

Factors Related to the Recovery of Subalpine Woodland on Mauna Kea, Hawaii¹

Steven C. Hess², Paul C. Banko, Gregory J. Brenner, and James D. Jacobi

U.S.G.S. Biological Resources Division, Pacific Island Ecosystems Research Center, P.O. Box 44, Hawaii National Park, Hawaii 96718, U.S.A.

ABSTRACT

We measured mature tree and sapling density, tree associations, crown size, age structure, recovery from ungulate browsing, and grass cover at four study sites in two types of subalpine woodland on Mauna Kea volcano, island of Hawaii. Beginning in 1981, introduced ungulates were reduced in number to allow regeneration of *Sophora chrysophylla* (mamane) in habitat supporting the endangered Hawaiian finch, *Loxioides bailleui* (palila). We found *Sophora* regeneration at all four study sites, but regeneration was higher in mixed species woodland with codominant *Myoporum sandwicense* (naio) than in areas where *Sophora* dominated. Regeneration of *Myoporum* was uniformly very low in comparison. Invasive grass cover, which suppresses *Sophora* germination, was highest in mid-elevation woodland where *Sophora* dominated. The distribution of mature and sapling *Sophora* were both related to study site, reflecting previous ungulate browsing and uneven recovery due to grasses. Densities of *Sophora* snags were not different among any of the sites, suggesting a more even distribution in the past. Selective browsing before ungulate reduction may have favored *Myoporum* over *Sophora*, leading to high densities of mature *Myoporum* in codominant woodland. After ungulate reduction, however, we found no pattern of competitive inhibition by *Myoporum* on regeneration of *Sophora*. Reduction of *Myoporum* is not likely to enhance habitat for *Loxioides* as much as supplemental plantings of *Sophora*, grass control, and continued ungulate eradication. Mid-elevation *Sophora* woodland areas, where *Loxioides* forage and nest in high densities, would benefit the most from these management actions.

Key words: browse damage; Hawaii; invasive grasses; *Loxioides*; mamane; palila; recovery; *Sophora*; subalpine woodland.

DRY FORESTS OF THE HAWAIIAN ISLANDS, like dry forests in other tropical regions, have been extensively altered by human activity (Murphy & Lugo 1986, Cuddihy & Stone 1990), and as in other tropical areas, Hawaiian dry forest avifaunas have fared worse than those of humid forests (Stotz *et al.* 1996). The endangered finch (Fringillidae: Drepanidinae), *Loxioides bailleui* Oustalet (palila), is now the only remaining endemic bird that requires dry forest, living exclusively in subalpine woodland of Mauna Kea volcano, island of Hawaii (Scott *et al.* 1986). *Loxioides* rely primarily on the green seeds of the endemic leguminous tree, *Sophora chrysophylla* Salisb. (Mamane), for food. They also eat *Sophora* flowers, flower buds, foliage flush (van Riper 1980a), and moth larvae that inhabit pods (Biological Resources Division, pers. comm.), and depend on *Sophora* for nesting and roosting sites. *Loxioides* were once more widely distributed in lowlands and on at least one other island before Polynesian contact (Olson & James 1982). They are currently restricted to 139 km², less than five per-

cent of their historical distribution (Scott *et al.* 1984, 1986; Jacobi *et al.* 1996).

