

Occurrence of Indigenous Plant Species in a Middle-Elevation *Melaleuca* Plantation on O'ahu (Hawaiian Islands)¹

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ABSTRACT: The occurrence of native species at a middle-elevation (265–290 m) site on the island of O'ahu is of interest because of the extremely disturbed character of the vegetation and paucity of native forest species in the vicinity and at these elevations generally. 'Ōhi'a (*Metrosideros polymorpha*) and native shrubs are understory elements in a plantation of *Melaleuca quinquenervia* that was planted in the early 1930s. The relatively open character of the stand (light levels underneath the canopy 20–50% of incident radiation) may allow enough penetration of light to the subcanopy for native woody plants while excluding more light-demanding alien taxa. The variety of *Metrosideros* present is the smooth-leaved form (*M. polymorpha* var. *glaberrima*) more prevalent in the later stages of succession. The findings presented here may be an example of a tree plantation acting to foster native species and promote forest regeneration, a phenomenon that has been reported in degraded lands elsewhere in the Tropics.

NATIVE VEGETATION over extensive areas of the low to middle elevations of the island of O'ahu has been greatly affected by disturbances such as fire and grazing and by naturalization of alien species. Hasty and Zamzow (1997) noted the near absence of native plants over elevations from 170 to 500 m in the back of Mānoa Valley near urban Honolulu. On one side of the valley is Wa'ahila Ridge, which also shows very limited occurrence of native species below 400 m. Much of the middle-elevation ridge top is covered by plantings of nonnative trees made in the 1930s for revegetation and watershed protection. These plantations are generally either monotypic or contain nonnative species as understory elements. A hiker along the ridge path sees few native species, yet just down-slope underneath a canopy of nonnative *Melaleuca quinquenervia* is an assortment of species including 'ōhi'a (*Metrosideros polymorpha*), a dominant tree of the Hawaiian

forests, and other native woody plants (*Wikstroemia oahuensis*, *Styphelia tameiameia*, *Osteomeles anthyllidifolia*, *Chamaesyce celastroides*, *Acacia koa*, and *Bidens sandvicensis*). Reestablishment of native species in this area is particularly important because much of the native forest of the lower-elevation areas of the Islands is often assumed to be lost (Kirch 1982). In this study we document the occurrence of native species at this site and look at some of the physical and biotic characteristics of the site that may explain the vegetation patterns seen.

What is known about vegetation history in the area begins with the coming of Polynesians and a drastic increase in fire frequency at lower to mid elevations (Egler 1947, Kirch 1982). During the mid to late 1800s, cattle grazing, burning practiced in conjunction with sandalwood (*Santalum* spp.) harvesting and for other purposes, and tree harvesting for firewood and charcoal put further pressure on woody species. Grasses were favored as a result, both natives and a succession of introduced species. The onslaught of alien species that accompanied the Europeans included woody taxa as well. Most woody species became established at

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low elevations, but some moved into mid-elevations, where fire-adapted and fire-promoting characteristics of many of these plants resulted in additional changes to the fire and disturbance regime.

In the early part of the century as cattle ranching gave way to agriculture, there was interest in revegetating the watersheds to create a buffer between higher-elevation forest and lower agricultural land, which was increasingly subject to flooding and siltation (R. G. Skolmen, pers. comm.). Because *Metrosideros* had been observed dying back over large areas and the native vegetation was not regarded as well adapted to the landscapes created by human activities (Nickerson 1955, Holt 1988), a wide variety of nonnative trees was introduced in experimental plantings, such as those on Wa'ahila Ridge. In the 1960s, *Andropogon virginicus* replaced *Paspalum dilatatum* and *Setaria gracilis* as the dominant grass at this location as in other mid-elevation grasslands on O'ahu (Kartawinata 1971, Kartawinata and Mueller-Dombois 1972). The thick, dry thatch of this very fire-adapted species increased probability of fire even more where it occurred. Reestablishment of woody vegetation at the low and mid elevations has been the trend at least since the 1970s (Kartawinata 1971, Kartawinata and Mueller-Dombois 1972).

