca. 25 m tall. We established two square 5 m × 5 m plots in the center of each gap, two on the edge of the gap, and two under the full canopy of the plantation adjacent to each gap. The ground in the gaps was covered with litter but little vegetation was present with the exception of a few ferns. We fenced one of each pair of plots with 10 cm mesh hog wire to a height of 1.2 m to exclude feral pigs and feral cattle. We monitored seedling regeneration in each plot each month for one year. In each enclosure, we placed four 84 cm × 42 cm rectangular trays to monitor seed rain from June 2000 through May 2001. Seed was collected monthly and dried and weighted. Seed rain was not monitored in the unfenced plots. We measured optical leaf area index (LAI) for plots in gaps, at gap edges, and under forest canopy using a LICOR LI2000 Plant Canopy Analyzer (LICOR, Lincoln, NE, USA). Measurements were taken in September 2000, when the *Fraxinus* trees were fully in leaf, and in January 2001, when they were largely deciduous. As the canopy gaps were small, we used only data from the first two concentric rings of the plant canopy analyzer. Five readings were taken at each location and averaged.

Soil nutrient sampling

To investigate possible soil nutrient influences on the distribution and spread of *Fraxinus*, in 2001 we sampled soils and plant tissues inside and outside the *Fraxinus* plantation. We established sample points along the five transects in middle block of the original study, as these transects traversed the original plantation. For three transects, we established one point in native forest on either side of the plantation, one at the edge of either side of the plantation, and one in the middle of the plantation. For two transects, we only established one point in the native forest, one on the edge of the plantation, and one

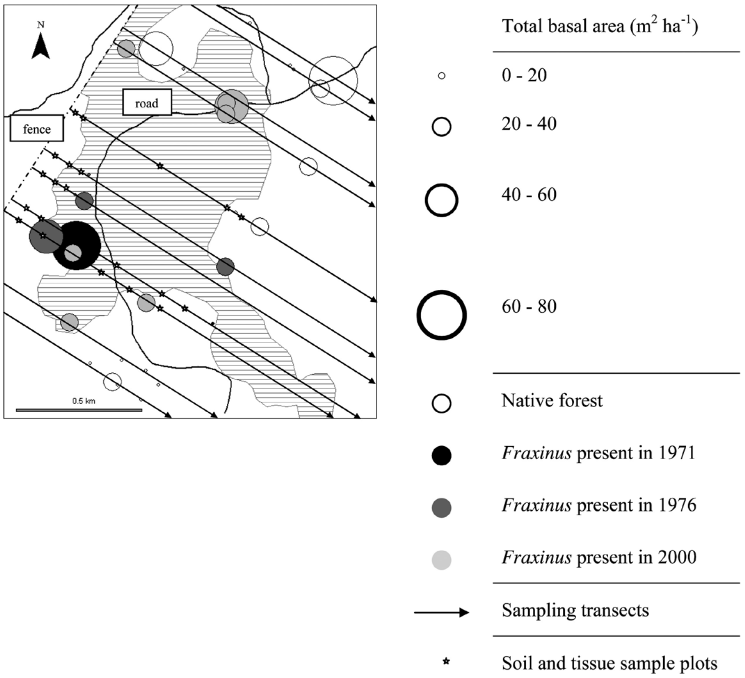

Fig. 2. Location, basal area, and composition of survey plots and soil and tissue sample plots in to perimeter of stand of *Fraxinus uhdei* (hatched the windward slopes of Mauna Kea, island of Hav of circles is proportional to basal area of the plots circles indicates the date of the first observation of in the plot.

inside the plantation. Thus we sampled a total of eight points in the native forest, eight on the edge of the plantation, and five inside the plantation. At each point, we measured the basal area and species of the surrounding trees by using a prism with a basal area factor of either 2.3 or 4.6 m^2.ha^{-1}. We sampled soils at depths of 0 to 5 cm and 5 to 20 cm. For points located on the edge of or within the plantation, we sampled fully expanded shade leaves from three to five *Fraxinus* seedlings.

Tissue samples were oven dried at 70 ºC and ground. Tissues and soils were analyzed by the University of Hawai‘i Agricultural Diagnostic Service Center laboratory. Soil samples were analysed for C and total N on a LECO C/N 2000 Analyzer (LECO Corp., St. Joseph, MI, USA, www.leco.com). Potassium, Ca, and Mg were extracted with 1N NH_4OAc, pH 7.0, and determined using inductively coupled plasma optical emission spectrometry. Phosphorus was extracted using a modified Truog method and P-concentration in extracts was determined by an automated colorimetric (molybdenum blue) method. Total N in leaf samples was determined using a LECO C/N 2000 analyzer and P, K, Ca, Mg, Mn, Fe, Cu, Zn, and B were determined in digests using inductively-coupled plasma optical emission spectrometry.

Statistical methods

Differences in basal area of different tree species between the 1976 and the 2000 inventories were tested using the a mixed model of repeated measures in SAS (Littell et al. 1996) with sampling date as fixed effect and plot as random effect.

For each main plot, we calculated the frequency of occurrence of each species in the 66 microplots. We analyzed for differences in occurrence among time intervals for each species by using a repeated measures ANOVA modified for uneven time intervals (Littell et al. 1996) on arcsine square root transformed data. We used Spearman Rank correlations to look for associations among the nine most common species in the understory plots (Ludwig & Reynolds 1988).

