ALIEN AND NATIVE PLANT RESPONSE TO RELEASE FROM FERAL SHEEP BROWSING ON MAUNA KEA

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ABSTRACT

Over 150 years of feral sheep damage to the subalpine woodlands on Mauna Kea, Hawai'i, ended when "eradication" of feral sheep *(Ovis aries)* was declared complete (even though a few sheep remained). Managers and others interested in conserving Mauna Kea's subalpine ecosystem are now concerned about the ability of native plants to reestablish dominance without the aid of humans in the absence of significant feral sheep grazing and browsing. Successful reestablishment will depend partly on the ability of native plants to compete with alien plants. Data from exclosures near tree line indicate that both herbaceous and woody native species establish in areas freed from sheep foraging pressure, in spite of alien plants, provided that the areas are not fully occupied by aliens. In areas that were densely populated by feral sheep before 1981, native and alien plants appear to be responding, as indicated in publications about earlier exclosure studies. Control of alien plants to favor native species does not now appear warranted. However, two noxious aliens, fountain grass *(Pennisetum setaceum)* and German ivy *(Senecio mikanioides)*, are established in the subalpine woodland and could become management problems in the future.

INTRODUCTION

Are native plants capable of successfully competing with introduced alien plants in insular terrestrial ecosystems? This question has been posed repeatedly in Hawai'i, where over 4,600 species of plants have been introduced over the last 200 years (St. John 1973). Of these species, 86 have been recognized as serious pests of native Hawaiian ecosystems (Smith 1985).

Answering the question is no simple task, because competitive interactions are not easily assessed in uncontrolled natural areas without experimentation. Furthermore, an answer based on native-alien plant interactions in one ecosystem cannot be generalized to others, especially in Hawai'i, where considerable terrestrial ecosystem diversity exists (*e.g.*, dry coastal lowlands, rain forests, and semiarid alpine tundra). The best one can hope for are answers on a case-by-case basis.

In this paper we examine alien and native plant responses to release from feral sheep grazing and browsing in the māmane *(Sophora chrysophylla)* forest on Mauna Kea, a subalpine woodland ecosystem that has been and remains the center of management controversy (Juvik and Juvik 1984). We also describe this woodland ecosystem, summarize the impacts of alien animals, and discuss potential interactions among native and alien plants and introduced ungulates. Specific objectives are: 1) to review responses of plants to release from sheep browsing in areas protected by exclosures prior to feral sheep eradication in 1981; 2) to describe plant responses inside and outside two exclosures five years after feral sheep "eradication;" and 3) to evaluate alien-native plant interactions in a portion of the Mauna Kea Forest Reserve that has been essentially sheep-free since about 1960 (R. Walker, pers. comm. 1986). We also address the question of whether plant recovery after "eradication" and outside exclosures follows a pattern similar to that observed inside exclosures before "eradication" and discuss suppression of native species by alien species.

The Subalpine Woodland Ecosystem

The subalpine ecosystem of Mauna Kea occurs between 5,900 and 9,840 ft (1,800-3,000 m) elevation and consists of two distinct woodland types: the māmane woodland and the naio *(Myoporum sandwicense)*-māmane woodland.

On eastern, northern, and western slopes of Mauna Kea, and also in a narrow band at tree line on the southern slope, māmane occurs in almost pure stands (Scott *et al.* 1984). Naio is absent in these areas, and other native tree species, such as pilo *(Coprosma montana)*, are scarce. The māmane trees average less than 26 ft (8 m) in height, and canopy cover ranges from very scattered (<5% cover) to partly closed (60% cover) (Scott *et al.* 1984), the latter being uncommon. Native woody species in the understory include pūkiawe (*Styphelia tameiameiae*), ʻōhelo (*Vaccinium* sp.), *Geranium cuneatum*, and *Dubautia arborea*. Herbaceous species are predominantly aliens and include several grasses: sweet vernalgrass, ripgut grass, hairy oatgrass, Kentucky bluegrass, needlegrass, and velvet grass *(Anthoxanthum odoratum, Bromus rigidus, Danthonia pilosa, Poa pratensis, Stipa cernua, Holcus lanatus)*. Native grasses are *Agrostis sandwicensis, Deschampsia nubigena*, and pili uka *(Trisetum glomeratum)*. Additional details about māmane woodland vegetation are given by Hartt and Neal (1940) and Mueller-Dombois and Krajina (1968).

The mixed naio-māmane woodland type is confined to the southwestern slopes of Mauna Kea (Scott *et al.* 1984). Naio accounts for 10 to over 85% of the trees, with māmane comprising most of the rest (van Riper 1980a). Other native tree species occurring as scattered individuals and colonies are *Dubautia arborea, Chamaesyce olowaluana*, and sandalwood (*Santalum ellipticum*). Tree heights average less than 26 ft (8 m), but tree canopy cover is generally higher than in the pure māmane forest and can exceed 85% (Scowcroft 1983). The shrubs in the mixed woodland are all native and include 'āweoweo, 'ūlei, and 'a'ali'i (*Chenopodium oahuense, Osteomeles anthyllidifolia, Dodonaea* sp.). Many of the herbaceous species found in the māmane woodland also occur in the naio-māmane woodland. Three noxious weeds are found in the mixed woodland: stinkweed, fountain grass, and German ivy (*Tagetes minuta, Pennisetum setaceum, Senecio mikanioides*) (Scott *et al.* 1984; Smith 1985).

The climate of the subalpine woodlands is a function of elevation and prevailing tradewinds. Temperatures range from nighttime lows near freezing to daytime highs above 68 F (20 C) (van Riper 1980a; Scowcroft 1981). The range of mean daily temperature over a year is smaller than the diurnal temperature range. The nighttime inversion layer, which generally lies below the subalpine woodland, breaks down by midday, and prevailing tradewinds bring fog or rain or both to northeastern to southeastern slopes. Median annual rainfall on windward slopes ranges from 28 in. (700 mm) at tree line (9,500 ft or 2,900 m elevation) to 63 in. (1,600 mm) at the lower boundary of the māmane woodland at 6,900 ft (2,100 m) elevation (Hawaii Division of Water and Land Development 1982). Rainfall is low at all elevations in the rain shadow of Mauna Kea, with an annual median of 16 in. (400 mm). Snow rarely falls in the subalpine woodlands, and if it does, it melts rapidly.

The soils are poorly developed, and in some cases plants are growing in undifferentiated parent material (cinders and volcanic sand). Where development has occurred, the soil is classified as a Typic Vitrandept, medial over cindery, isomesic (U.S. Soil Conservation Service 1973). Coarse structure and low amounts of organic matter result in low water-holding capacity. Steep slopes and coarse texture of cinders and ash result in unstable soils. In general, the edaphic conditions of the subalpine woodlands are harsh for plant growth (Hartt and Neal 1940).

Historical Impact of Ungulates

Domestic livestock were introduced to the Hawaiian Islands late in the 18th century (Kramer 1971). Feral populations of cattle, sheep, and goats (*Bos taurus, Ovis aries, Capra hircus*) soon became established in forests. By 1825, feral sheep had established in Mauna Kea's subalpine woodland. Lacking natural predators except for wild dogs (*Canis domesticus*), the sheep population reached about 40,000 animals by the early 1930s, one for every 5 a (2 ha) of habitat (Bryan 1937a). Sheep suppressed māmane and other tree reproduction over large areas, stripped bark from tree stems, and consumed herbaceous vegetation, thereby leaving the soil exposed to accelerated erosion (Warner 1960). Because damage to the ecosystem was severe and because feral sheep competed with commercial flocks (Judd 1936), Hawai'i Territorial foresters built a stock-proof fence around the Mauna Kea Forest Reserve (Bryan 1937b) and reduced the population through sheep drives and hunter-guide programs. Fewer than 500 feral sheep were left by 1950 (Bryan 1950). Control efforts were then relaxed, and populations increased.

Sustained yield management for public hunting was started in 1955, with the population kept below 5,000 animals. During the 1970s, the population averaged 1,500 animals. Even at this relatively low level, vegetation continued to deteriorate where sheep concentrated, especially at tree line (Scowcroft 1983; Scowcroft and Giffin 1983; Scowcroft and Sakai 1983).

Ecosystem damage has also been caused by mouflon sheep (*Ovis musimon*), which were released in the Mauna Kea Forest Reserve starting in 1962 (Giffin 1982). Food preferences, grazing and browsing behavior, and herding habits are similar to those of feral sheep, and native plants are particularly susceptible to damage by mouflon. In 1986, the largest concentrations of mouflon were on the southeastern and northwestern flanks of the mountain, and animals were moving into areas formerly occupied by feral sheep. The mouflon population was estimated at 500 animals (R.E. Bachman, pers. comm. 1986).

Continued degradation of the māmane woodland in the late 1970s posed a significant threat to the palila *(Loxioides bailleui)*, an endangered endemic Hawaiian bird now found only in the subalpine woodland of Mauna Kea (Berger 1972; van Riper *et al.* 1978; Scott *et al.* 1984). Palila depend on māmane and, to a lesser extent, on naio trees for food and nest sites (van Riper 1980b). Critical habitat for palila was designated in 1977 and included almost all State-owned māmane and naio-māmane woodlands on Mauna Kea (U.S. Fish and Wildlife Service 1977).

Because of continued habitat degradation and the attendant threat to the palila, a suit on behalf of the palila was brought by conservationists against the state of Hawai'i. Noncompliance with the U.S. Endangered Species Act of 1973 was charged. A detailed account of the initial palila lawsuit and events that preceded was given by Juvik and Juvik (1984). The suit was decided in favor of the bird, and the State was ordered to remove feral sheep and feral goats completely and permanently from those portions of the māmane forest designated as critical palila habitat. The status of mouflon sheep was not affected by the court order.

The feral sheep and goat "eradication" effort was completed in 1981. Five years later, it was evident that a few feral sheep had escaped death, as expected. The authors have seen a flock of 20 feral sheep at tree line on the western side of Mauna Kea. Sheep tracks and signs of recent browsing were common in the vicinity of that sighting.

Potential Plant-Animal Interactions

The interactions among native plants, alien plants, and alien ungulates are often manifest in composition of the plant communities and species densities. Relative species composition is the percent contribution of each species to total plant cover in a given area. Potential interactions among aliens and natives may be considered in terms of species composition and density of each group in a community.