MATERIALS AND METHODS

Study Site

Wa'ahila Ridge (21° 17' N, 157° 52' W) extends along the southeastern flank of Mānoa Valley and ranges in elevation from 40 to 757 m, where it meets the Ko'olau summit crest on the windward coast of the island. The climate is characterized by a low range of mean annual temperature and high spatial variability of precipitation. Rainfall is 800 mm (30 inches) or less on the lower end of the ridge toward the ocean and increases, over a distance of 4 km, to close to 4000 mm (157 inches) at the higher elevations (Giambelluca et al. 1986). Xerophytic vegetation

consisting of nonnative species that both dominate and are present in high diversity is characteristic of the lower-elevation areas. Plantation trees are found mainly at middle elevations and occur with many naturalized species, including woody taxa presenting serious control problems such as *Psidium cattleianum*. Only at higher elevations (above 550 m) do native species dominate.

Of the 44 taxa, both native and nonnative, that were planted in the area, mainly in the early 1930s during planting trials (Skolmen 1980), substantial stands exist of *Melaleuca quinquenervia*, *Casuarina equisetifolia*, *Araucaria* spp., and *Syncarpia glomulifera* (Figure 1). Several thousand individuals of *Melaleuca*, now 4.5–5.5 m tall, were planted in 1932 and 1935 on either side of the ridge trail. A part of this plantation extends downslope toward Mānoa Valley in a narrow band that runs along the ridgeline. We studied the central portion of this stand, which is bounded on each end by cleared areas (power line clearing, etc.). The site is at an elevation of 260 to 295 m on a slope of 30–35 degrees that faces northwest. Median annual precipitation is estimated at 1000 mm or more (Giambelluca et al. 1986). Mean annual temperature is 22–23°C.

Sampling

Our sampling strategy was twofold. We first surveyed vegetation and various physical parameters along a 90-m transect following the 275-m contour to arrive at an idea of the range of variation present within the stand and how vegetation patterns might vary with differences in aspect and degree of canopy closure. The transect started and ended at the cleared areas that delimit the central portion of the stand. Linear extent of each species along the transect was used to calculate percentage cover. Photosynthetically active radiation (PAR) was measured underneath the canopy, at ground level, and at a height of approximately 1 m every 10 m along the transect, using a Decagon Sunfleck Cepometer (Pullman, Washington), which provided a measurement of average radiation over a distance of 0.8 m. Simultaneous mea-