In the gap experiments, we used a one-way ANOVA to test for differences in seed rain and seedling recruitment among the three locations (gap, edge, and under the canopy) with two replications.

We regressed *Fraxinus* basal area against pH and soil nutrients at both soil sample depths for the new plots that we had established across the plantation. We used a one-way ANOVA to test for differences in leaf tissue nutrients between *Fraxinus* seedlings growing on the edge of the plantation and in the center of the plantation.

Statistical calculations were performed using SAS (www.sas.com) and Statistix for Windows (Analytical Software, www.statistix.com).

Results

The surveys tallied a total of 18 species of ferns (all native to Hawai‘i), 25 species of forbs (five native and 20 alien), eight species of grasses or sedges (two native and six alien), eight species of shrubs or vines

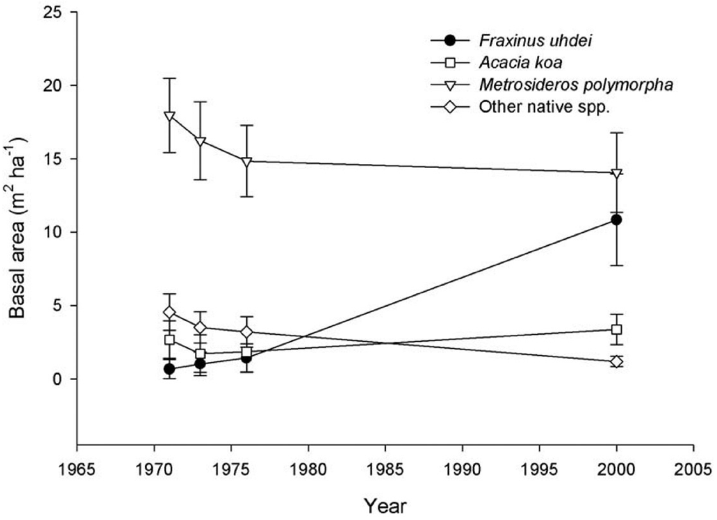

Fig. 3. Changes in basal area of the alien tree *Fraxinus uhdei* and the native trees *Acacia koa* and *Metrosideros polymorpha* after logging in a forest on the windward slopes of Mauna Kea, island of Hawai‘i. Error bars represent standard errors.

(five native and three alien), and nine species of trees (eight native and one alien) (App. 1.) Plots within and adjacent to the former plantation were dominated by *Fraxinus*, while plots further away were dominated by native plants (Fig. 2).

Forest structure and growth rates

While some plots were clearly in the center of the original *Fraxinus* plantation, as shown by straight rows of very large (up to 1.4 m diameter) trees, other plots included a mixture of either original or naturally regenerated *Fraxinus* and native forest species. Average diameter increment of *Fraxinus* trees that were present in the time interval from 1976 to 2000 was 0.8 $cm.a^{-1}$, four times that of *Metrosideros*, the most common native tree, at 0.2 $cm.a^{-1}$.

Total basal area of the forest decreased from 26 $m^2.ha^{-1}$in 1971 to 21 $m^2.ha^{-1}$ in 1976 after logging, although the change was not statistically significant. By 2000, though, total basal area of the forest had recovered to 29 $m^2.ha^{-1}$ ($p < 0.0005$). Almost all the increase in basal area was for *Fraxinus*, which increased from 0.7 $m^2.ha^{-1}$ in 1971 to 10.8 $m^2.ha^{-1}$ in 2000 ($p < 0.001$) (Fig. 3). Most of this increase was new regeneration and ingrowth rather than increase in DBH of trees present in 1976. Basal area of *Acacia* tended to decrease after logging and then recover to 3.4 $m^2.ha^{-1}$, although changes were not statistically significant. In contrast, basal area of *Metrosideros* tended to decline over the time period, although the change was again not statistically significant ($p = 0.06$). Basal area of other native trees, largely tree ferns *(Cibotium* spp.) declined by 74% from 1971 to 2000 ($p = 0.005$). Plot by plot, the basal area of *Fraxinus* was negatively correlated with basal area of *Acacia* and *Metrosideros* (Fig. 4). However, there were no correlations between plot by plot basal area increments of *Fraxinus* and basal area increments of *Acacia*, *Metrosideros*, or other native species (data not shown). Abundance of *Cibotium* spp. decreased from an average of 72 $stems.ha^{-1}$ in 1971 to 10 $stems.ha^{-1}$ in 2000.

Stem diameter distribution of *Fraxinus* showed many small individuals and relatively few large ones, indicating that *Fraxinus* is still prolifically regenerating in the forest (Fig. 5). In contrast, *Acacia* diameter size distribution showed mostly medium-sized individuals and few small ones, indicating a marked slowdown of regeneration.