Species Composition. Differential grazing may favor alien plants, which appear to be less palatable than some native plants. For instance, māmane is sometimes called an "ice cream plant" because it is preferentially browsed by sheep. The native climax perennial grasses in the Mauna Kea subalpine woodlands seem to be preferred by sheep over alien perennial grasses such as sweet vernalgrass.

The effect of sheep grazing on survival of native climax grasses may involve more than palatability. Williams (1968) and Williams and Roe (1975) reported that sheep-grazing decreased the probability of survival of climax grasses in semiarid portions of Australia. In contrast, the life spans of dominant disclimax grasses there were enhanced by grazing. On Mauna Kea the climax native grasses are tufted perennials, such as pili uka, which have their perennating buds above ground where they are susceptible to grazing damage. In contrast, several alien grasses (*e.g.*, Kentucky bluegrass, hairy oatgrass) have perennating buds below ground.

When released from grazing pressure, aliens may grow more rapidly and disperse more seeds over a larger area than native species. Thus, aliens may simply outcompete native species and dominate recovering plant communities. Kilcher and Looman (1983) concluded that most of the native grasses they studied in a temperate ecosystem did not have the potential to be competitive with adapted introduced and domesticated species and cultivars.

Conversely, although aliens may dominate a grazed plant community, they are not necessarily more competitive than native species. Rabinowitz *et al.* (1984) postulated that competitive inferiority may be a sufficient explanation for sparsity of certain herbaceous species in a plant community. But if abundance is regulated by another cause, such as differential herbivory, then competitive superiority may be a necessary conditon of persistence. In such a situation, we would expect the competitively superior but suppressed species to respond positively to release from grazing and become a biologically significant component of the community.

Plant Density. The reproductive capacity and population growth potential of alien plants may exceed that of native species. The greater potential of an alien may be genetically determined (*e.g.*, the growth potential for mullein (*Verbascum thapsus*), an alien species, is remarkable (Juvik and Juvik, this volume)). Lower population growth potential of native plants could also result from greater herbivory reducing the supply of photosynthate available for reproduction (Harper 1977). Ungulates may also preferentially eat germinants of native species even when native germinants are scarce.

Smith (1985) noted that some alien plant pests are known or suspected of allelopathy. Although true allelopathic effects are difficult to separate from other competitive interactions, allelopathy could be a mechanism controlling density of native competitors. Conversely, some native species, like ʻāweoweo, may be allelopathic.

Suitability of Alien and Native Species for Forage

We have assembled information from published sources about the forage value, relative palatability, and susceptibility to animal damage of many common plant species in the Mauna Kea Forest Reserve (Table 1). Four native species on the list are highly palatable and susceptible to grazing or browsing damage: pili uka, *Agrostis avenacea*, ʻāweoweo, and

Table 1. Relative forage value, relative palatability, and susceptibility to browsing or grazing damage of some common plant species in the Mauna Kea Forest Reserve, island of Hawai'i.

Species	Relative forage value	Relative palatability	Susceptibility to grazing/ browsing damage	References
GRASSES				
*Agrostis avenacea**	?	High	?	Whitney *et al.* 1939
Anthoxanthum odoratum	Low	Low	Low	Ripperton *et al.* 1933
*Bromus rigidus***	None	None	?	Whitney *et al.* 1939
Dactylis glomerata	High	High	Moderate	Ripperton *et al.* 1933
Danthonia pilosa	?	Moderate	Low	Whitney *et al.* 1939
*Deschampsia nubigena**	?	Low	?	Ripperton *et al.* 1933
Holcus lanatus	High	High	Moderate	Ripperton *et al.* 1933
Pennisetum setaceum	Low	Low	Low	Hosaka & Thistle 1954
Poa pratensis	High	High	Low	Ripperton *et al.* 1933
Trisetum glomeratum	?	High	High	Giffin 1982; Scowcroft & Giffin 1983; Ripperton *et al.* 1933
*Vulpia myuros***	?	Low-Moderate	?	Ripperton *et al.* 1933
FERN				
Pteridium aquilinum	Poisonous	Low	Low	Giffin 1982
HERBS AND FORBS				
*Bidens pilosa***	Low	Low	Low	McClelland 1915
Cirsium vulgare	Low	Low	Low	Giffin 1976
Epilobium billardierianum	High	High	High	Giffin 1976
*Erodium cicutarium***	Low	Moderate	Low	McClelland 1915; Giffin 1976
Hypochoeris radicata	Moderate	Moderate	Low	McClelland 1915; Giffin 1976; Giffin 1982; Ripperton *et al.* 1933

Species	Relative forage value	Relative palatability	Susceptibility to grazing/ browsing damage	References
Rumex acetosella	?	Moderate	Moderate	Giffin 1982
*Senecio sylvaticus***	?	Low	Moderate	Giffin 1976
*Sonchus oleraceus***	Moderate	High	Moderate	McClelland 1915; Giffin 1976
*Tagetes minuta***	None	None	Low	Hosaka & Thistle 1954
Taraxacum officinale	Moderate	Moderate	Low	McClelland 1915
*Urtica urens***	Low	Low	Moderate	Giffin 1976
*Verbascum thapsus***	Low	Low	Low	Giffin 1982
SHRUBS				
*Chenopodium oahuense**	?	High	High	Giffin 1976
Dodonaea sp.*	?	Low	Low	Giffin 1982
Dubautia sp.*	?	Low-Moderate	High	Giffin 1982
Geranium sp.*	?	Moderate	Moderate	Giffin 1982
*Styphelia tameiameiae**	Low	Low-Moderate	Low	Hosaka & Thistle 1954; Giffin 1976, 1982
Vaccinium sp.*	Low	Moderate	Moderate	McClelland 1915; Giffin 1982
TREES				
Coprosma sp.*	?	Low	Moderate	Giffin 1982
Euphorbia sp.*	?	Low	Moderate	McClelland 1915
*Myoporum sandwicense**	Low	Low	Moderate	Giffin 1976
*Sophora chrysophylla**	High	High	High	Giffin 1976, 1982

*Native species.
**Species with annual or biennial life spans. All others are perennials.

māmane. *Agrostis sandwicensis*, a native grass not listed in Table 1, is probably highly palatable and easily damaged also (Scowcroft and Giffin 1983). Several alien plant species are highly palatable: cocksfoot (*Dactylis glomerata*), velvet grass, Kentucky bluegrass, *Epilobium billardierianum*, and *Sonchus oleraceus*. However, susceptibility to damage by sheep for these and other alien plants is generally lower than for the native plants. Plant responses to release from grazing and browsing pressure in light of their forage characteristics will be discussed later.

RECOVERY OF ALIEN AND NATIVE PLANTS

Study Sites

Thirteen exclosures have been established within the Mauna Kea Forest Reserve (Loope and Scowcroft 1985). Quantitative data have been collected from six of these exclosures: Pu'u Nanahā, Pu'u Kole, Kaluamakani, Pu'u o Ka'uha, Wailuku, and Hale Pōhaku. All six exclosures are located at or near tree line (about 9,020 ft or 2,750 m elevation). Site attributes of the six exclosures are described by Scowcroft and Giffin (1983).

Methods

Methods used to study vegetation recovery at five of the exclosure sites before feral sheep "eradication" in 1981 were described by Scowcroft and Giffin (1983). At the sixth site, the Wailuku exclosure, data were collected four years after construction using stratified random sampling, but results were not published. Three strata were mapped and sampled inside Wailuku: a light grass stratum with eight sample quadrats, a cinders stratum with ten sample quadrats, and a rock stratum with three sample quadrats. Mature māmane trees and the vegetation under them constituted a fourth stratum, but it was not sampled. Quadrats measured 10 x 10 ft (3.05 x 3.05 m), and 3-6% of each stratum was sampled. The basal area of each plant was determined by species (Scowcroft and Giffin 1983). Mean basal area estimates were calculated, by species, for each stratum and for the whole exclosure.

Herbaceous vegetation was resampled in April and May 1986 at two of the six exclosures -- Pu'u o Ka'uha in the rain shadow on the western side of Mauna Kea, and Wailuku on the wetter, eastern side of the mountain. Methodology in 1986 differed from that used earlier. We reestablished the same sample quadrats used previously, but instead of measuring all plants in each quadrat, we subsampled as described by Cochran (1963). Each large quadrat (cluster) was divided into 36 cells measuring 0.8 x 0.8 ft (0.25 x 0.25 m). Twelve cells per cluster were randomly selected, and plants were measured for projected crown area, basal area, and height, by species. Overall means and standard errors were calculated according to Cochran (1963).

All pairwise comparisons in this paper were made using the Games and Howell (1976) procedure (see also Keselman and Rogan 1978). The Bonferroni "z" value (df = infinity) was used to calculate confidence limits for the difference between means (Bailey 1977).

We also estimated the percentage of each cell covered by rock, bare ground, litter, and live plants, regardless of species. We defined cover in this instance as vertical projected cover. Total cover for each cell had to equal 100%.

Woody species, which were exclusively native plants, were not as abundant as the herbaceous species, so we measured every individual inside the Wailuku exclosure and inside and outside the Pu'u o Ka'uha exclosure. Data included species, height, crown spread, and stem diameter 12 in. (30 cm) above the ground. For plants with multiple stems at 30 cm, we estimated the diameter of the "average"-sized stem. Mature individuals were tallied separately from immatures.

The māmane woodland was also sampled, along transects running along the contour and to either side of the Pu'u o Ka'uha exclosure, to determine if plant responses at the exclosure site were representative of the surrounding area. Samples were not taken outside the Wailuku exclosure, because grazing and browsing by mouflon sheep continued unabated there.

Using stopwatch, compass, and altimeter, we walked along the contour at the same elevation as the Pu'u o Ka'uha exclosure (9,020 ft or 2,750 m) and established five sample points 15 minutes apart. We estimated that the transects were about 1.24 mi (2 km) long. At each sample point we laid out two nested circular plots; the area of the inner one was 1,076 ft^2 (100 m^2), and the area of the outer one was 3,390 ft^2 (315 m^2). Vertical projected areas of rock, litter (including logs and branches), bare soil, and live herbaceous foliar cover, by species, were estimated within the smaller plots. Woody plant heights and crown diameters were measured in the larger plots, by species.

A similar pair of transects and set of nested plots were established near the Pu'u La'au cabin at an elevation of 7,710 ft (2,350 m). The woodland at this elevation has been essentially sheep-free since about 1960. The southern transect lies entirely within the mouflon-holding pen, which was built in 1960. Data collected along the lower-elevation transects were identical to those collected along the upper-elevation transects.