Subalpine woodlands dominated by *Sophora* developed in the absence of herbivorous mammals, as did all other Hawaiian forests (Carlquist 1970). The largest remaining stand of *Sophora* subalpine woodland, a unique forest of the world, is on Mauna Kea volcano. Rain shadow effects of Mauna Kea and extreme substrate drainage account for the semiarid aspect of the woodland. All of the dominant tree species are endemic to the Hawaiian Islands where it is cooler than lowland tropical or subtropical dry forests (Murphy & Lugo 1986), with frequent freezing temperatures, relatively aseasonal precipitation, and substantial cloud-water interception (Juvik & Nullet 1993, Juvik *et al.* 1993). Herbivorous mammals, including feral sheep (*Ovis aries*), mouflon sheep (*O. musimon*), feral goats (*Capris hircus*), feral cattle (*Bos taurus*), and feral horses (*Equus caballus*) repeatedly have reached high population densities on Mauna Kea and suppressed regeneration of *Sophora* since their introductions beginning in 1793. (Hartt & Neal 1940, Warner 1960, Giffin 1976, 1982; Scowcroft & Giffin 1983, Scowcroft & Sakai 1983, Scowcroft 1983, Juvik & Juvik 1984, Mountainspring *et al.* 1987). Alien grasses, such as *Dactylus glom-*

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² Present Address: Fish & Wildlife Management Program, Montana State University, P.O. Box 173460, 301 D Lewis Hall, Bozeman Montana 59717-3460, U.S.A.

erata, *Holcus lanatus*, *Anthoxanthum odoratum*, and *Poa pratensis*, now dominate understory vegetation in subalpine woodland on Mauna Kea (Smith & Tunison 1992, Amarasekare 1993, Williams 1994). *Sophora* facilitates grass growth by providing a high nutrient environment, with germination of *Sophora* being also suppressed by grasses (Williams 1994). Fires in subalpine woodland are rare natural events, but invasive grasses have added continuous fine fuels (Smith & Tunison 1992), increasing the likelihood of intense fires that could result in the short-term destruction of *Loxioides* habitat.

Selective browsing of *Sophora* by feral mammals may have caused increased densities of *Myoporum sandwicense* A. Gray (Myoporaceae; naio) in areas where these trees codominated (van Riper 1980b, Cuddihy & Stone 1990). Hunting pressure caused feral mammals to concentrate browsing at high elevation and in other areas not accessible by road (Giffin 1976, 1982; Scowcroft & Giffin 1983). The current pattern of *Sophora* distribution on Mauna Kea may have been affected by a combination of localized browsing, seedling suppression from introduced grasses, and possibly, competitive suppression from other native plants. These factors, as well as existing feral *Ovis* spp. populations in some areas, may currently control regeneration in subalpine woodland.

The recovery plan for *Loxioides* calls for sustaining and expanding *Sophora* forest and preventing further damage by removing, excluding, and fencing feral animals from *Loxioides* habitat (U.S. Fish and Wildlife Service 1986). Federal court rulings in 1979 and 1986 mandated removal of feral *Ovis* spp. and *Capris* to allow regeneration of *Sophora* trees for *Loxioides*. Monitoring of vegetation condition and trend was also recommended, but no monitoring programs were established after animals were reduced beginning in 1981 (Scowcroft & Giffin 1983, Scott *et al.* 1986). Mountainspring *et al.* (1987), using semiquantitative methods, concluded that *Sophora* regeneration occurred in response to reduced browsing pressure. They also concluded that *Sophora* was replacing *Myoporum* in areas where the two species codominate. Reduction of *Myoporum* has been considered as a potential management action to improve *Loxioides* habitat with the implicit assumption that it limits *Sophora* through competition; however, there have been no studies to determine if such an interaction exists. If there is no negative association between these species, then *Myoporum* reduction is not likely to be an effective management action.

We measured mature tree and sapling density,

tree associations, crown size, age structure, and grass cover to describe woodland structure and to identify factors correlated with *Sophora* recovery from ungulate browsing in habitat supporting *Loxioides* on the west slope of Mauna Kea. The objectives of this study were to determine: (1) if there are differences in regeneration, age structure, and crown size of *Sophora* related to woodland type, site, or elevation; (2) if *Myoporum* or grasses are negatively associated with *Sophora* regeneration; and (3) estimate current ungulate browse damage on *Sophora* regeneration. Additionally, this data establishes a background for habitat structure comparisons with subalpine woodland ecosystems in other areas on the island of Hawaii that are being considered for restoration of *Loxioides*.