Despite the prolific regeneration and rapid growth of *Fraxinus*, plots where it was present in 2000 were no more than 500 m away from plots where it was located in 1971 (Fig. 2). Individual trees, however, were found

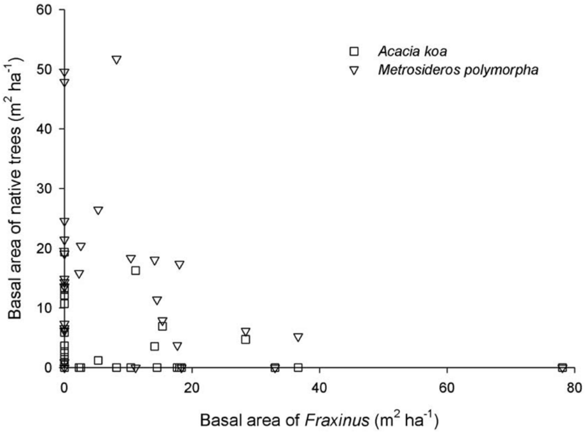

Fig. 4. Comparison of basal area of the alien tree *Fraxinus uhdei* with basal area of the native trees *Acacia koa* and *Metrosideros polymorpha* in the year 2000 in 32 0.04-ha plots on the windward slopes of Mauna Kea, island of Hawai‘i.

Table 1. Spearman Rank Correlations among frequencies of occurrences of trees and understory species in understory plots in a forest on the windward slopes of Mauna Kea, island of Hawai‘i.

	ASCA	ATMI	DRWA	**EHST**	**FRUH**	MEPO	NORU	PATA	**POGL**
ATMI	-								
DRWA	-	-							
EHST	-	-	0.38						
FRUH	-	– 0.41	– 0.46**	– 0.79**					
MEPO	-	-	-	-	-				
NORU	-	0.38	-	0.46**	-0.50**	-			
PATA	-	-	-	-	-	-	-		
POGL	-	0.44	0.44	0.68**	– 0.74**	-	-	-	
RUAR	0.39	0.39	-	0.39	– 0.41	-	0.42	-	0.44

ASCA = *Asplenium contiguum* (fern), ATMI = *Athyrium microphyllum* (fern), DRWA = *Dryopteris wallichiana* (fern), **EHST = *Ehrharta stipoides* (grass)**, **FRUH = *Fraxinus uhdei* (tree)**, MEPO = *Metrosideros polymorpha* (tree), NORU = *Nothoperanema rubiginosa* (fern), PATA = *Passiflora tarminiana* (vine), POGL = *Polygonum glabrum* (fern), **RUAR = *Rubus argutus* (shrub).** Alien species indicated in boldface type.
** denotes significance at $p < 0.01$; other values shown are significant at $p < 0.05$.

spread along several kilometers along the access road and have been found at many other sites in the forest, some several kilometers from the plantation.

Herbaceous-layer vegetation

The occurrence of invasive herbaceous species in the understory declined throughout the study (Fig. 6a). The occurrence of *Passiflora* decreased steadily and by 2000 it was 71% less than in 1971 ($p < 0.0001$). The alien grass *Ehrharta stipoides* increased in frequency after logging but then decreased by 44% between 1976 and 2000 ($p < 0.0001$). The alien herb *Polygonum glabrum* showed the same pattern, decreasing by 61% between 1973 and 2000 ($p < 0.0001$). Native ferns collectively showed the reverse pattern, increasing their occurrence by 109% in 2000 as compared with 1971 ($p < 0.001$).

Tree regeneration

Tree species, however, showed the opposite pattern of occurrence than that of herbaceous species, with *Fraxinus* greatly outnumbering the native species by 2000 (Fig. 6b). While *Acacia* occurrence showed a significant increase of 105% between 1971 and 1973 ($p = 0.001$), from 1973 to 2000 it declined by 73%

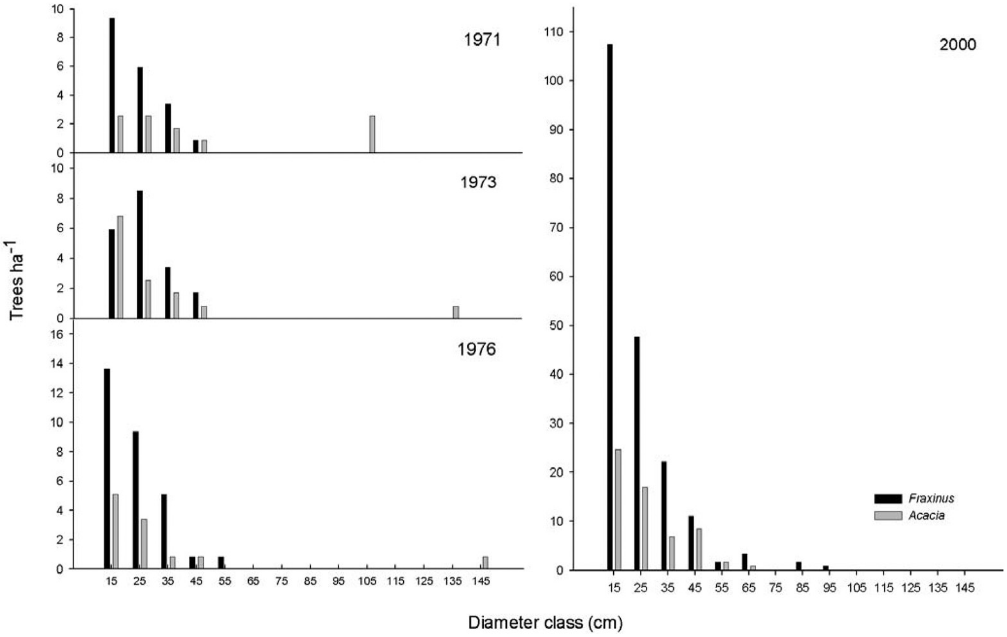

Fig. 5. Changes in stem diameter distributions for the native tree *Acacia koa* and the alien tree *Fraxinus uhdei* in a forest on the windward slopes of Mauna Kea, island of Hawai‘i.