Results and Discussion

Recovery Before Feral Sheep Eradication. After 12 years of protection from sheep grazing, aerial cover of alien and native herbaceous species was generally greater inside than outside the Pu'u Nanahā, Pu'u Kole, and Kaluamakani exclosures. Total herbaceous cover was 24.5% inside and 9.2% outside at Pu'u Nanahā; 21.5% inside and 7.2% outside at Pu'u Kole; and 1.2% inside and <0.1% outside at Kaluamakani. Apparently, both alien and native species responded favorably to release from grazing.

Recompiled data from Scowcroft and Giffin (1983, Table 2) show that aliens comprised smaller proportions of total herbaceous aerial cover inside than outside the three old exclosures: alien aerial cover was 91% inside and 98% outside the Pu'u Nanahā exclosure; alien aerial cover was 79% inside and >99% outside the Pu'u Kole exclosure.

Native species became reestablished inside the exclosure in spite of alien species. The increased cover of native species was mainly due to reestablishment of the native grasses pili uka, *Agrostis sandwicensis*, and *Deschampsia nubigena*. These grasses were only found inside the exclosures.

Herbaceous species were taller inside than outside the three old exclosures (Scowcroft and Giffin 1983). Sample sizes for hairy oatgrass, velvet grass, gosmore (*Hypochoeris radicata*), sweet vernalgrass, and sheep sorrel (*Rumex acetosella*) were large enough to statistically compare mean height inside with that outside. All of these alien species were significantly taller inside than outside ($p < 0.05$).

Changes in basal area of alien and native herbaceous species after three years of protection from sheep browsing were reported for the Pu'u o Ka'uha and Hale Pōhaku exclosures, which were built in 1972 (Scowcroft and Giffin 1983).

Alien plant basal area increased significantly over a three-year period inside and outside the Pu'u o Ka'uha exclosure. No difference in mean alien basal area was detected between fenced and unfenced populations, which could indicate 1) that growth and reproduction of alien populations were not limited by feral sheep grazing, 2) that feral sheep avoided the areas in the immediate vicinity of the exclosure, or 3) that alien plants that established inside the exclosure served as a population center and source of propagules for colonization of adjacent sparsely occupied sites. We believe all three situations were operative, at least to some degree. As stated, feral sheep did affect aerial cover of aliens outside the older exclosures (Pu'u Nanahā, Pu'u Kole, and Kaluamakani), the effect being most pronounced at the last and harshest of the six sites.

Alien plant basal area did not change significantly inside or outside the Hale Pōhaku exclosure. Also, alien basal area after three years of protection was not significantly greater inside than outside the exclosure. This site, which was on the inside of a cinder cone and characterized by a steep slope and unstable, coarse sandy soil (like the Kaluamakani exclosure), is harsher than the Pu'u o Ka'uha site, so the lack of a significant increase in alien basal cover is not surprising. Hale Pōhaku was also the least impacted by sheep.

Māmane regeneration and establishment was observed only inside exclosures. The native shrub 'āweoweo became established inside but not outside the Pu'u o Ka'uha exclosure. Scowcroft and Giffin (1983) did not comment about possible inhibition of native woody plant regeneration by alien plants.

Recovery After Feral Sheep Eradication. In this section we detail the result of vegetation sampling done in April and May 1986 at Wailuku and Pu'u o Ka'uha exclosures, both erected in 1972. Data from Scowcroft and Giffin (1983) are presented to complement the 1986 data for Pu'u o Ka'uha.

The Wailuku Exclosure. Inside the Wailuku exclosure, basal area for alien herbaceous species in 1976 averaged 200 $\pm$ 25 cm^2/m^2, whereas in 1986 it averaged 232 $\pm$ 41 cm^2/m^2 (Fig. 1). The difference in basal area was not statistically different, however ($p > 0.05$). Likewise, changes in alien plant basal area within individual strata between years were not statistically significant (Table 2).

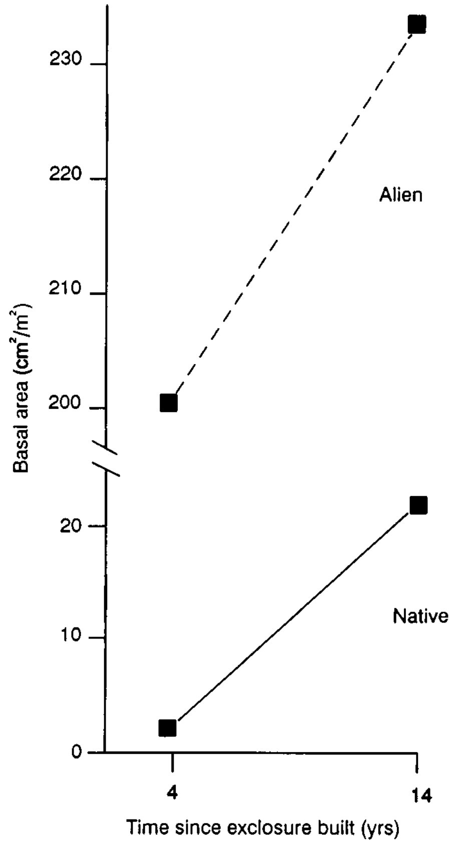

Figure 1. Basal area of alien and native herbaceous species inside the Wailuku exclosure at tree line on the east flank of Mauna Kea, by elapsed time since the exclosure was built.

We believe basal area changes in the cinders stratum were biologically significant, but because our sample size was small, we could not declare the difference statistically significant. In 1976, alien basal area averaged 47 $\pm$ 25 cm^2/m^2 (Table 2). By 1986, it had increased to 113 $\pm$ 62 $cm^2/m.^2$ These data, together with our observations of unsampled portions of the cinders stratum during the period 1976 to 1986, indicate that alien species were colonizing the previously sparsely populated cinders stratum. Hairy oatgrass in particular was establishing in the coarse cinders (Table 2). We suspect that the decrease in alien plant basal area in the rock stratum may also have biological significance. Some alien species may be poorly equipped to cope with the harsh

Table 2. Mean basal area cover (cm^2/m^2) of herbaceous species in the Wailuku exclosure in 1976 and 1986 by major strata.

Species	Light grass stratum 1976	Light grass stratum 1986	Cinders stratum 1976	Cinders stratum 1986	Rock stratum 1976	Rock stratum 1986	Entire exclosure 1976	Entire exclosure 1986
GRASSES AND SEDGES								
*Agrostis avenacea**	t**	--	--	--	--	--	t	--
*Agrostis sandwicensis**	--	0.1 (0.1)***	t	11.7 (11.4)	4.0 (2.3)	1.6 (1.6)	0.4 (0.2)	5.6 (5.3)
Anthoxanthum odoratum	78.2 (19.3)	123.5 (43.7)	31.6 (18.5)	55.2 (23.2)	26.5 (9.2)	15.7 (9.8)	52.3 (12.3)	82.9 (22.5)
Bromus carinatus	--	--	--	--	--	10.4 (10.2)	--	0.9 (0.8)
Bromus rigidus	--	--	0.2 (0.2)	--	--	--	0.1 (0.1)	--
Danthonia pilosa	263.9 (54.3)	188.1 (52.1)	8.8 (4.0)	54.0 (40.0)	74.7 (29.6)	10.7 (5.0)	129.7 (24.8)	111.1 (30.0)
*Luzula hawaiiensis**	0.8 (0.8)	--	--	--	1.8 (1.8)	t	0.5 (0.4)	t
Poa pratensis	--	t	--	--	--	--	--	--
Vulpia myuros	0.2 (0.2)	--	--	--	--	--	0.1 (0.1)	--

Species	Light grass stratum 1976	1986	Cinders stratum 1976	1986	Rock stratum 1976	1986	Entire exclosure 1976	1986
HERBS AND FORBS								
*Argyroxiphium sandwicense**	--	--	--	30.2 (29.9)	--	--	--	14.0 (13.9)
Hypochoeris radicata	6.5 (4.0)	73.0 (8.6)	6.8 (3.6)	4.0 (2.6)	89.5 (45.4)	24.3 (6.2)	13.5 (4.5)	36.9 (10.4)
Rumex acetosella	9.5 (9.4)	0.4 (0.4)	--	--	--	--	4.3 (4.2)	0.2 (0.2)
Senecio sylvaticus	t	--	t	--	t	--	t	--
*Tetramolopium humile**	3.0 (2.9)	0.7 (0.6)	--	t	3.2 (1.5)	1.4 (0.8)	1.6 (1.3)	0.4 (0.3)
FERNS								
*Asplenium trichomanes**	--	0.2 (0.2)	--	--	3.5 (3.0)	5.2 (3.7)	0.3 (0.3)	0.5 (0.3)
*Pellaea ternifolia**	t	1.5 (1.4)	--	--	2.0 (1.7)	6.1 (3.7)	0.2 (0.1)	1.2 (0.7)
Pteridium aquilinum	--	t	t	--	--	t	t	t

Table 2, continued.

Table 2, continued.

Species	Light grass stratum 1976	1986	Cinders stratum 1976	1986	Rock stratum 1976	1986	Entire exclosure 1976	1986
Alien species	358.3	385.0	47.4	113.2	190.7	61.1	200.0	232.0
	(46.1)	(63.9)	(25.1)	(62.2)	(80.2)	(24.8)	(24.8)	(41.2)
Native species	3.8	2.5	t	41.9	14.5	14.3	3.0	21.7
	(2.9)	(1.5)		(30.7)	(5.8)	(6.1)	(1.4)	(14.3)
Combined species	362.1	387.5	47.4	155.1	205.2	75.4	203.0	253.7
	(48.0)	(64.0)	(25.1)	(67.3)	(75.0)	(23.9)	(25.5)	(42.7)

*Native species.
**Trace amount, <0.1 cm^2/m^2.
***Values in parentheses are standard errors of the means.

conditions prevalent in the rock stratum, particularly the shallowness or complete absence of soil. About one-half of the decrease in alien basal area was due to hairy oatgrass (Table 2). Inside the Wailuku exclosure, total basal area for native herbaceous species, as shown in Figure 1, averaged 3 $\pm$ 1 cm^2/m^2 in 1976, and 22 $\pm$ 14 cm^2/m^2 in 1986. The difference between years was not statistically significant.