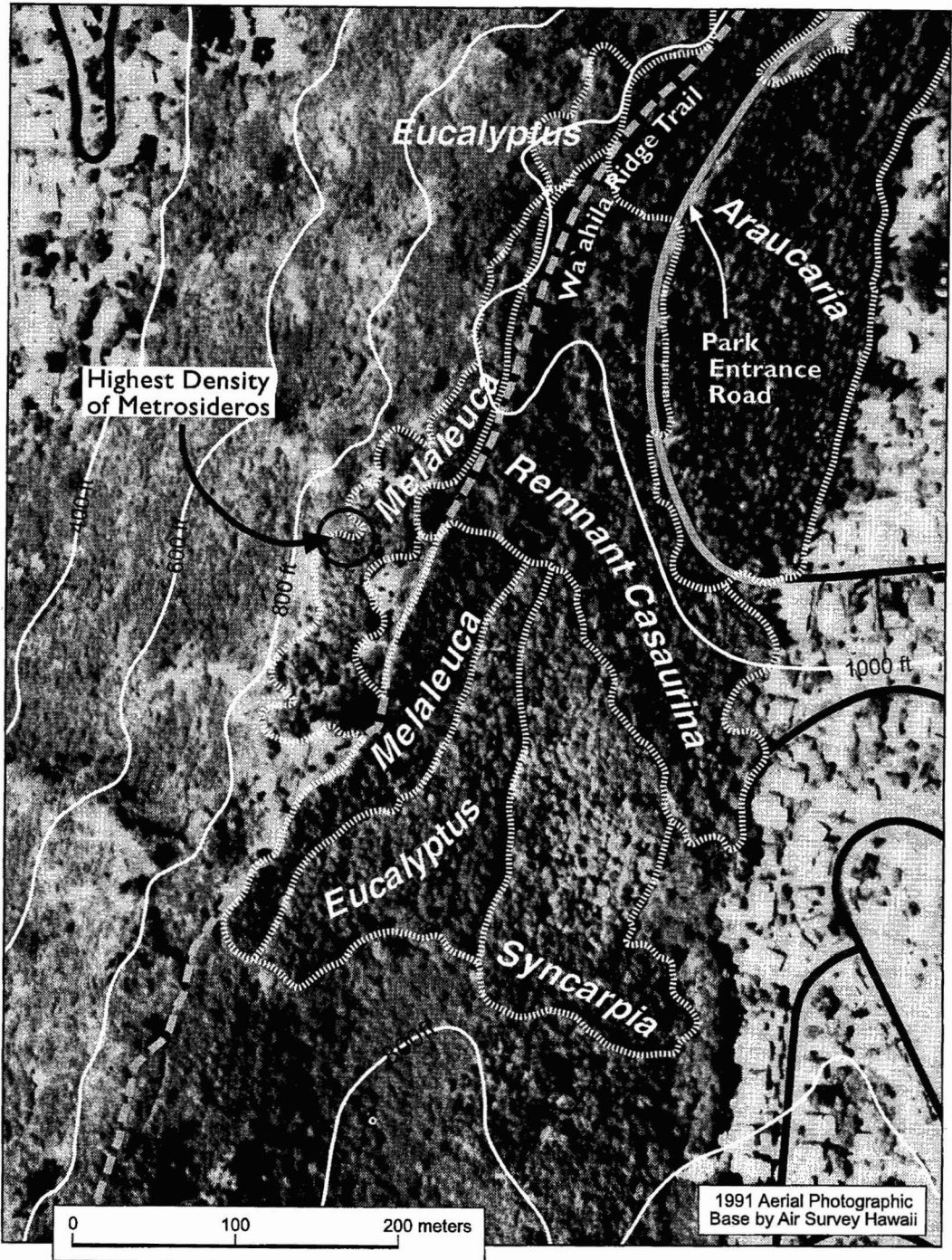


FIGURE 1. Map showing the Wa'ahila Ridge tree plantations. Mānoa Valley is on the left side, St. Louis Heights on the right.

surements of unobstructed PAR were also obtained using a Delta-T Quantum Sensor located in an adjacent clearing. Radiation measurements are presented as percentage of unobstructed radiation at two heights under the canopy. We took measurements morning, midday, and afternoon on 22 October 1995, when solar zenith angle is 32° . Light received on a horizontal surface at that time of year is approximately 80% of that received at the summer solstice. The annual attenuation cycle at the field site is accentuated by its northwest aspect. Values were averaged at each measurement point to give an idea of the general variation in radiation receipts underneath the canopy. Soil was sampled by means of a 132-cm³ core sampler every 20 m along the transect at the surface below the litter layer and at a depth of 10–16 cm. Soil moisture was determined gravimetrically. Bulk density was also determined.

The transect data identified three parts of the stand (see Results): a region where guava (*Psidium cattleianum*) is dominant to the exclusion of most other species; a region where native plants are present at higher frequency; and a region where grasses predominate. We conducted further sampling in two 250-m² plots just upslope of the transect to get a more detailed idea of the vegetation in the native plants and grass associations. Vegetation was sampled by point-intercept method, with all individuals impinging on a vertical line recorded at 0.25-m intervals along north-south and east-west axes of the plots. Sampling in the plots followed the protocol of The Nature Conservancy of Hawai'i for long-term vegetation monitoring (The Nature Conservancy 1993). Number of individuals of each species expressed as percentage of total was used as a measure of relative density in the plots. In addition, all woody species (with the exception of *Psidium cattleianum*, which was present throughout) were counted in each plot.