($p < 0.0001$). There was a significant increase in the occurrence of *Fraxinus;* in 1971 it occurred in only 3% of the microplots compared with 16% in 2000 ($p = 0.017$). There were no significant differences in occurrence of *Metrosideros*. *Fraxinus* occurrence was generally negatively correlated with the occurrence both of alien species such as *Ehrharta*, *Polygonum*, and *Rubus,* and native ferns (Table 1). The occurrence of the alien grass *Ehrharta* was positively correlated with both *Polygonum* and *Rubus* and two species of native ferns.

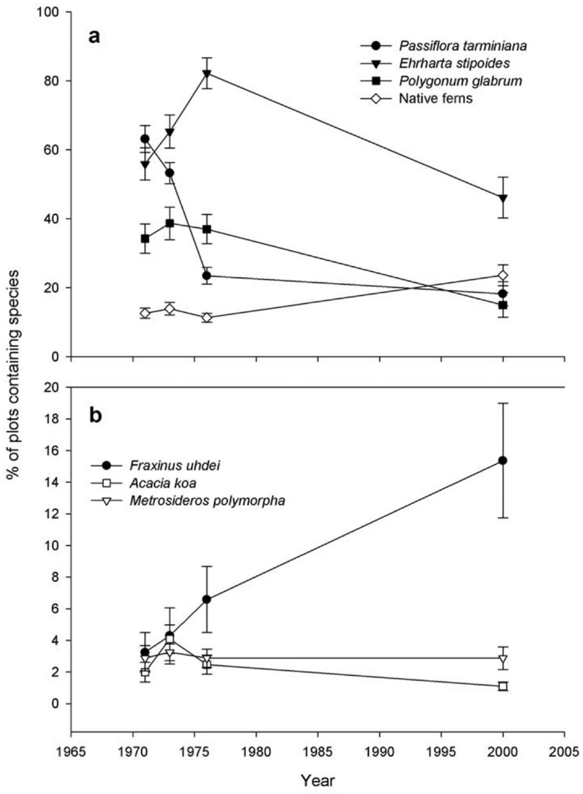

Fig. 6. Changes in occurrence of (**a**) the alien vine *Passiflora tarminiana*, alien grass *Ehrharta stipoides*, alien forb *Polygonum glabrum*, and native fern species, and (**b**) seedlings of the alien tree *Fraxinus uhdei* and the native trees *Acacia koa* and *Metrosideros polymorpha* in understory plots on the windward slopes of Mauna Kea, island of Hawai‘i. Error bars represent standard errors.

Seed rain and regeneration in experimental gaps

Optical leaf area index, as measured by the LICOR LI2000 Plant Canopy Analyzer, was four-fold less in the experimental gaps than under intact plantation canopies, irrespective of whether *Fraxinus* trees were in full leaf or not (Table 2). That LAI was not zero in the gaps was due to the lens sensing leaves and branches of trees at the edges of the relatively small gaps. *Fraxinus* seeds averaged 115 seeds.g^{-1}. Although seed rain was substantial under the plantation, up to 7800 seeds.m^{-2} in one plot over the year when it was collected, large amounts of seed also fell in the gaps, such that differences in seed rain among locations were not significant (Table 2). In contrast, recruitment of *Fraxinus* seedlings was prolific and was significantly greater in gaps than at the edge of gaps or under intact forest canopy. No *Fraxinus* seedlings emerged under the closed plantation canopy (Table 2). *Acacia* seedlings emerged in only one pair of fenced/unfenced plots and only in the open gap. On average, the number of *Acacia* seedlings recruited in the open gap plots was significantly less than the number of *Fraxinus* in the same plots (1200 *Acacia* seedlings. ha^{-1} vs. 8600 *Fraxinus* seedlings/ha; $p = 0.011$). Some mortality of *Acacia* seedlings was observed. Only three other seedlings of native tree species (two of *Coprosma* spec. and one *of Myrsine lessertiana*) were recruited during the course of the experiment. Keeping feral pigs out by fencing had no significant effect on the density of seedling regeneration, however, *Fraxinus* seedlings in unfenced plots were later observed to have been damaged by browsing, either by feral pigs or by feral cattle.

Soil and leaf nutrients

Soil pH values were moderately to strongly acidic, ranging from 6.0 to 3.8. Basal area of *Fraxinus* was positively related with soil pH at the 0-5 cm depth ($p < 0.0001$; $r^2 = 0.30$) and at the 5-20 cm depth ($p < 0.0001$, r^2

Table 2. Seed rain and seedling regeneration for the alien tree *Fraxinus uhdei* in artificial gaps created within a plantation on the windward slopes of Mauna Kea, island of Hawai‘i. Numbers within columns with the same letter do not differ significantly ($p > 0.05$). Leaf area index (LAI) was determined optically from center of plots.

Plot location	Seed rain	Seedling recruitment Unfenced	Seedling recruitment Fenced	LAI Sep	LAI Jan
	# m^{-2}	# m^{-2}	# m^{-2}	m^2.m^{-2}	m^2.m^{-2}
Gap	900a	1.1a	0.6a	1.7	1.1
Gap edge	3100a	0.3b	0.2b	5.7	2.5
Under canopy	5300a	0.0b	0.0b	7.2	4.4

= 0.36). There were no significant relationships between basal area of *Fraxinus* and soil C, N, P, K, Ca, or Mg at either soil depth (data not shown).