An examination of total native basal area data for individual strata shows that only the cinders community showed a change that could be interpreted as biologically significant (Table 2): 0.05 $\pm$ 0.05 cm^2/m^2 in 1976 and 42 $\pm$ 31 cm^2/m^2 in 1986. The primary native herbaceous colonizers of the cinders stratum were *Agrostis sandwicensis*, a perennial bunch grass that is conspicuously scarce in mouflon-browsed areas surrounding the Wailuku exclosure, and *Argyroxiphium sandwicense* var. *sandwicense*, the Mauna Kea silversword (Table 2). Data from a survey done in 1973, one year after the exclosure was built, showed that *Agrostis sandwicensis* was not found in the cinders stratum. In fact, we recorded only one individual at that time in the entire exclosure, and it was in the rock stratum. The silverswords in our sample and those found elsewhere in the cinders stratum are the result of natural regeneration by a small population planted by the Hawaii Division of Forestry and Wildlife in 1973 (Loope and Scowcroft 1985; C. Wakida, pers. comm. 1986; E. Powell, unpub. data). The data show that in the cinders stratum, the relative increase in basal cover was 9% per year for alien species, and 96% per year for native species.

Foliar cover inside the Wailuku exclosure was measured in 1986 for herbaceous species (Table 3). Aliens accounted for 99% of the foliar cover in the light grass community, 83% in the cinders community, and 92% in the rock community. Hairy oatgrass, sweet vernalgrass, and gosmore contributed most to alien foliar cover in all three communities.

Agrostis sandwicensis accounted for 40% of the native foliar cover in the cinders community. As we indicated earlier, this bunch grass seems to be an aggressive colonizer of barren cinder. The species comprised about 7% and 33% of the native herbaceous foliar cover in the light grass and rock communities.

The density of alien and native herbaceous species, each taken as a group, did not change significantly from 1976 to 1986, either in the separate strata or in the exclosure as a whole (Table 4). Generally, this result was also true for individual species. Hairy oatgrass in the rock stratum was an exception. Density of this alien grass decreased significantly from 26 plants/m^2 in 1976 to about 4 plants/m^2 in 1986. The decrease in basal area of hairy oatgrass noted earlier was apparently due to whole-plant mortality rather than death of portions of individuals. Gosmore in the light grass stratum was another individual species whose density changed significantly between measurements. It increased from less than 1 plant/m^2 in 1976 to over 16 plants/m^2 in 1986 (Table 4).

Table 3. Mean foliar cover (cm^2/m^2) for herbaceous species in the Wailuku exclosure in 1986, by major strata.

Species	Light grass stratum	Cinders stratum	Rock stratum	Entire exclosure
GRASSES AND SEDGES				
*Agrostis sandwicensis**	0.8 (0.8)**	30.8 (28.2)	3.3 (3.2)	14.9 (13.1)
Anthoxanthum odoratum	382.1 (131.8)	137.5 (49.9)	76.6 (55.5)	243.2 (64.2)
Bromus carinatus	--	--	71.2 (69.6)	5.9 (5.8)
Danthonia pilosa	469.0 (135.1)	140.3 (105.0)	45.9 (28.1)	281.3 (78.3)
*Luzula hawaiiensis**	--	--	0.4 (0.3)	t***
Poa pratensis	t	--	--	t
HERBS AND FORBS				
*Argyroxiphium sandwicense**	--	45.3 (44.8)	--	21.1 (20.8)
Hypochoeris radicata	349.5 (151.7)	91.9 (59.1)	347.8 (103.2)	229.7 (74.4)
Rumex acetosella	9.1 (8.1)	--	--	4.1 (3.7)
*tetramolopium humile**	6.2 (4.2)	0.4 (0.4)	8.6 (4.7)	3.7 (2.0)
FERNS				
*Asplenium trichomanes**	0.6 (0.6)	--	11.0 (8.8)	1.2 (0.8)
*Pellaea ternifolia**	3.9 (2.9)	--	26.1 (20.6)	3.9 (2.2)
Pteridium aquilinum	0.4 (0.3)	--	t	0.2 (0.2)
Alien species	1210.2 (292.0)	369.7 (207.4)	541.5 (219.9)	764.4 (164.6)
Native species	11.6 (5.0)	76.6 (50.0)	49.3 (17.1)	44.9 (23.4)
Combined species	1221.8 (291.9)	446.3 (205.9)	590.8 (228.6)	809.3 (164.2)

*Native species.
**Values in parentheses are standard errors of the means.
***Trace amount, < 0.1 cm^2/m^2.

Table 4. Mean plant density* (no./m^2) in the Wailuku exclosure in 1976 and 1986, by major strata.

Species	Light grass stratum 1976	Light grass stratum 1986	Cinders stratum 1976	Cinders stratum 1986	Rock stratum 1976	Rock stratum 1986	Entire exclosure 1976	Entire exclosure 1986
GRASSES AND SEDGES								
*Agrostis avenacea***	0.2 (0.2)***	--	--	--	--	--	0.1 (0.1)	--
*Agrostis sandwicensis***	--	t#	t	0.3 (0.3)	0.2 (0.1)	0.2 (0.2)	t	0.2 (0.1)
Anthoxanthum odoratum	7.6 (1.9)	12.0 (3.1)	1.9 (1.1)	3.5 (1.0)	7.0 (2.7)	5.0 (3.0)	4.9 (1.0)	7.5 (1.5)
Bromus carinatus	--	--	--	--	--	0.7 (0.6)	--	t
Bromus rigidus	--	--	1.2 (1.2)	--	--	--	0.6 (0.5)	--
Danthonia pilosa	15.7 (3.5)	17.9 (3.9)	0.8 (0.4)	3.8 (2.1)	26.0 (7.2)	4.3 (1.2)	9.6 (1.7)	10.2 (2.0)
*Luzula hawaiiensis***	t	--	--	--	0.4 (0.4)	0.1 (0.1)	t	t
Poa pratensis##	--	t	--	--	--	--	--	t
Vulpia myuros	42.6 (40.7)	--	--	--	--	--	19.3 (18.4)	--

Table 4, continued.

Table 4, continued.

Species	Light grass stratum 1976	Light grass stratum 1986	Cinders stratum 1976	Cinders stratum 1986	Rock stratum 1976	Rock stratum 1986	Entire exclosure 1976	Entire exclosure 1986
HERBS AND FORBS								
*Argyroxiphium sandwicense***	--	--	--	t	--	--	--	t
Hypochoeris radicata	0.6 (0.4)	16.3 (5.8)	0.5 (0.3)	6.7 (4.0)	17.4 (8.6)	18.6 (4.0)	1.9 (0.7)	12.0 (3.2)
Rumex acetosella	11.0 (10.8)	2.5 (2.2)	--	--	--	--	5.0 (4.9)	1.1 (1.0)
Senecio sylvaticus	0.4 (0.4)	--	t	--	3.2 (3.1)	--	0.5 (0.3)	--
*Tetramolopium humile***	0.3 (0.2)	0.5 (0.4)	--	t	1.5 (0.5)	0.4 (0.2)	0.2 (0.1)	0.3 (0.2)
FERNS								
*Asplenium trichomanes***	--	0.2 (0.2)	--	--	0.5 (0.4)	0.6 (0.4)	t	0.1 (0.1)
*Pellaea ternifolia***	t	0.2 (0.1)	--	--	0.6 (0.5)	0.3 (0.2)	t	0.1 (0.1)
Pteridium aquilinum	--	0.2 (0.1)	t	--	--	0.1 (0.1)	t	0.1 (0.1)

Species	Light grass stratum		Cinders stratum		Rock stratum		Entire exclosure	
	1976	1986	1976	1986	1976	1986	1976	1986
Alien species	77.8	48.9	4.4	14.0	53.6	28.7	41.8	30.9
	(54.0)	(9.4)	(2.9)	(6.8)	(12.1)	(6.0)	(24.5)	(5.3)
Native species	0.5	0.9	t	0.3	3.2	1.6	0.3	0.7
	(0.3)	(0.4)		(0.3)	(1.3)	(1.0)	(0.2)	(0.2)
Combined species	78.4	49.8	4.4	14.3	56.8	30.3	42.1	31.6
	(53.9)	(9.6)	(2.9)	(6.7)	(12.3)	(6.1)	(24.5)	(5.4)

*Densities for 1976 based on number of rooted plants/sampling unit; densities for 1986.
based on number of plants either rooted in or overhanging each sampling unit. Consequently, estimates for 1986 are slightly inflated.
**Native species.
***Values in parentheses are standard errors of the means.
#Trace amount, <0.1 plant/m^2.
##Mean number of *Poa pratensis* patches, not individual plants.

The amount of ground covered by live herbaceous foliage, irrespective of species, inside the Wailuku exclosure was quite small -- only 843 cm^2/m^2 or about 8% (Table 5). Litter, including woody detritus, covered 8% of the ground, and rock covered 40%. The remaining 44% was bare soil and coarse cinders. The area of each stratum in each of the four ground cover categories is also shown in Table 5.

Without grazing, growth of alien grasses was lush under māmane trees inside the exclosure. Although the vegetation under māmane trees was not sampled, we made a few incidental measurements of grass heights inside as well as outside the exclosure. Kentucky bluegrass, which was a common grass beneath māmane, averaged about 18 in. (45 cm) tall inside the exclosure, but only 2.4 in. (6 cm) tall outside. Kentucky bluegrass litter formed a thick dense mat inside, but not outside. Sweet vernalgrass averaged 31 in. (79 cm) tall inside the exclosure and only 4 in. (11 cm) tall outside.

Characteristics of the woody plant population inside the Wailuku exclosure are listed in Table 6. All woody plants are native species. Of the five species represented, māmane, pūkiawe, and ʻōhelo were regenerating, although ʻōhelo was doing so slowly (*i.e.*, only one seedling after 14 years without sheep browsing). In comparison, māmane was regenerating rapidly, with 136 seedlings and 37 sprouts tallied in 1986. Most māmane seedlings established in the light grass stratum and under the canopy edge of seed trees. *Dubautia arborea*, an endangered species, was represented by a single flowering adult.

A survey of the woodlands adjacent to the Wailuku exclosure revealed no woody regeneration, even though alien plant cover generally appeared similar to that inside. We concluded that herbaceous vegetation at these densities in general, and alien herbaceous vegetation in particular, does not prevent reestablishment of native woody species.

Puʻu o Kaʻuha Exclosure. Inside the Puʻu o Kaʻuha exclosure, alien and native herbaceous basal areas increased at the same rate (Fig. 2). Initially, herbaceous basal area was very small for both alien and native species: basal area of each represented less than 0.03% of the exclosure surface area. After 14 years of no grazing, basal area was 184 $\pm$ 65 cm^2/m^2 for aliens, and 167 $\pm$ 57 cm^2/m^2 for natives, or the equivalent of 1.8% and 1.7% basal cover. Alien and native basal areas were both significantly greater in 1986 than in 1975 ($p < 0.05$).