RESULTS

Vegetation data from the transect and corresponding radiation measurements are

presented in Figure 2. In the subcanopy along the transect, *Psidium cattleianum* gives way to vegetation dominated by greater prevalence of woody natives (*Metrosideros polymorpha*, *Wikstroemia oahuensis*, *Styphelia tameiameia*) and the fern *Odontosoria chinensis* and then to *Andropogon virginicus* with *Psidium*. Percentage cover of woody natives plus *Odontosoria* varies inversely with that of *Psidium* and *Andropogon*, with native species most prevalent in the stand interior.

Light levels below the *Melaleuca* (Figure 2b) range from 17 to 47% of that incident at the top of the canopy, with values lowest ($\sim 20\%$) near the middle of the transect and higher (30–45%) in the area where *Andropogon* occurs. The average was 440 $\mu\text{mole cm}^{-2} \text{sec}^{-1}$ at midday on a sunny day. Native woody plants occur over most of the range of light levels present in the stand. Light at the soil surface ranges from 5 to 30% of unobstructed radiation. There appears to be a consistent attenuation by the subcanopy vegetation of 15–25%.

Soil moisture at the surface and subsurface (10–16 cm) averaged 43 and 42% by mass, respectively. The only notable variation was at the end of the transect where *Andropogon* is dominant; there values of soil moisture were 10–20% higher. Bulk density exhibited even less variation, averaging 0.79 Mg m^{-3} at the surface and 0.86 Mg m^{-3} at 10–16 cm. These values are consistent with a porous, deeply weathered soil with little organic matter.

Figure 3 shows the percentage occurrence of various taxa in the two survey plots. Apart from *Psidium cattleianum*, an important common element, the plots differ in that *Odontosoria* and native woody species are prevalent in plot 1, whereas *Andropogon* dominates in plot 2. The list of understory species (Table 1) shows that plot 1 has many more woody species and also that natives are more prevalent than nonnatives.

Metrosideros is present at one individual per 10 m² in plot 1, but the form is generally that of a low bush and no individuals are taller than 1.5 m. Several large (3 m tall), dead individuals of this species were found within the stand and living specimens 4 m tall