Fraxinus leaf-N-concentrations ranged from 1.7 to 2.2%. There were no significant differences in leaf tissue concentrations of N, P, Ca, Mg, Na, Mn, Fe, Cu, Zn, or B between seedlings in the center of the *Fraxinus* stand and seedlings at the invasion front at the edge of the plantation. Leaf-Ca-concentration was weakly correlated with soil extractable Ca ($p = 0.013$, $r^2 = 0.23$). There was no correlation between total soil N and leaf N concentrations or between soil extractable K, P, or Mg and leaf tissue concentrations of these elements (data not shown).

Discussion

Forest structure and growth rates

Total forest basal area increased over the course of the study despite the harvest of *Acacia koa*. Decreases in the basal area of native species were offset by increases in basal area of *Fraxinus*, indicating an overall increase in the plant biomass of the forest. This was likely because *Fraxinus* occupied growing space that the native trees were unable to exploit.

Native Hawaiian forests are composed of few species relative to mainland tropical forests (Mueller-Dombois & Fosberg 1998), which suggests that some ecological niches are not occupied. The emergent tree canopy probably is one such niche. While Hawaiian rain forests have many shade-tolerant understory tree species, they have limited height growth potential and seldom become part of the general forest canopy (Mueller-Dombois & Fosberg 1998). The native overstory in the study area was originally composed solely of *Metrosideros* and *Acacia*. With the introduction of *Fraxinus*, a third species had potential to become part of the forest canopy in this area.

Most of the spread of *Fraxinus* in the current study appears related to disturbance history. Logging opened the forest canopy and generated seedbeds where *Fraxinus* became established. Remnant skid roads could still be seen in the forest in 2000, and these were often colonized by young *Fraxinus* seedlings, provided they were close enough to a seed source. Denslow (2003) suggests that an important reason that alien species are able to establish in disturbed areas on tropical islands is that the native species are not able to take advantage of the resources released during a disturbance as quickly as can alien species. *Fraxinus* seedlings store more non-structural carbohydrates and N in their roots and stems than *Acacia* seedlings. Therefore, *Fraxinus* can survive defoliation better (Gleason & Ares 2004) and thus it can also recover better from partial damage during disturbances such as logging than the native *Acacia* seedlings.

While surveying the forest in 2000, we frequently encountered groves of *Fraxinus* trees, many over 20 cm DBH, which had been absent or too small to sample in 1976. In terms of both numbers of trees and biomass in the sample plots, *Fraxinus* is overwhelming the native trees in the forest. An apparently young, healthy *Fraxinus* tree could frequently be seen dominating the growing space of an apparently older *Acacia* or *Metrosideros* tree with a partial crown. Visually, *Fraxinus* has a much denser canopy than *Acacia* and *Metrosideros*, and these native trees do not seem to be able to compete with *Fraxinus* of similar size.

Many more plots had *Fraxinus* in 2000 than in 1971, but the farthest away of these was only 500 m from the borders of the original plantation. Plots farther than 500 m remained un-invaded, although little of the native forest beyond the logged area was sampled (Fig. 2). In our surveys, *Fraxinus* seedlings were rarely seen in intact native forest, although *Fraxinus* has been found in numerous locations across the forest as far as several km from the original plantation (C. Giardina, pers. comm.). The overall pattern is of dense *Fraxinus* regeneration in disturbed areas near the original plantation and scattered trees becoming established in intact native forest, sometimes at some distance from the seed source.

Dispersal of Fraxinus

The winged seeds of *Fraxinus* are windblown (Fournier 2002) but probably do not travel far once they fall below the canopy. However, eddies produced by strong winds can lift winged tree seeds above the canopy where they may be transported long distances (Horn et al. 2001). Prevailing easterly trade winds at the site run lengthwise to the plantation, but down slope winds occur at night as cool air flows down the mountain and local windstorms are common. Young *Fraxinus* seedlings were found at distances of up to several km along the road down slope from the stand. These seeds could have been distributed by water flowing along the road or by vehicles. Although no perennial streams run through the plantation, they do occur elsewhere in the forest and would facilitate seed dispersal (Thébaud & Debussche 1991).

Resilience of Acacia koa

Despite the invasion of *Fraxinus* over much of the area, *Acacia koa* proved resilient after the harvesting in the early 1970s. Basal area of *Acacia* more than doubled from 1976 to 2000 (Fig. 4). A single tree with a diameter of 142 cm constituted 74% of the *Acacia* basal area in 1976, however. This tree fell over in early 2000, shortly before the inventory (Fig. 5). The average basal area for *Acacia* in the other 28 plots averaged only 0.5 $m^2.ha^{-1}$ in 1976, after the harvest, but increased seven-fold to 3.5 m^2.ha^{-1} by 2000. The average basal area of 3.4 m^2.ha^{-1} for all 29 plots in this mixed forest thirty years after harvesting compares well with basal areas of 10 to 40 m^2.ha^{-1} in pure *Acacia* stands in other forests on leeward Hawai'i Island (Ares & Fownes 1999; Baker & Scowcroft 2005) and on Kaua'i (Harrington et al. 1995). Several small pure *Acacia* stands nearby, which probably regenerated after the same logging disturbances, vary from 26 to 48 m^2.ha^{-1} in basal area (Meason, Idol, and Friday, unpubl. data). Seedling recruitment probably did not limit the regeneration of *Acacia*. The 2400 *Acacia* seedlings.ha^{-1} recruited in the gap created in the *Fraxinus* canopy would certainly have been enough to reestablish an *Acacia* stand in the absence of invasive plant species or herbivores.