Two alien species, Kentucky bluegrass and mullein, made up about 98% of the alien basal area inside the exclosure in 1986 (Table 7). However, the data indicated that only mullein had significantly more basal area in 1986 than in 1975. Juvik and Juvik (this volume) report on the phenomenal spread and adaptation of this alien species to Mauna Kea's subalpine woodland.

Table 5. Mean vertical projected area (cm^2/m^2) of live aerial herbaceous plant cover, litter, bare soil, and rock in the Wailuku exclosure in 1986.

	Projected area by ground cover category			
Stratum	Herbaceous cover	Litter	Bare soil	Rock
Light grass	1,303(317)*	1,431(329)	3,655(669)	3,611(679)
Cinders	422(227)	251(88)	5,602(775)	3,725(688)
Rock	689(313)	967(127)	1,269(359)	7,075(184)
Entire exclosure	843(116)	844(155)	4,363(471)	3,950(444)

*Values in parentheses are standard errors of the mean.

Table 6. Woody plant population characteristics in the Wailuku exclosure in 1986.

Species	Density (Plants/ha)	Height (m)	Plant crown (m^2/plant)	Total crown (m^2/ha)
Sophora chrysophylla				
mature trees	19	4.6(0.2)*	24.2(0.8)	460.4
sprouts**	37	1.2(0.5)	1.3(1.3)	47.4
seedlings	136	0.8(0.7)	0.4(1.8)	55.8
Styphelia tameiameiae				
mature shrubs	141	0.6(0.5)	1.3(2.2)	184.7
seedlings	11	0.2(0.4)	t***	0.4
Dubautia arborea	1	1.7(-)	4.5(-)	4.5
Dubautia ciliolata	1	0.5(-)	0.5(-)	0.5
Vaccinium sp.				
mature shrubs	14	0.9(0.3)	0.2(1.1)	2.2
seedlings	1	0.2(-)	t	t

*Values in parentheses are coefficients of variation.
**Statistics are for sprout clumps rather than individual stems.
***Trace amount, <0.1 m^2/plant or <0.1 m^2/ha.

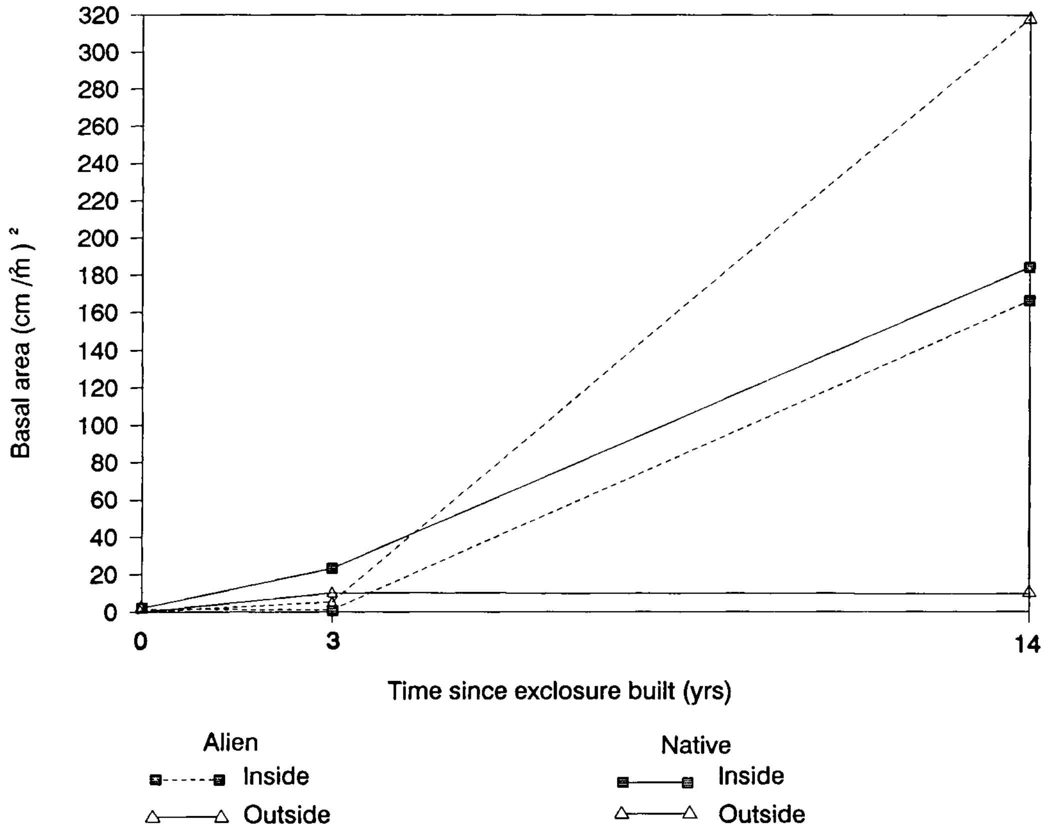

Figure 2. Basal area of alien and native herbaceous species inside and outside the Pu'u o Ka'uha exclosure near tree line on the west flank of Mauna Kea, by elapsed time since the exclosure was built.

Two native species, *Agrostis sandwicensis* and pili uka, comprised more than 99% of the native basal area in 1986. Only pili uka had significantly more basal area in 1986 than in 1975. Based on these data inside the exclosure, we conclude that native herbaceous species are reestablishing in spite of alien species. Probably interspecific competition is not widespread as yet inside the Pu'u o Ka'uha exclosure.

Plotted data for alien and native species just outside the exclosure appeared to indicate that basal area of aliens increased more rapidly than basal area of natives (Fig. 2). However, basal area variability for aliens was so large in 1986 that no significant difference was detected between years or between native and alien species in 1986 (Table 7). The large

Table 7. Average basal area (cm^2/m^2) of herbaceous plant species inside and outside Pu'u o Ka'uha sheep exclosure 2 months to almost 15 years after construction.*

Species	Inside 1972	Inside 1975	Inside 1986	Outside 1972	Outside 1975	Outside 1986
GRASSES AND SEDGES						
*Agrostis avenacea***	0.8(0.4)	8.8(3.2)	0.2(0.2)	0.1(0.1)	10.2(2.8)	1.1(0.4)
*Agrostis sandwicensis***	t#	0.1(0.1)	6.5(3.9)	--	t	--
Bromus rigidus	t	0.1(0.1)	t	--	--	0.4(0.1)
*Carex macloviana***	0.2(0.2)	4.8(4.5)	t	--	--	0.4(0.3)
Danthonia pilosa	--	--	--	--	--	0.1(0.1)
Hordeum murinum	--	t	--	--	--	t
Poa pratensis	--	t	95.5(57.3)	--	5.4(4.8)	255.2(222.3)
Stipa cernua	--	0.8(0.8)	2.9(1.7)	--	--	36.1(15.9)
*Trisetum glomeratum***	t	8.6(3.6)	177.2(66.1)	--	--	8.2(4.6)
Vulpia myuros	--	t	0.2(0.2)	--	t	t
FERN						
*Pellaea ternifolia***	0.2(0.2)	--	--	t	t	--
HERBS AND FORBS						
*Argemone glauca***	t	--	--	--	--	--
Cirsium vulgare	t	--	--	t	t	--
Epilobium billardierianum	--	--	--	--	--	2.8(2.7)
Erigeron sp.	--	--	--	--	0.1(0.1)	0.1(0.1)
Erodium cicutarium	t	t	--	--	t	t
*Gnaphalium purpureum***	0.9(0.1)	t	--	t	t	--
*Gnaphalium sandwicensium***	t	1.1(0.5)	0.2(0.1)	--	t	t
Heterotheca grandiflora	t	0.3(0.2)	0.5(0.2)	t	--	5.8(2.0)
Hypochoeris radicata	--	--	--	--	t	--

Table 7, continued.

Table 7, continued.

Species	Inside			Outside		
	1972	1975	1986	1972	1975	1986
Senecio sylvaticus	1.4(1.5)	t	--	0.1(0.0)	t	--
Sonchus oleraceus	t	0.1(0.1)	--	t	--	--
Taraxacum officinale	0.2(0.1)	t	--	t	t	t
Verbascum thapsus	t	0.2(0.0)	67.3(15.2)	t	t	17.3(3.6)
Alien species	1.6(0.6)	1.5(0.4)	166.4(56.9)	0.2(0.1)	5.6(5.2)	318.0(222.3)
Native species	2.1(n/a)##	23.4(n/a)	184.1(65.5)	0.2(0.1)	10.2	9.7(4.6)
Combined species	3.7(n/a)	24.9(n/a)	350.5(90.1)	0.4(n/a)	15.8(n/a)	327.7(222.0)

*1972 and 1975 based on Table 2 in Scowcroft and Giffin (1983).
**Native species.
#Trace amount, <0.1 cm^2/m^2.
##Equivalent standard errors not given in Scowcroft and Giffin (1983).

alien mean and standard error were mainly due to Kentucky bluegrass, which was patchily distributed. Thus, our data indicated no significant increase in basal area of either alien or native species in the 11 years since 1975. Even without the inflationary effect of Kentucky bluegrass, we suspect that increases would not have been significant. We suggest that continued grazing outside the exclosure up to 1981 retarded plant establishment and growth, and that too little time had elapsed since 1981 for manifestation of basal area differences comparable to those inside the exclosure.

In 1986, mean foliar cover for all herbaceous species combined, like mean basal area for all species combined, was not statistically greater inside than outside the Pu'u o Ka'uha exclosure: 1,485 $\pm$ 230 cm^2/m^2 inside, versus 1,046 $\pm$ 236 cm^2/m^2 outside (Table 8). Similarly, mean foliar cover of aliens inside the exclosure was not significantly different from that outside. On the other hand, native foliar cover was significantly greater inside than outside the exclosure: 772 $\pm$ 175 cm^2/m^2 inside, versus 85 $\pm$ 56 cm^2/m^2 outside. Most of the native foliar cover was due to pili uka.

Plant density was significantly greater in 1986 than in 1972 just after the exclosure was built (Table 9). This finding was true for alien, native, and all species combined. The exceptionally large density values for aliens in 1975 and 1986 were due to two annual species, ripgut grass and rat tail fescue (*Vulpia myuros*).