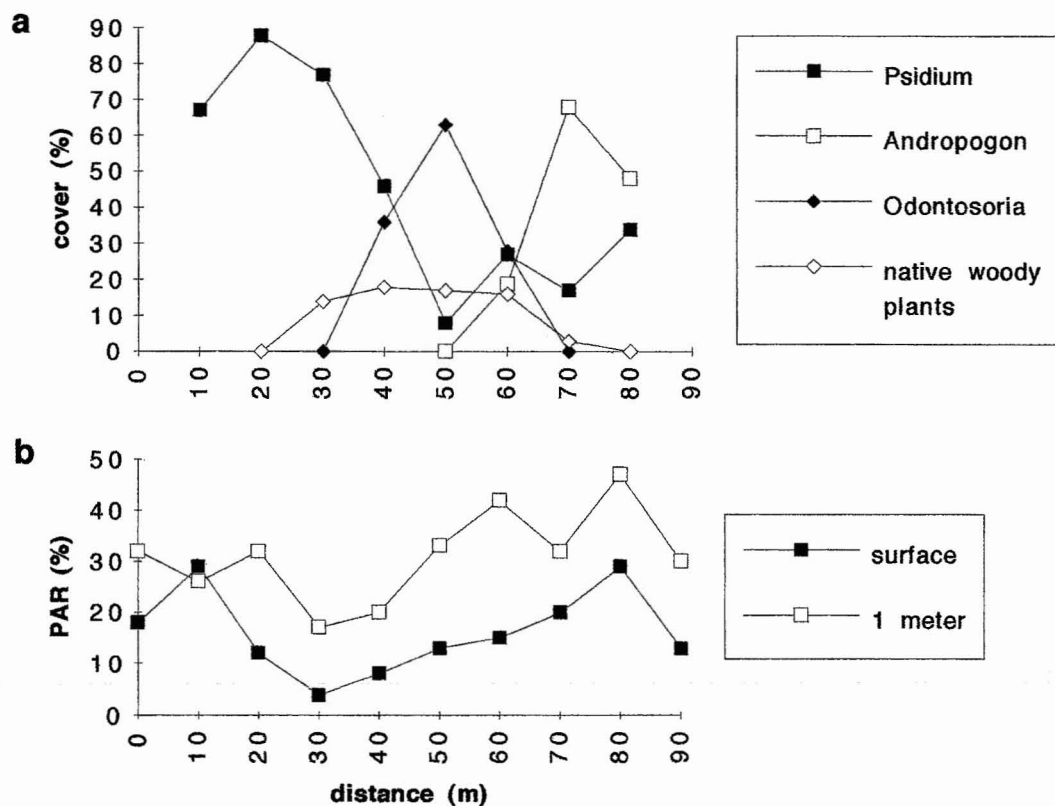


FIGURE 2. *a*, Percentage cover along the 90-m transect. Values are grouped by 10-m intervals. *b*, Percentage of unobstructed photosynthetically active radiation (PAR) below the canopy at a height of 1 m and at the surface.

occur nearby on the ridge. Tall individuals on the ridge tend to have small leaves that are pubescent on their undersurface, whereas the understory plants are generally the smooth-leaved variety (var. *glaberrima*) linked with later stages of succession (Mueller-Dombois 1983, Stemmermann 1983). Whether these trees represent a viable reproducing population is not known.

DISCUSSION

The species composition of the subcanopy (see Appendix) exhibits similarities with that of the subhumid grassland community described by Kartawinata and Mueller-Dombois (1972). *Andropogon virginicus* is the dominant grass, occurring with the grasses

Setaria gracilis and *Paspalum conjugatum*, the fern *Odontosoria chinensis*, shrubs including *Psidium cattleianum*, and *Metrosideros polymorpha*. This association occurs on slopes and moderate-relief areas on the windward side of the island and less frequently on the leeward wide. Water availability and soil pH appear to be important in delimiting the main grassland associations studied, with high soil moisture and pH of 4.5–5.0 characterizing *Andropogon*-dominated areas (Kartawinata and Mueller-Dombois 1972). The woody composite *Bidens sandvicensis*, which is common at the site, often occurs in disturbed shrubland (Wagner et al. 1990).

It is somewhat surprising to find young *Metrosideros* under the shade of a forest canopy because this species most often be-

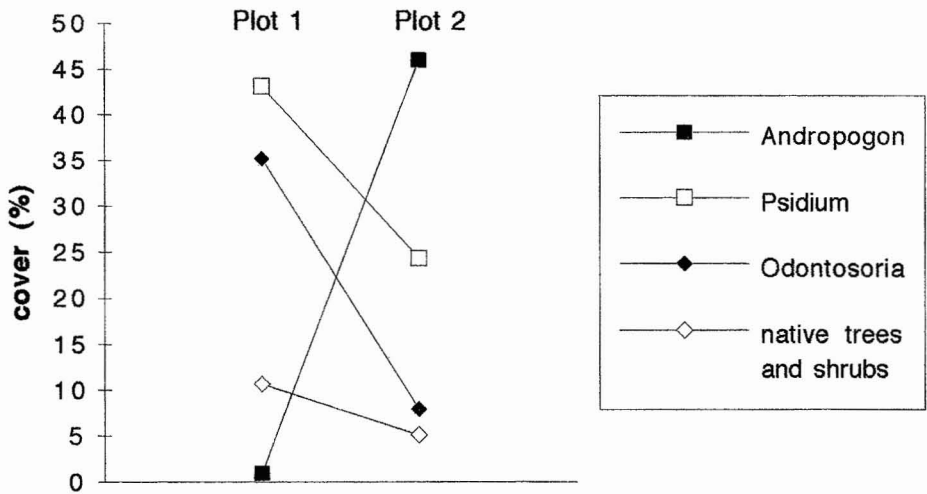


FIGURE 3. Percentage occurrence of various taxa and taxon groupings in plots 1 and 2.