The native co-dominant Metrosideros and the tree fern understory

In contrast to the *Acacia*, basal area of *Metrosideros* did not recover after logging. While *Metrosideros* itself was not harvested, the tree is highly susceptible to physical damage (Friday & Herbert 2006). The decrease in basal area is probably due to a combination of mortality from damage during the logging operations and competition from *Fraxinus*.

We found only 14% of the number of tree ferns that were located in 1971, and most of the ferns disappeared after the 1976 survey. Tree ferns are long-lived species, and with typical growth rates of 2.0 to 3.2 cm.a^{-1} in height (Durand & Goldstein 2001). Feral pigs are abundant in the forest, as shown by large areas disturbed by their rooting, and it is known that feral pigs knock down tree ferns to get at the starchy pith in the stem. Feral cattle also were present in the forest. The loss of the tree fern understory may also increase the invasibility of the native forest, as the tree fern understory intercepts significant light that otherwise becomes available to alien grasses and tree seedlings (Cordell & Goldstein 1999). Burton & Mueller-Dombois found that removing the tree fern understory in a *Metrosideros*-dominated forest increased the light available to seedlings on the forest floor from 10.1% to 42.5% of incident radiation. Few tree ferns were found under a closed canopy of *Fraxinus*.

Herbaceous-layer vegetation and tree regeneration

When the *Acacia* harvest was first proposed in the 1970s, environmental concerns were raised about *Passiflora tarminiana*, a climbing vine that can persist in the forest understory and grow rapidly to take advantage of full light in gaps created by disturbances such as logging (LaRosa 1992). A bio-control agent, the leaf-spot fungus *Septoria passiflorae* was introduced at the site in 1996 and by 2000 was causing severe *Passiflora* defoliation and mortality in the forest nearby (Trujillo et al. 2001). The decline in the number of *Passiflora* stems counted in our survey, however, occurred between 1970 and 1976, before the introduction of the pathogen. Most likely the population of *Passiflora* rose after the forest canopy was opened during logging operations and declined as the canopy recovered. While climbing vines are often thought of as particularly aggressive invasive species, in the present case the invasive trees have had a much greater impact on the native ecosystem. In some forests in Hawai'i, one invasive species has been shown to facilitate invasion by others. For example, the nitrogen-fixing tree *Falcataria moluccana* has invaded native *Metrosideros* forest in east Hawai'i, increased N-cycling, and facilitated invasion of the understory tree *Psidium cattleianum* (Hughes & Denslow 2005). In contrast, we found that *Fraxinus* competed with and tended to exclude both native and alien plants, as shown by the negative correlations between *Fraxinus* and both native and alien understory plants (Table 1) and the decrease in density of understory alien plants over time (Fig. 6). The positive correlation observed between the alien grass *Ehrharta* and native ferns is probably caused by both being excluded by *Fraxinus*. We did not see evidence in our plots of *Ehrharta* excluding native species. In a grass removal study in an *Acacia* forest on the leeward side of Mauna Loa, Denslow et al. (2006) found that dense *Ehrharta* cover can inhibit the recruitment of native tree species. That forest, however, was not subject to invasion by an alien tree species that would dominate understory plants.

While feral pigs were abundant at our research site, they do not appear to limit regeneration of *Fraxinus*, as both fenced and unfenced plots supported abundant regeneration. Nor was bare soil necessary, as regeneration occurred on surfaces covered with leaf litter. It is possible that the dense carpet of *Ehrharta stipoides* in undisturbed native forest areas suppresses *Fraxinus* seed germination, and disturbances to the grass mat by feral pigs or might facilitate the spread of *Fraxinus*. Our data from the understory sampling plots showed a negative correlation between the frequency of *Fraxinus* occurrence and frequency of occurrence of *Ehrharta*, but either the *Fraxinus* could be shading out the grass or the *Fraxinus* seeds could be germinating where the grass is disturbed.

Forest light environment and shade tolerance

Regeneration of any kind under stands of *Fraxinus* is sparse partly because of the dense shade created by the high LAI of *Fraxinus* trees. Ares (1998) calculated a low value of 0.91 of the extinction coefficient (k) for *Fraxinus* on Hawai'i Island by regressing measured light transmittance against optically derived LAI. With an LAI of 7.2

$m^2.m^{-2}$, *Fraxinus* stands in this study would transmit less than 1% of incident radiation. In contrast, optical LAI in a nearby *Metrosideros*-dominated forest was only 3.0 (Herbert & Fownes 1999). With a light extinction coefficient of 0.56 (Herbert, unpublished data), the *Metrosideros* canopy would transmit 19% of incident radiation. Allometrically-determined LAI for *Acacia* in four nearby pure stands averaged 3.1 (Meason & Friday, unpublished data). Ares (1998) calculated a light extinction coefficient of 0.43 for *Acacia* from allometrically-derived leaf area and light transmittance, and Grace (1995) similarly calculated an extinction coefficient of 0.5 for *Acacia*. If an average *k*-value of 0.465 is used in calculations, the canopy in the *Acacia* stands with an LAI of 3.1 would be expected to transmit 24% of incident radiation. Thus, these native-dominated forest canopies allow more light to reach the forest understory, making the probability of successful establishment of regeneration greater.