Recovery trends for alien and native species outside Pu'u o Ka'uha in the years since sheep "eradication" appear to be following the general trend observed inside during the first few years after fencing. Total alien and total native plant densities in 1975 inside the exclosure were not significantly different from those in 1986 outside the exclosure. Only two individual species, both aliens, were significantly more abundant in 1986 outside than in 1975 inside -- *Heterotheca grandiflora* and mullein. Both are prolific seed producers, and mullein is aggressively colonizing the southern and western flanks of Mauna Kea, as we noted earlier. Furthermore, neither is an important forage species, so their populations probably were expanding even when sheep were grazing.

None of the native plant species were more abundant in 1986 outside than in 1975 inside. For example, density of pili uka, the more common native perennial bunch grass, was 0.35 $\pm$ 0.23 cm^2/m^2 outside the exclosure after about five years without sheep grazing. This density was not significantly different from that inside the exclosure in 1975, after three years of freedom from sheep grazing.

The amount of ground covered by live herbaceous vegetation inside and outside the Pu'u o Ka'uha exclosure, irrespective of species, was small, as it was at Wailuku -- 1,485 cm^2/m^2, or 14.8%, inside, and 1,046 cm^2/m^2, or about 10.5%, outside (Table 10). Bare soil comprised about 26% of ground cover inside and about 40% of the ground cover outside the exclosure. Rocks comprised 42% and 26% of the ground

Table 8. Mean aerial cover (cm^2/m^2) of herbaceous species inside and outside the Pu'u o Ka'uha exclosure and in surrounding woodland at the same elevation (2,750 m) and in woodland at a lower elevation (2,350 m) in 1986.

Species	Exclosure		2750 m		2350 m	
	Inside	Outside	South	North	South	North
GRASSES AND SEDGES						
*Agrostis avenacea**	t**	t	t	t	--	--
*Agrostis sandwicensis**	29(16)#	--	--	--	--	--
Anthoxanthum odoratum	--	--	--	t	250(189)	620(177)
Bromus rigidus	t	t	t	120(58)	t	--
Bromus sp.	--	--	--	--	--	t
*Carex macloviana**	t	t	--	--	--	t
Dactylis glomerata	--	--	--	t	1650(1007)	2200(921)
Danthonia pilosa	--	t	520(309)	1440(520)	--	--
Danthonia sp.	--	--	--	t	--	--
Holcus lanatus	--		--	--	25(1164)	1460(588)
Hordeum murinum	--	t	--	--	--	--
Lolium sp.	--		--	--	50(50)	t
Pennisetum setaceum	--	--	--	20(20)	--	--
Poa pratensis	96(58)	257(223)	--	620(571)	725(345)	940(492)
Stipa cernua	24(14)	176(70)	120(120)	120(80)	--	
*Trisetum glomeratum**	740(179)	82(56)	20(20)	--	300(191)	--
Vulpia myuros	t	t	--	--	--	--
FERNS						
Asplenium trichomanes	--	--	--	t	--	t
Pellaea ternifolia	--	--	--	t	--	--
Pteridium aquilinum	--	--	--	t	--	--
HERBS AND FORBS						
Cirsium vulgare	--	--	--	t	50(50)	t
Epilobium billardierianum	--	t	--	80(80)	t	t

Species	Exclosure Inside	Exclosure Outside	2750 m South	2750 m North	2350 m South	2350 m North
Erigeron sp.	--	t	t	t	t	--
Erodium cicutarium	--	t	t	t	--	--
Geranium homeanum	--	--	--	--	--	t
*Gnaphalium sandwicensium**	t	t	t	t	t	t
Heterotheca grandiflora	25(8)	173(34)	100(55)	120(80)	--	t
Hypochoeris radicata	--	--	--	--	--	20(20)
Medicago lupulina	--	--	--	--	50(50)	440(250)
Oxalis corniculata	--	--	--	--	t	--
Plantago sp.	--	--	--	--	--	t
Rumex acetosella	--	--	--	--	t	220(102)
Senecio sylvaticus	--	--	--	t	t	--
Sonchus oleraceus	--	--	t	--	t	--
Stenogyne sp.*	--	--	--	--	25(25)	--
Tagetes minuta	--	--	--	t	--	--
Taraxacum officinale	--	t	--	t	25(25)	2(20)
Urtica urens	--	--	--	--	t	--
Verbascum thapsus	564(136)	321(81)	460(214)	620(49)	100(71)	60(60)
Verbesina encelioides	--	--	--	t	--	--
Veronica serpyllifolia	--	--	--	--	--	t
Alien species##	713(141)	961(232)	1280(485)	3260(747)	4550(1805)	6120(306)
Native species##	772(175)	85(56)	40(24)	0(--)	300(192)	0(--)
All species combined##	1485(230)	1046(236)	1320(491)	3260(747)	4850(1618)	6120(306)

*Native species.
**Only trace amount found on sample plots.
#Values in parentheses are standard errors of the mean.
##Inclusion of trace amounts in summations results in subtotals that exceed the sum of tabled values for individual species.

Table 9. Average density* (no./m^2) of herbaceous plants inside and outside Pu'u o Ka'uha sheep exclosure 2 months to almost 15 years after construction.

Species	Inside			Outside		
	1972	1975	1986	1972	1975	1986
GRASSES AND SEDGES						
*Agrostis avenacea***	0.5(0.2)#	5.4(1.4)	0.2(0.1)	t##	6.7(1.9)	0.9(0.4)
*Agrostis sandwicensis***	t	t	0.2(0.1)	--	t	--
Bromus rigidus	t	17.8(16.9)	0.4(0.3)	--	t	56.5(17.7)
*Carex macloviana***	t	t	t	--	--	t
Danthonia pilosa	--	--	--	--	--	t
Hordeum murinum	--	0.2(0.1)	--	--	--	0.8(0.8)
Poa pratensis###	--	t	0.3(0.1)	--	0.2(0.2)	0.5(0.3)
Stipa cernua	t	t	0.3(0.2)	--	--	2.7(1.6)
*Trisetum glomeratum***	t	0.2(0.1)	2.8(0.6)	--	t	0.4(0.2)
Vulpia myuros	--	17.8(7.7)	t	--	1.0(0.8)	t
FERN						
*Pellaea ternifolia***	t	--	--	t	t	--
HERBS						
*Argemone glauca***	t	t	--	--	--	--
Cirsium vulgare	t	--	--	t	t	--
Epilobium billardierianum	--	--	--	--	--	t
Erigeron sp.	--	--	--	--	t	0.3(<0.1)
Erodium cicutarium	t	0.3(0.2)	--	--	t	8.0(3.6)
*Gnaphalium purpureum***	0.6(0.1)	1.4(0.4)	--	t	0.8(0.2)	--
*Gnaphalium sandwicensium***	t	1.1(0.6)	0.5(0.2)	--	t	0.2(0.1)
Heterotheca grandiflora	t	t	1.5(0.6)	--	t	15.6(3.4)
Hypochoeris radicata	--	--	--	--	t	--

Species	Inside 1972	Inside 1975	Inside 1986	Outside 1972	Outside 1975	Outside 1986
Senecio sylvaticus	0.3(0.1)	t	--	t	0.4 (0.2)	--
Sonchus oleraceus	t	t	--	t	--	--
Taraxacum officinale	t	t	--	t	t	t
Urtica urens	--	--	--	--	t	--
Verbascum thapsus	t	t	6.8 (2.1)	--	t	3.4 (0.8)
Alien Species	0.3(0.1)	36.3 (17.1)	9.3 (2.6)	0.2(0.1)	12.0 (0.5)	88.0 (18.4)
Native Species	1.2(0.2)	8.0 (1.1)	3.8 (0.5)	0.1(0.0)	7.5 (1.2)	1.5 (0.2)
Combined Species	1.5(0.3)	44.3 (18.1)	13.0 (2.7)	0.3(0.1)	9.1 (2.7)	89.5 (18.4)

*Densities for 1976 based on number of rooted plants in each sampling unit and densities for 1986 based on number of plants either rooted in or overhanging each sampling unit. Consequently, estimates for 1986 are slightly inflated.

**Native species.

#Values in parentheses are standard errors of the means.

##Trace amount, $<0.1/m^2$.

###Mean number of *Poa pratensis* patches, not individual plants.

Table 10. Mean vertical projected cover (cm^2/m^2) by cover class and data collection site at 2,750 m elevation in and around the Pu'u o Ka'uha exclosure in 1986.

Cover class	North transect	Pu'u o Ka'uha exclosure Inside	Pu'u o Ka'uha exclosure Outside	South transect
Herbaceous cover	3260(747)*	1485(230)	1046(236)	1320(491)
Litter	2340(435)	1762(419)	2377(397)	1600(601)
Bare Ground	1140(808)	2580(289)	3977(396)	2140(730)
Rock	3260(568)	4173(504)	2600(337)	4940(816)

*Values in parentheses are standard errors of the mean.

cover inside and outside, with litter making up the rest of the ground cover. None of the differences between inside and outside were statistically significant ($p > 0.05$).

Māmane seedlings were more numerous outside than inside the Pu'u o Ka'uha exclosure (Table 11). A partial explanation for the higher seedling density outside is that the seed reserve outside was slightly larger than inside (Scowcroft and Giffin 1983). The ratio of seed density inside to outside was 0.59, and the ratio of seedling density inside to outside was 0.63.

Mean height and crown area were not significantly different for the two māmane seedling populations. Initially, we could not understand why the population means should be so similar when we knew that few seedlings survived outside before 1981 (Scowcroft and Giffin 1983). The explanation is that the distributions for seedling height and crown area (Fig. 3) were not the same inside and outside, and the variances were so large that statistical differences were not detectable. The distribution inside tended to be bimodal, thus indicating that some seedlings were older (larger) than the rest (*i.e.*, more advanced stand development inside). This result was expected because recovery inside had a nine-year head start on recovery outside.

More than twice as many adult 'āweoweo shrubs were found inside as outside Pu'u o Ka'uha. Mean plant height and canopy area for the two populations were not significantly different ($p > 0.05$). 'Āweoweo seedlings were over 13 times as abundant inside than outside. We believe that the greater abundance of both adult and seedling 'āweoweo inside the exclosure are due to heavier seed rain over a longer period. As Scowcroft and Giffin (1983) reported, 'āweoweo was among the first native woody species to establish inside Pu'u o Ka'uha, and its growth was rapid. Outside, sheep kept the species completely suppressed until about 1981 when the sheep were eliminated.