TABLE 1
WOODY PLANTS IN PLOTS 1 AND 2

AREA	PLOT 1	NO.	PLOT 2	NO.
Canopy	<i>Melaleuca quinquenervia</i>	20	<i>Melaleuca quinquenervia</i>	23
	<i>Araucaria</i> sp.	1		
Understory	* <i>Styphelia tameiameia</i>	37	* <i>Styphelia tameiameia</i>	11
	* <i>Metrosideros polymorpha</i>	24 ^a	<i>Melaleuca quinquenervia</i>	1
	* <i>Wikstroemia oahuensis</i>	17	<i>Araucaria</i> sp.	1
	<i>Schinus terebinthifolius</i>	17	<i>Schinus terebinthifolius</i>	1
	<i>Citharexylum caudatum</i>	17	<i>Citharexylum caudatum</i>	1
	<i>Araucaria</i> sp.	2		
	<i>Melaleuca quinquenervia</i>	2		
	<i>Lantana camara</i>	1		
	<i>Schefflera actinophylla</i>	1		
	<i>Tecoma</i> sp.	2		

NOTE: In both plots *Psidium cattleianum* is dominant in the understory (26–50% cover). Plot area is 250 m².

*Native species.

^aPlus two dead trees.

comes established in the open. A study of seedling establishment and growth in different light regimes indicates that *Metrosideros* is moderately shade tolerant in spite of being a pioneer species (Burton and Mueller-Dombois 1984). In Burton and Mueller-Dombois' (1984) study, which was carried out in a rain forest location on the Big Island (Hawai'i), seedling mortality was lowest at 5–45% relative irradiance and growth was at a maximum at 50% irradiance. Light levels within

the *Melaleuca* stand (20–45% of unobstructed radiation under the canopy and <30% of unobstructed radiation at the soil surface) are thus within the range that should promote seedling establishment. These findings taken together indicate that *Metrosideros* can participate in gap-phase as well as primary succession and suggest that light levels within the plantation may approximate those in gaps in closed-canopy native forest. In fact, relatively uniform gap-phase con-

ditions is one explanation for the vegetation patterns seen. This interpretation is supported by the occurrence of smooth-leaved *Metrosideros*, which is described as the later-successional form (Mueller-Dombois 1983, Stemmermann 1983).

Variation in physical characteristics (light, aspect) does not explain the vegetation pattern within the stand. Occurrence of native species at maximum frequency in the center of the stand is probably not coincidental. Decreased competition from light-demanding aliens colonizing from the periphery and lesser amounts of disturbance away from the edges may be key factors. Presence of *Andropogon* along the last 30 m of the transect and in plot 2 is indicative of fire in the fairly recent past. Occasional fires should act to promote grassy vegetation and suppress growth of woody plants. Parman and Wampler (1977) found that individuals of *Metrosideros* less than 1 m high were killed by fire, although larger trees sprouted from the roots.

The following factors may be important in explaining the occurrence of native species at this site. First, the sparse crown and open quality of the *Melaleuca* stand may allow establishment of taxa (*Metrosideros*, *Andropogon*) more commonly found in more open areas. The sloping nature of the site undoubtedly results in greater light penetration than in corresponding flatter areas. (At the higher elevations where native trees are clearly in evidence, they often appear more prevalent on steeper slopes.) Light levels may be high enough to allow establishment of *Metrosideros* and other native species but low enough to exclude at least some potential competitors. The light litter layer (and absence of allelopathic substances?) may also be important in allowing seedling establishment. Although some adult *Metrosideros* occur in the vicinity and there are more extensive populations downwind of the site at higher elevation, seed dispersal in this species, which has wind-dispersed seeds, may not be a limiting factor (Drake 1992). In the case of *Styphelia* and *Wikstroemia*, both of which have fleshy fruits, overstory trees may promote seedling establishment by providing roosting areas for birds. Parrotta (1992)

noted the prevalence of taxa with bird- and bat-dispersed fruits in plantations on degraded lands in Puerto Rico. Last, and perhaps most important, natural successional processes may have had sufficient time with disturbance absent or minimal for native species to become established.