METHODS

We used the point-centered quarter method, a transect-based distance method (Mueller-Dombois & Ellenberg 1974), to estimate densities of all mature trees, saplings, and tree associations at four established *Loxioides* study sites on the west slope of Mauna Kea, island of Hawaii (19°50'N, 155°35'W). The four study sites were arranged on an elevational gradient that extends 1978–2816 m in dry subalpine woodland of the Mauna Kea Forest Reserve (Fig. 1).

Substrates were severely drained vitrandepts composed of volcanic cinder and ash with exposed basaltic lava flows. Surface substrate age was between 4000 and 14,000 years (Wolfe & Morris 1996). Much of the organic soil layer has been lost to erosion and grazing since European colonization (Warner 1960). Temperature averages $11.1 \pm 1.5^\circ$ C annually and rainfall averages 511 mm (Juvik & Nullet 1993). January through April and August are the wettest months with average rainfall > 50 mm/mo. June is the driest month with < 20 mm/mo (Juvik, pers. comm.). In addition to rainfall, there is also substantial fog-drip interception by trees from a cyclic diurnal influx of humid, low elevation air that may account for as much as 38 percent additional precipitation (Juvik & Nullet 1993).

The study sites were designated in order of descending elevation: upper, mid-elevation north, mid-elevation south, and lower. Although the mid-elevation north site overlapped 74 percent of the mid-elevation south site in altitude, the sites contained different woodland types (Fig. 1). The upper and mid-elevation north sites were comprised almost exclusively of *Sophora* with 5–30 percent canopy cover, and the mid-elevation south and lower sites con-

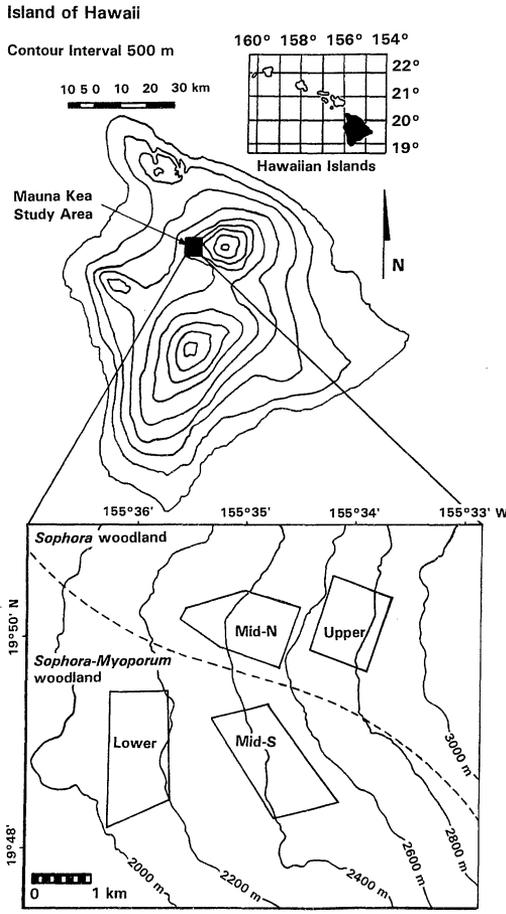


FIGURE 1. Map of study area with 200 m elevation contours, study sites, and approximate boundary of *Sophora* woodland and mixed *Myoporum-Sophora* woodland on the west slope of Mauna Kea, Hawaii.

tained a high proportion of codominant *Myoporum* with as much as 60 percent total canopy cover. Overall canopy cover averaged 30 percent and canopy height was generally short (3–10 m). Other woodland species included in this study were *Dodonaea viscosa* (Sapindaceae) and *Chenopodium oahuense* (Chenopodiaceae), which were found primarily in the mid-elevation south and lower elevation sites. Additional tree species present in subalpine woodlands of Mauna Kea but not encountered during sampling included: *Chamaesyce olowaluana* (Euphorbiaceae), *Dubautia arborea* (Asteraceae), and *Santalalum ellipticum* (Santalaceae). Vegetation in the study area was described previously by van Riper (1980b) and Scowcroft and Giffin (1983). Other subalpine areas on Mauna Kea have been described by Hartt and Neal (1940).