Table 11. Woody plant population characteristics in the Pu'u o Ka'uha exclosure and in a comparable area outside the exclosure in 1986.

Species	Density (Plants/ha)		Height (meters)		Plant Crown (sq. m/plant)		Total Crown (sq. m/ha)	
	Inside	Outside	Inside	Outside	Inside	Outside	Inside	Outside
Chenopodium oahuense								
Mature shrubs	391	183	1.2(0.4)*	1.4(0.3)	1.7(2.1)	1.6(0.9)	668.6	287.3
Seedlings	415	31	0.5(0.5)	0.6(0.4)	<0.1(1.7)	<0.1(0.9)	8.3	0.6
Myoporum sandwicense								
Mature trees	--	6	--	3.1(0.1)	--	17.8(0.6)	--	107.1
Seedlings	--	3	--	0.4(--)	--	0.3(--)	--	0.8
Sophora chrysophylla								
Mature trees	14	17	5.4(0.2)	5.8(0.3)	41.5(0.5)	36.1(0.6)	581.3	614.4
Sprouts**	34	23	2.5(0.4)	1.8(0.2)	12.0(2.2)	7.0(1.6)	409.4	160.8
Seedlings	204	326	1.7(0.7)	0.9(0.8)	2.0(1.2)	0.7(1.8)	406.0	224.9

*Value in parentheses is coefficient of variation.
**Statistics are for sprout clumps rather than individual stems.

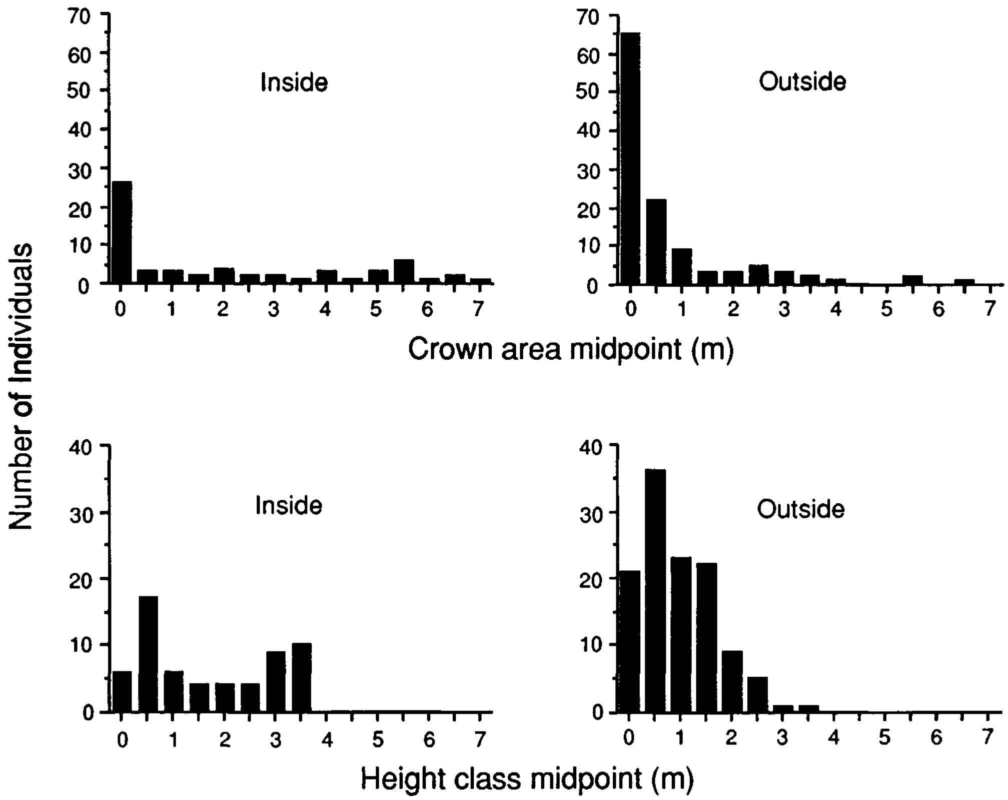

Figure 3. Height and crown area class distributions for seedling *Sophora chrysophylla* populations inside and outside the Pu'u o Ka'uha exclosure in 1986.

The more advanced recovery of vegetation inside the exclosure was not evident from examination of height and crown area data for 'āweoweo (Fig. 4). This species lives only about 10 years, and the original colonizers, although they had individual crown areas greater than 52 ft^2 (16 m^2), were all dead by 1986. The plants we measured were their progeny. Possibly, some of the adult 'āweoweo outside were also the offspring of the original colonizers inside the exclosure.

Naio was found outside the exclosure, but not inside (Table 11). When the exclosure was built, no naio trees were in the immediate vicinity. No seedlings or trees occurred within study boundaries in 1975 (Scowcroft and Giffin 1983). Based on mean height and canopy area data, we conclude that naio grows more rapidly than māmane in this tree line zone. The species is regenerating from seed.

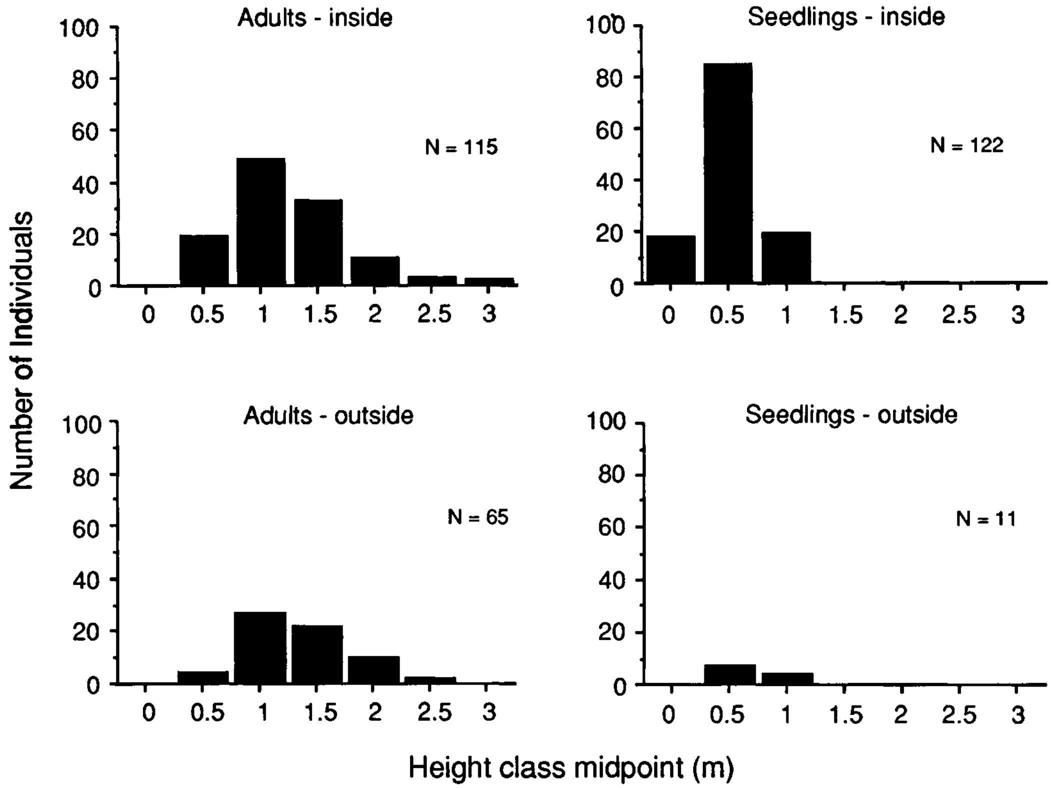

Figure 4. Height class distributions for adult and seedling *Chenopodium oahuense* populations inside and outside the Pu'u o Ka'uha exclosure in 1986.

Tree Line Zone Either Side of Pu'u o Ka'uha. We found no evidence that recovery of alien or native herbaceous species elsewhere in the tree line zone was different from that just outside the Pu'u o Ka'uha exclosure. Mean foliar cover estimates along transects at 9,020 ft (2,750 m) elevation were not significantly different from the estimate outside the exclosure (Table 8). The average proportions of ground covered by litter, bare soil, and rock along the two transects (Table 10) were not significantly different from outside the exclosure either. We conclude that the outside study area at Pu'u o Ka'uha is representative of the tree line zone on the western flank of the mountain.

Recovery of native herbaceous species inside the Pu'u o Ka'uha exclosure was more advanced than elsewhere in the tree line zone, *i.e.*, significantly more total native foliar cover occurred inside the exclosure than along the two transects at 9,020 ft (2,750 m) elevation (Table 8).

Recovery had been underway for 14 years inside, but only for five years elsewhere in the tree line zone. In contrast, judging from estimates of total alien foliar cover, recovery of alien herbaceous species inside the exclosure was not more advanced than elsewhere in the tree line zone (Table 8).

We call attention to the presence of fountain grass, along the north transect at 9,020 ft elevation (Table 8). This grass is a potential fire hazard and threatens native species, most of which are vulnerable to burning. We had not encountered it at this elevation in previous years, but a small population of scattered individuals has established in what we hope is an isolated situation. However, the seed source now exists near tree line to support expansion of this noxious species.

The only new woody species encountered along the 9,020 ft elevation transects was ʻaʻaliʻi, which was represented by one adult and one seedling in our sample (Table 12). No adult māmane trees occurred within sample plots, although scattered individuals grew all along the transects.

Naio was encountered only along the southern transect at 9,020 ft elevation and in the study area outside the Puʻu o Kaʻuha exclosure. Apparently the exclosure is located at an ecotone between māmane woodland to the north and naio-māmane woodland to the south. Characteristics of māmane seedling populations were not statistically different ($p > 0.05$) between the two woodland communities (Table 12). *Chenopodium* seedlings were found along the north transect in the māmane woodland, but not along the south transect in the naio-māmane woodland. Even adult ʻāweoweo shrubs were sparse in the mixed woodland.

Recovery of woody plant populations at the Puʻu o Kaʻuha exclosure (both inside and outside) was more advanced than elsewhere in the tree line zone (Tables 11 and 12). Crown area and average height of māmane seedlings were greater at the exclosure site than along the two transects established to either side of the exclosure site. Similarly, crown areas and density of ʻāweoweo adults and seedlings were greater inside and outside the exclosure than along transects to either side.