Whether the process of forest regeneration will continue is uncertain because of the competing influences present. Fire (or other types of disturbance) would encourage *Andropogon* and maintain the mosaic of *Psidium*, grasses, and other alien species much in evidence in the area, and protection from fire and other disturbances seems to be the clearest requirement if the process of succession is to continue. It is possible also that alien species may be poised to advance into the area, even in the absence of disturbance. *Araucaria* is invading gradually from the mature plantation nearby. There are numerous seedlings and saplings of *Citharexylum caudatum* present in the stand and it appears to share with *Psidium cattleianum* the ability to become established in full sunlight or some degree of shade. Also present are saplings of *Tabebuia* sp. that may have the potential to be a dominant canopy element. All of the latter taxa are currently being planted as ornamentals and/or street trees in urban Honolulu surrounding the ridge. In addition, introductions of woody exotics continue.

Tropical tree plantations are known to affect understory diversity, soil and litter characteristics, and nutrient recycling differently than primary or secondary forest (Lugo 1992, Michelsen et al. 1996). In Hawai'i, Harrington and Ewel (1997) found that abundance of native plants is directly related to basal area and abundance of nonnative species. *Fraxinus* was associated with more natives than either *Eucalyptus* or *Flindersia*. Plantations of these tree species are at higher elevation and experience substantially higher precipitation than the site studied here. In addition, they are adjacent to native forest. More closely analogous to the situation reported here is a study done in Puerto Rico in an area of degraded (grazed and otherwise disturbed) land with grasses dominant and few woody plants (Parrotta 1992, 1993). A

few years after planting, secondary forest species appeared within a plantation of *Albizia lebbek*. The conclusion that plantations accelerate natural forest regeneration has also been made for *Eucalyptus* plantations in southeastern Brazil (da Silva et al. 1995). These researchers regard *Eucalyptus* as a "nurse tree" species capable of speeding the course of forest succession by mimicking the role of early successional taxa. It is possible that plantation species such as *Melaleuca* may be capable of playing a similar role in the Hawaiian Islands. Finally, these findings suggest that forest regeneration can occur at low elevations in locations that have been severely disturbed and that it may be possible to manage Hawai'i's extensive "unnatural" landscapes to maximize the possibility of native forest regeneration.

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APPENDIX

SPECIES LIST FOR THE WA‘AHILA RIDGE SITE

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- Ageratina riparia* (Regel) R. King & H. Robinson [herb]
Andropogon virginicus L. [grass]
Araucaria cf. *heterophylla* [tree]
 **Bidens sandvicensis* Less. [woody composite]
Citharexylum caudatum L. [tree]
 **Cocculus trilobus* (Thunb.) DC [herb]
Epidendrum × *obrienianum* Rolfe [orchid]
Erigeron karvinskianus DC [herb]
Lantana camara L. [shrub]
 **Metrosideros polymorpha* Gaud. [tree]
Melaleuca quinquenervia (Cav.) S. T. Blake [tree]
Nephrolepis sp. [fern]
 **Odontosoria chinensis* (L.) J. Sm. [fern]
 **Osteomeles anthyllidifolia* (Sm.) Lindl. [shrub]
Paspalum dilatatum Poir. [grass]
Passiflora edulis Sims [herb]
Phymatosorus scolopendria [fern]
Psidium cattleianum Sabine [shrub/tree]
 **Pilotum nudum* (L.) Griseb. [lower vascular plant]
 **Pteridium aquilinum* (L.) Kuhn [fern]
Schefflera actinophylla (Endl.) Harms [shrub/tree]
Schinus terebinthifolius Raddi [tree]
Setaria gracilis Kunth [grass]
Spathoglottis plicata Blume [fern]
Stachytarpheta jamaicensis (L.) Vahl [herb]
 **Styphelia tameiameia* (Cham. & Schlechtend.) F.v. Muell. [shrub]
Tabebuia sp. [tree]
 **Wikstroemia oahuensis* (A. Gray) Rock [shrub]
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*Native species.

Authorities for names are Wagner et al. (1990) and *Index Filicum*.