At each of the four sites, we selected three transects randomly to estimate tree and sapling density. Transect length varied 1050–1200 m. In each study area, we randomly placed 20 point-centers along two transects and 10 point-centers along the third transect for a total of 50 point-centers per study site, except at the upper site where 20 point-centers were chosen for all three transects. Within each quarter, we selected the nearest mature tree of crown size > 2 m tall and the nearest sapling tree with a crown height < 2 m but > 0.5 m. We also selected the nearest standing dead tree to each point that had attained a height > 2 m. We measured the distance from each selected tree crown center to the sample point to ± 0.5 m. We considered all conspecific stems emerging from the ground within a 1-m radius of the selected individual to come from the same individual. Because *Sophora* trees have irregular growth forms and diameter may not be a reliable indicator of size or age, we used crown height and width as a measure of size. We measured the crown width to ± 0.5 m at the widest point for mature trees. We visually estimated crown height for mature trees to ± 0.5 m; observers were trained in height estimation to reduce errors. We measured elevation at each point-center with a Thommen handheld altimeter.

We estimated three age categories for all mature *Sophora* trees by the following method: (1) trees with recumbent dead branches were considered senescent; (2) trees without dead recumbent branches, but having deeply fissured bark and lichens on the branches, were considered mature; and (3) trees with smooth bark and lacking lichens were considered young.

We randomly selected a transect from each site to estimate ungulate browse damage. We recorded the presence of recent browse damage on each of the trees selected for density estimation. We sampled grass cover at 30 m intervals on two transects to relate the association of grasses with tree regeneration. One transect bisected the upper and mid-elevation north sites and the other bisected the mid-elevation south and lower sites. We used a 1-m² frame with 10 \times 10 cm cells to estimate the area within the frame containing grass cover of any species.

We calculated density estimates for each point-center with Pollard's (1971) formula for an unbiased population density estimate of the point-centered quarter method where N_p = the population density estimate, n = the number of random points, and r_{ij} = the distance from the random point i to the nearest organism in quadrant j .

TABLE 1. Densities (no./ha^{-1}) of trees <2 m tall but >0.5 m tall, trees >2 m tall, and snags of *Sophora chrysophylla*, *Myoporum sandwicense*, *Chenopodium oahuense*, *Dodonaea viscosa*, all species combined, and elevation at four sites on the west slope of Mauna Kea, Hawaii. Mean *Sophora* densities with the same superscripts are not significantly different (Tukey grouping, $\alpha = 0.05$). *Sophora* snag densities did not differ among sites.

Site	Upper	Mid-N	Mid-S	Lower
Elevation range	2816–2599 m	2575–2317 m	2437–2274 m	2128–1978 m
Trees <2 m tall	49.1	16.4	120.8	67.8
<i>Sophora</i>	48.5 ^a	16.0 ^b	21.7 ^{a,b}	36.9 ^a
<i>Myoporum</i>	0.2	—	1.2	3.1
<i>Chenopodium</i>	0.4	0.3	96.0	7.5
<i>Dodonaea</i>	—	0.1	1.2	0.3
Trees >2 m tall	118.4	51.3	77.9	249.8
<i>Sophora</i>	118.4 ^a	50.9 ^b	28.4 ^b	48.7 ^b
<i>Myoporum</i>	—	0.3	48.7	199.8
<i>Chenopodium</i>	—	—	0.07	—
Snags	48.0	27.7	65.0	48.1
<i>Sophora</i>	48.0	27.7	42.3	21.6
<i>Myoporum</i>	—	—	3.3	26.5
<i>Chenopodium</i>	—	—	19.5	—

$$N_p = 4(4n - 1)/\pi \sum (r_{ij}^2)$$

We calculated snag density at each point-center with Cottam and Curtis's (1956) formula adjusted for sampling a single individual at each point, where Q_1 = the distance to the nearest snag at a point and MA = the equivalent of the mean area occupied by snags in each of the four quarters: $Q_1 = 0.5\sqrt{MA}$.