<u>Lower-elevation Woodland Around Puʻu Laʻau</u>. The woodland around Puʻu Laʻau has been relatively free of sheep for 20 to 30 years due to frequent human disturbance and the tendency of feral sheep to avoid areas with tall grass (Giffin 1976). Examination of vegetation recovery along a southern and northern transect at 7,710 ft (2,350 m) elevation showed that alien herbaceous species dominate the herbaceous community (Table 8). Total alien foliar cover averaged 4,550 $\pm$ 1,805 and 6,120 $\pm$ 306 cm^2/m^2 along the southern and northern transects. Total alien foliar cover was significantly greater along the north transect at 7,710 ft elevation than in the tree line zone. The only native herbaceous species with more than trace amounts of foliar cover were pili uka and *Stenogyne* sp., both of which were encountered only along the southern transect.

The proportion of ground covered by litter, rock, and moss or as exposed bare soil is shown in Figure 5. Significantly less rock cover existed at

Table 12. Woody plant population characteristics along transects at 2,350 and 2,750 m elevation on the west flank of Mauna Kea.

Transect	Elevation (m)	Species	Density* (no./ha)	Crown area* (m^2/ha)	Height** (m)
South	2350	*Sophora chrysophylla*			
		adults	151(78)	2346(1273)	4.7(2.6)
		seedlings	239(181)	38(36)	0.5(0.7)
		sprouts#	64(45)	46(45)	2.7(0.2)
		Chenopodium oahuense			
		seedlings	10(10)	< 1(< 1)	0.4(-)
North	2350	*Sophora chrysophylla*			
		adults	108(13)	2384(279)	4.9(2.0)
		seedlings	140(54)	17(8)	0.5(0.6)
		sprouts	38(38)	43(43)	1.8(1.1)
		Coprosma sp.			
		seedlings	13(8)	< 1(< 1)	0.6(0.3)
South	2750	*Sophora chrysophylla*			
		seedlings	471(308)	61(49)	0.5(0.6)
		Chenopodium oahuense			
		adults	13(13)	23(22)	1.2(0.8)
		Dodonaea sp.			
		adults	6(6)	5(5)	0.3(-)
		seedlings	6(6)	< 1(< 1)	0.3(-)
		Myoporum sandwicense			
		adults	102(78)	2059(914)	3.2(1.1)
		seedlings	153(102)	48(30)	0.7(0.8)
North	2750	*Sophora chrysophylla*			
		seedlings	414(334)	79(67)	0.5(0.5)
		sprouts	45(30)	272(143)	1.8(1.2)
		Chenopodium oahuense			
		adults	108(76)	243(168)	1.6(0.5)
		seedlings	57(42)	6(6)	0.5(0.3)

*Mean density and crown area per sample plot expanded to means per hectare and associated standard errors of the means.
**Mean height per individual and associated standard deviation in parentheses.
#Characteristics are for sprout clumps, not individual sprouts.

7,710 ft (2,350 m) elevation than at tree line. Moss-covered soil was found only along the lower transects and probably indicates moister conditions there owing to frequent afternoon fog and mist. Bare soil comprised less than 1% of the cover along the north transect at 7,710 ft elevation, but more than 29% of the cover along the south transect. Herbaceous plants occupied most of the available space along the north transect, whereas along the south transect, space was still available for alien and native plant establishment.

Recovery of two woody species in the low-elevation woodland was like that observed in the tree line woodland (Table 12). Māmane seedlings were just as numerous and about the same size at 7,710 ft (2,350 m) as at

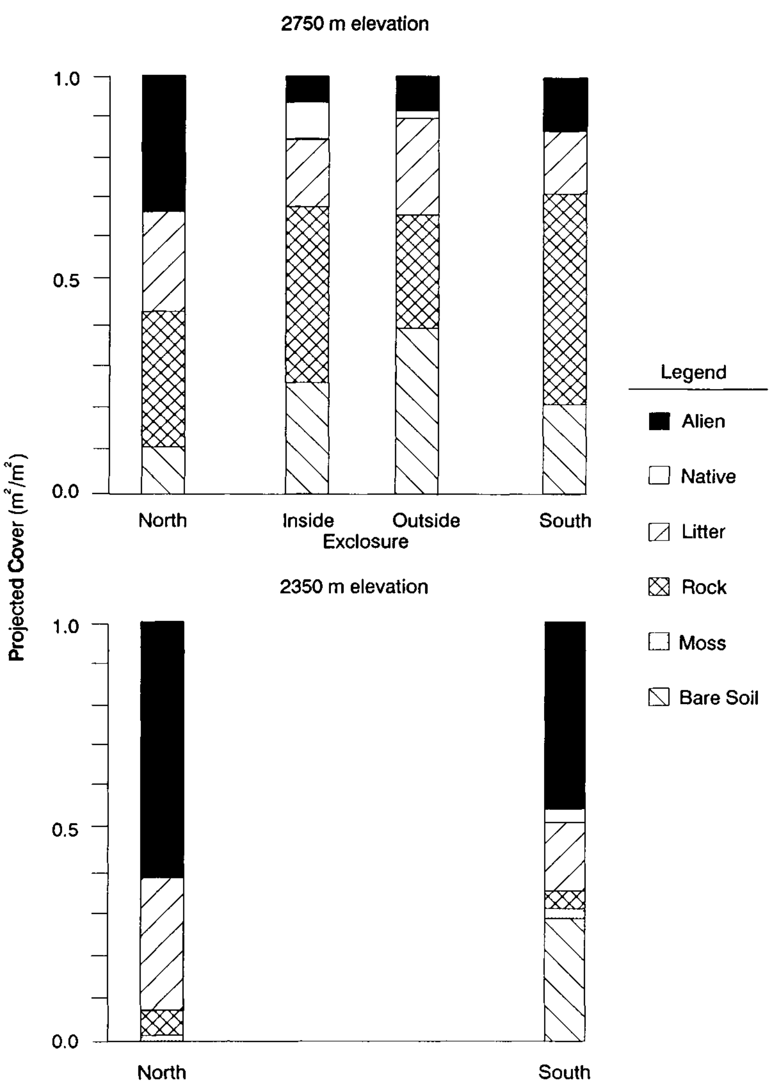

Figure 5. Projected cover of alien and native herbaceous plants, litter, rock, moss, and bare soil inside, outside, and in the vicinity of the Pu'u o Ka'uha exclosure and in the māmane woodland at 2,350 m elevation near Pu'u La'au, 1986.

9,020 ft (2,750 m) elevation. Density and size of ‘āweoweo seedings were also alike at the two elevations.

If sheep foraging pressure has been low in the low elevation woodland for 20 to 30 years, why are populations of māmane and ‘āweoweo regeneration not more advanced in terms of both density and size characteristics? Mature māmane trees appear more numerous and more vigorous in the lower stands than in the upper stands, and we would expect seed production and soil seed reserves to be greater as well. We doubt that lack of seed accounts for the lack of advanced regeneration. Pilo seedlings occurred at 7,710 ft (2,350 m) elevation, but not at the higher elevation. On the other hand, ‘a‘ali‘i and naio reproduction were only found at higher elevation. Possibly, dense alien herbaceous cover inhibited woody native plant establishment at the low elevation. Our impression is that alien grass cover along the northern transect at 7,710 ft (2,350 m) elevation is dense enough now to interfere with establishment of native woody species. Whether it has been dense enough to do so for the past 20 to 30 years is unknown.

CONCLUSIONS

Release from grazing and browsing has not resulted in significant increases in basal area, density, or foliar cover of most alien plant species in the māmane woodland of Mauna Kea. Mullein increased significantly at the Pu‘u o Ka‘uha exclosure, but we saw no evidence that the increase was due to release from sheep grazing. Rather, the unpalatable, prolific seed-producing species appeared to aggressively colonize sites regardless of grazing pressure.

Release from grazing and browsing has benefitted native species in tree line communities, however, especially those species that are highly palatable and highly susceptible to damage (*e.g.*, māmane, ‘āweoweo, pili uka, and *Agrostis sandwicensis*). The colonization and reestablishment of these species inside exclosures as well as outside exclosures after eradication of feral sheep indicates that these natives were able to persist in an ecosystem damaged by animals. As Rabinowitz *et al.* (1984) suggested, the persistence and ultimate resurgence of native grass species may be indicative of competitive superiority in the somewhat harsh environment of Mauna Kea's subalpine woodlands. Mueller-Dombois (1981) concluded that native Hawaiian plants cannot be considered weak competitors.

On the basis of our findings, we believe that control of most alien plant populations on upper Mauna Kea is unwarranted. Native species are recovering in spite of alien species. Even at lower elevation in the māmane woodland, recovery of native woody species is evident, although circumstantial evidence suggests that the rate of recovery is slower there than in the tree line zone.

Control of two alien species, fountain grass and possibly German ivy, may be desirable while their populations are still relatively small.

Fountain grass is not yet interfering with recovery of native plants in the māmane woodlands we examined, but it has the potential to do so. Furthermore, it is a fire-adapted species that is capable of replacing nearly all of the native ground layer species (Jacobi and Scott 1985). Repeated fires may result in the elimination of native woody plants as well. German ivy was not encountered in our sampling, but it is established nearby in the Kaohe Game Management Area just below Pu'u La'au. Both species have been declared noxious by the Hawaii Department of Agriculture (Hawaii Revised Statutes, Ch. 68, Noxious Weed Rules).

Data from Pu'u o Ka'uha and vicinity clearly show that native species will recover once sheep foraging pressure is eliminated. Data from Wailuku indicate that a similar native vegetation response can be expected on that side of the mountain if mouflon are eliminated. Both māmane and *Agrostis sandwicensis* reestablished at Wailuku in the absence of grazing and browsing. Neither species establishes where mouflon sheep can get to them. On the basis of these results and those of Scowcroft and Giffin (1983), we conclude that maintenance of mouflon sheep at 1986 population levels will prevent recovery of native species in those portions of the Mauna Kea Forest Reserve where the animals concentrate. Furthermore, should feral sheep reestablish, they too will interfere with native species recovery wherever the animals concentrate.

Because mouflon and feral sheep are problems only as defined by management objectives, managers must have a clear statement of land management policy for the land in question, especially if the land use is zoned Conservation (Riney 1964). With a clear statement of policy, managers can examine ecosystem trends and decide if they will continue to the detriment of the land. If the trends indicate that maintenance of large herbivores is in conflict with the policy statement, either in part or whole, then one of three decisions should be made: change the policy, get rid of the animals, or both. This is the prerogative of policy makers, not managers or researchers.

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