Acacia is a shade-intolerant species (Whitesell 1990). Walters (1981) found that biomass of 160-day-old *Acacia* seedlings was reduced by 81% when grown at 19% of full light in comparison with seedlings grown at 70% of full light. *Acacia* seedlings grown under 25% of full light failed to develop the mature phyllodes characteristic of the species and retained juvenile leaves (Walters & Bartholomew 1990). *Fraxinus* seedlings have light compensation points, maximum CO_2 assimilation rates, and dark respiration rates that are similar to those of *Acacia* seedlings (Gleason & Ares 2004), and they are just as shade intolerant. The likelihood of seedling survival for either species in dense shade is low, as our gap data indicates. By 2007 there was abundant *Fraxinus* regeneration in the plots at the edges of the gaps we had created and some sparse regeneration under the canopy shade.

An earlier study of regeneration under a low elevation *Fraxinus* plantation on the eastern flank of Mauna Loa volcano also showed that *Fraxinus* did not regenerate beneath its own canopy (Harrington & Ewel 1997), and average LAI at their site (4.1 $m^2.m^{-2}$) was lower than at our site. *Metrosideros* germinants are shade-tolerant but seedlings need light exposure to grow into the sapling stage. Burton & Mueller-Dombois (1984) found high (57% per year) mortality in *Metrosideros* seedlings receiving less than 5% of incident radiation. Naturally-regenerated seedlings growing on the forest floor received an average of 10% of incident radiation, although the average light reaching the forest floor was only 1.9%. In our *study Metrosideros* failed to regenerate under *Fraxinus*. The failure was most likely due to a combination of lack of suitable seedbeds (i.e. moss-covered decomposed logs), frequent feral pig rooting, and low light. In the *Fraxinus* plantation studied by Harrington & Ewel (1997), *Metrosideros* and *Cibotium glaucum* were found in the understory, perhaps due to less frequent pig rooting or to increased light availability.

Soil and leaf nutrients

We found no relationship between soil nutrients and basal area of *Fraxinus*. There was a weak correlation between *Fraxinus* basal area and pH, likely because *Fraxinus* increased pH over time through deposition of Ca-rich leaf litter. *Fraxinus* stands ranging in age from 30 to 36 years in the Hōnaunau forest on the leeward side of the island of Hawai‘i had an average soil pH of 5.7 ± 0.12 at 0 to 15 cm depth compared to 5.0 ± 0.22 in naturally-regenerated koa stands ranging in age between 28 and 37 years growing on similar soils (A. Ares, pers. obs.). Although *Fraxinus* has been shown to accelerate nutrient cycling in our study area by increasing both litter fall and litter decomposition rates (Rothstein et al. 2004), *Fraxinus* basal area was not correlated with concentrations of any soil nutrient. Our study only measured total N in the soils and not N mineralization rates, which may have differed across the different soil series present in the study site and between sites with and without *Fraxinus* (Rothstein et al. 2004). In contrast to our results, *Fraxinus* basal area was positively related with soil and foliar N in the Hōnaunau forest, and *Fraxinus* responded to N additions (Ares & Fownes 2001). This response occurred, however, on shallow and stony Histosols whereas basal area of *Fraxinus* was markedly greater in Andisols derived from volcanic ash in the same area. The Andisols resemble the soils in the present study in Laupāhoehoe where *Fraxinus* foliar N was high (i.e., 1.7 - 2.2%).

Closing observations

With the increase of *Acacia koa* stumpage prices during the 1990s, private landowners in Hawai‘i have a renewed interest in sustainable *Acacia* forestry (Pechar & Press 2006), including timber harvesting. Forest managers in Hawai‘i would like to harvest the *Fraxinus* and restore native *Acacia* forests. However, invasion by *Fraxinus* would make sustainable harvesting and regeneration of *Acacia* difficult in forests adjacent to *Fraxinus* plantations in several key areas. Any harvesting without appropriate control measures would allow dense regeneration of *Fraxinus* rather than of *Acacia* and other native tree species. Herbicides could be used to control *Fraxinus* regeneration, and trials in Hawai‘i have shown that *Fraxinus* is susceptible to several commonly used herbicides (Motooka et al. 2003). However, work at Hawai‘i Volcanoes National Park has indicated that *Fraxinus* seed banks are viable for up to eight years

(Tunison 1995). Herbicidal control of *Fraxinus* regeneration might therefore require repeated applications and *Acacia* seedlings would likely be killed in the process. Although it would be fairly simple to regenerate a native *Acacia* forest from seed following harvests, the presence of the alien *Fraxinus* makes the possibility of sustainable forestry more uncertain. It is ironic that a tree introduced initially for forestry purposes now presents a management obstacle to sustainable forestry.

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*For App. 1, see below (online version)
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App. 1. Plant species identified during surveys in 1971, 1973, 1976, and 2000 on the windward slopes of Mauna Kea, island of Hawai‘i.