ANALYSIS.—We tested mature *Sophora* tree and sapling densities for effects of site, elevation, and their interaction at each point-center by two-way ANOVA (SAS Institute 1985). *Myoporum* densities were tested only for differences among sites because of distinct distributional limits that do not correspond to elevation (van Riper 1980b). We used Tukey's studentized range test and ANOVA contrasts to determine which sites differed from each other, and the probability of difference. We analyzed crown size and grass cover in the same manner. Age categories between sites were compared with Chi-square tests. We log transformed all density data and square root transformed grass cover data before analysis.

RESULTS

SAPLING DENSITIES.—*Sophora* sapling densities differed among study sites (ANOVA, $P = 0.002$, Table 1), and were not related to elevation ($P > 0.6$). They were related, however, to the interaction of study site and elevation ($P < 0.04$). *Sophora* sapling densities were higher in the two mixed *Myoporum-*

Sophora study sites than in the two *Sophora*-dominated study sites ($P = 0.021$). The *Sophora*-dominated mid-elevation north site did not differ from the mixed *Myoporum-Sophora* mid-elevation south site in *Sophora* sapling density ($P > 0.21$). *Myoporum* sapling density was extremely low and not significantly different among any of the sites.

MATURE TREE DENSITIES.—Mature *Sophora* densities differed among study sites (ANOVA, $P < 0.0001$; Table 1) and also were related to elevation ($P < 0.0001$), but were not related to the interaction of study site and elevation ($P > 0.09$). Mature *Sophora* densities were higher on the upper study site ($P = 0.021$) than the three other study sites. They, however, did not differ between the two *Sophora*-dominated sites and the two mixed *Myoporum-Sophora* sites ($P > 0.16$). Mature *Myoporum* densities were higher in the mid-elevation south and lower sites than the mid-elevation north and upper sites ($P < 0.0001$), where the species was virtually absent. Only one mature *Myoporum* tree was sampled above 2286 m elevation. *Chenopodium oahuense* occurred as mature trees only at the mid-elevation south site and only one individual of *Dodonaea viscosa* > 2 m tall was encountered.

SNAG DENSITIES.—There were no significant differences in *Sophora* snag densities between sites (ANOVA, $P > 0.15$; Table 1). There were also no effects of elevation, site, or their interaction on *Sophora* snag density. We did not encounter *Myoporum* or *Chenopodium* snags in the upper and mid-elevation north sites.

TABLE 2. Mean heights and widths (m) of *Sophora chrysophylla* trees >2 m tall at four sites on the west slope of Mauna Kea, Hawaii. Means with the same superscripts are not significantly different (Tukey grouping, $\alpha = 0.05$).

Site	<i>Sophora</i> height	<i>Sophora</i> width
Upper	3.961 ^a	5.341 ^a
Mid-N	4.827 ^b	6.702 ^b
Mid-S	4.753 ^b	6.182 ^{a,b}
Lower	4.269 ^a	3.897 ^c

CROWN SIZES.—There was a significant effect of both site (ANOVA, $P < 0.0001$; Table 2) and elevation ($P < 0.0001$) and also an interaction effect of site and elevation on mature *Sophora* tree height ($P < 0.001$). The upper site and the lower site contained significantly shorter mature *Sophora* trees overall than the two mid-elevation sites ($P < 0.001$).

There was a significant effect of site (ANOVA, $P < 0.0001$; Table 2) and an interaction effect of site and elevation on mature *Sophora* crown width ($P < 0.0001$), but there was no effect of elevation alone ($P = 0.647$). The upper, mid-elevation north, and mid-elevation south sites had significantly wider crowned trees than the lower site ($P = 0.041$).

AGE CATEGORIES.—*Sophora* age distributions differed (χ^2 test, $P = 0.003$; Table 3) between upper and lower sites, with the proportion of young trees much higher in the lower site than the upper site. The upper site also had over twice the proportion of mature trees than the lower site, while the proportion of senescent trees was similar between the upper and lower sites.

BROWSE DAMAGE.—There was no detectable browse damage on *Sophora* on the upper and mid-elevation sites. In the lower site, 11 of 13 (85%) mature trees and 11 of 13 saplings had browse damage. The bark of many young *Sophora* and *Myoporum* trees was stripped off; there was evidence of browsing on *Sophora* leaves, but no evidence of browsing on *Myoporum* leaves.

GRASS COVER.—Grass cover differed by study site (ANOVA, $P < 0.0001$; Fig. 2) and was also related to the interaction of study site and elevation ($P < 0.0001$). Elevation alone was not related to grass cover ($P > 0.33$). The mid-elevation north site, where *Sophora* regeneration was lowest, had signif-

TABLE 3. Percent *Sophora chrysophylla* trees (>2 m tall) and sample sizes in three age categories at four sites on the west slope of Mauna Kea, Hawaii.

Site	Sample size	Young	Mature	Senescent
Upper	(N = 239)	22.2	46.4	31.4
Mid-N	(N = 200)	14.0	54.5	31.5
Mid-S	(N = 71)	22.5	31.0	46.5
Lower	(N = 38)	44.7	21.1	34.2

icantly higher grass cover than the other sites ($P < 0.0001$). The upper site and the lower site, where *Sophora* regeneration was highest, contained lower grass cover overall than the two mid-elevation sites ($P < 0.031$).

DISCUSSION

Fifteen years after ungulate reduction began, we found *Sophora* regeneration occurring across the entire study area. Sapling densities, however, were higher in *Myoporum-Sophora* woodland than in *Sophora* woodland. *Sophora* sapling densities were not related to elevation, but were most strongly affected by site. Regeneration was much greater in the upper and lower sites than in the other sites. It was lowest in the mid-elevation north site where grass cover was highest and *Myoporum* was virtually absent. These local effects probably result from the intensity of browsing regimes in different areas and the subsequent colonization by alien grasses, which suppressed germination (Williams 1994). Physiological limitations may prevent exotic grasses from invading high elevation areas, allowing higher *So-*

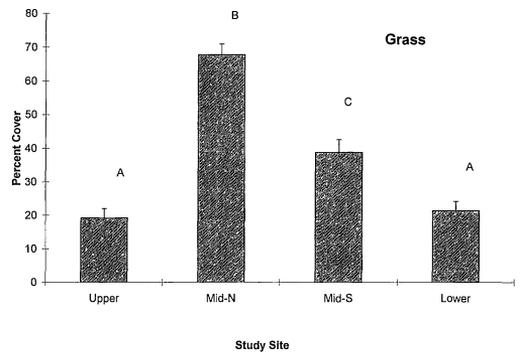


FIGURE 2. Mean percent grass cover by site and standard error on the west slope of Mauna Kea volcano, Hawaii. Means with the same superscripts are not significantly different ($N = 70$ /site; Tukey grouping, $\alpha = 0.05$).

phora regeneration. High elevation slopes may have been affected severely by a greater intensity of browsing if ungulates sought refuge from hunting after road access increased in the 1960s (Giffin 1976, 1982; Scowcroft & Giffin 1983). The extreme climate near treeline, however, apparently does not affect regeneration as much as dense grasses in mid-elevation areas, where sapling densities measure less than one-third of the upper site.

An alternative that was not investigated is *Sophora* seed bank impoverishment in mid-elevation areas. Although Hartt and Neal (1940) and Scowcroft and Giffin (1983) stated that seeds of this species are widespread and remain viable in the soil for years, no studies have quantified soil seed bank or viability on Mauna Kea. Repeated mortality of seedlings caused by browsing and competitive interactions with other plants could result in exhaustion of the soil seed bank in areas of low mature tree density, where seeds are not continually replenished.