	Scientific Name	Origin	Common name
Ferns	*Asplenium contiguum* Kaulf.	Endemic	forest spleenwort
	Asplenium insiticium Brack.	Indigenous	pi‘ipi‘i lau manamana, royal spleenwort
	Asplenium lobulatum Mett.	Indigenous	pi‘ipi‘i lau manamana
	Asplenium normale D. Don	Indigenous	rainforest spleenwort
	Athyrium microphyllum (Sm.) Alston	Endemic	‘ākōlea
	Cibotium glaucum (Sm.) Hook. & Arn.	Endemic	hāpu‘u pulu
	Cibotium menziesii Hook.	Endemic	hāpu‘u ‘i‘i
	Diplazium sandwichianum (C. Presl) Diels	Endemic	hō‘i‘o
	Dryopteris hawaiiensis (Hillebr.) W. J. Rob.	Endemic	Hawaiian woodfern
	Dryopteris sandwicensis (Hook. & Arn.) C. Chr.	Endemic	Pacific woodfern
	Dryopteris wallichiana (Spreng.) Hyl.	Indigenous	‘i‘o nui, oak fern
	Elaphoglossum paleaceum (Hook. & Grev.) Sledge	Endemic	‘ēkaha, māku‘e
	Lepisorus thunbergianus (Kaulf.) Ching	Indigenous	pākahakaha
	Microlepia strigosa (Thunb.) C. Presl	Indigenous	palapalai
	Nothoperanema rubiginosa (Brack.) A. R. Sm. & D. D. Palmer	Endemic	
	Polypodium pellucidum Kaulf.	Endemic	‘ae
	Sadleria cyatheoides Kaulf.	Endemic	ama‘u
	Vandenboschia davallioides (Gaudich.) Copel.	Endemic	kīlau
Forbs	*Astelia menziesiana* Sm.	Endemic	kaluaha
	Cyrtandra spp.	Endemic	hahale
	Peperomia spec.	Endemic or indigenous	‘ala ‘ala wai nui
	Solanum americanum Mill.	Indigenous or Alien	pōpolo
	Uncinia uncinata (L. f.) Kükenth.	Indigenous	
	Ageratina riparia (Regel) R. King & H. Robinson	Alien	Hāmākua pamakani
	Cardamine flexuosa With.	Alien	bittercress
	Cirsium vulgare (Savi) Ten.	Alien	bull thistle
	Conyza bonariensis (L.) Cronq.	Alien	hairy horseweed
	Epilobium billardierianum Ser.	Alien	willowweed
	Erechtites valerianifolia (Wolf) DC	Alien	fireweed
	Geranium homeanum Turcz.	Alien	cranes bill
	Lapsana communis L.	Alien	nipplewort
	Modiola caroliniana (L.) G. Don	Alien	
	Oxalis corniculata L.	Alien	yellow wood sorrel
	Physalis peruviana L.	Alien	pohā
	Polygonum glabrum Willd.	Alien	kāmole
	Rumex acetosella L.	Alien	sheep sorrel
	Rumex obtusifolius L.	Alien	bitter dock
	Senecio sylvaticus L.	Alien	wood groundsel
	Trifolium repens L.	Alien	white clover
	Verbena litoralis Kunth	Alien	vervain
	Veronica plebeia R. Br.	Alien	common speedwell
	Veronica serpyllifolia L.	Alien	thyme-leaved speedwell
	Youngia japonica (L.) DC	Alien	oriental hawksbeard
Grasses and sedges	*Carex alligata* Boott	Endemic	Hawaiian sedge
	Carex macloviana var. *subfusa* Dum. d'Urv.	Indigenous	
	Anthoxanthum odoratum L.	Alien	sweet vernal grass
	Ehrharta stipoides Labill.	Alien	meadow rice grass
	Holcus lanatus L.	Alien	velvet grass
	Paspalum urvillei Steud.	Alien	Vasey grass
	Pennisetum clandestinum Chiov.	Alien	kikuyu grass
	Poa annua L.	Alien	annual bluegrass
Shrubs and vines	*Alyxia oliviformis* Gaud.	Endemic	maile
	Phytolacca sandwicensis Endl.	Endemic	pokeberry
	Rubus hawaiiensis A. Gray	Endemic	‘ākala
	Styphelia tameiameiae (Cham. & Schlechtend.) F. v. Muell.	Indigenous	pukiawe
	Vaccinium calycinum Sm.	Endemic	‘ōhelo
	Passiflora tarminiana Coppens & Barney	Alien	banana poka
	Rubus argutus Link	Alien	blackberry
	Rubus rosifolius Sm.	Alien	thimbleberry
Trees	*Acacia koa* A. Gray	Endemic	koa
	Cheirodendron trigynum (Gaud.) A. Heller	Endemic	‘ōlapa
	Coprosma rhynchocarpa A. Gray	Endemic	pilo
	Hedyotis terminalis (Hook. & Arnott) W. L. Wagner & Herbst	Endemic	manono
	Ilex anomala (Hook. & Arnott)	Indigenous	kāwa‘u
	Metrosideros polymorpha Gaud.	Endemic	‘ōhi‘a
	Myrsine lessertiana A. DC	Endemic	kōlea
	Psychotria hawaiiensis (A. Gray) Fosb.	Endemic	kōpiko ula
	Fraxinus uhdei (Wenzig) Lingelsh.	Alien	tropical ash

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