Sophora snag densities were not different among any of the sites. Because precipitation was not related to elevation (Juvik *et al.* 1993), we may assume that snags, which do not intercept substantial fog drip, decay, and fall at similar rates, suggest the species was more evenly distributed in the past. *Sophora* population recovery from browse damage, however, was not evenly distributed due to grass colonization or reduced seed bank in mid-elevation areas.

The low density of *Sophora* saplings in the mid-elevation sites relative to the other sites suggests that the *Sophora* woodland in these areas will continue to be less dense than in the other areas unless supplemental plantings are made. This area, which has a high density of *Loxioides* and a high nesting density, may be critically important for *Loxioides*, which occur in higher density in *Sophora* woodland than in mixed woodland (Hess *et al.*, in press; Fig. 3). Supplemental plantings in areas formerly forested with *Sophora*, as recommended by Giffin (1982), may benefit *Loxioides* nesting success and juvenile survivorship, which are both positively correlated with *Sophora* pod production (Lindsey *et al.* 1995).

The upper and mid-elevation north sites were comprised almost exclusively of *Sophora*, while the mid-elevation south and lower sites contained a high proportion of codominant *Myoporum*, even though the two mid-elevation sites overlapped extensively in altitude. Van Riper (1980b) attributed this distinct distributional limit to substrate. Regeneration of *Myoporum* was less than one-tenth of

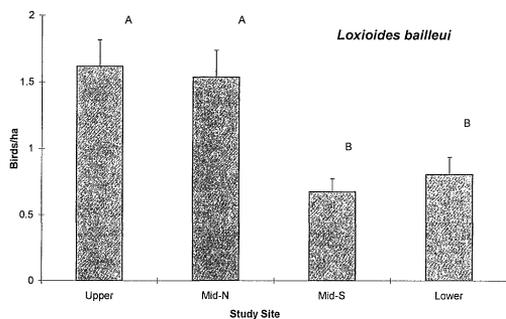


FIGURE 3. Mean density (no./ha \pm SE) of *Loxioides bailleui* per sampling station at four study sites on the west slope of Mauna Kea, Hawaii. Auditory counts ($N = 40$ stations/study site) sampled six times July 1994–August 1996. Means with the same superscripts are not significantly different (Tukey grouping, $\alpha = 0.05$).

Sophora regeneration in the mid-elevation south and lower sites, and almost absent in the upper and mid-elevation north sites. Low *Myoporum* regeneration suggests that this species will become less dense in codominant areas, and will be replaced by *Sophora* as an apparent result of ungulate reduction (van Riper 1980b, Cuddihy & Stone 1990). Mountainspring *et al.* (1987) also found *Sophora* regeneration, but low *Myoporum* regeneration after ungulate reduction. Other comparable subalpine woodland sites with high ungulate browsing pressure, such as Kipuka Alala on Mauna Loa, exhibit extremely high *Myoporum* regeneration concurrent with low *Sophora* regeneration (Banko 1997).

There was no evidence of a negative association between *Sophora* and mature *Myoporum* trees on the spatial scale of this study. Smaller-scale interactions may affect local establishment, but *Sophora* sapling densities were actually higher in mixed species woodland. This pattern of association suggests that competitive suppression by *Myoporum* is not as important in the establishment of *Sophora* as grasses. While *Sophora* facilitates grasses (Williams 1994), *Myoporum* apparently does not have the same effect. If *Myoporum* actually inhibits grasses, reduction of this species may lead to more extensive grass invasion in mixed woodland. In the Puu Ahumoa area of Mauna Kea, where swaths of mixed woodland have been cleared by bulldozers and invaded by grasses, there is no detectable regeneration of any trees. Reduction of *Myoporum* would not likely be as successful in enhancing *Sophora* woodlands or improving habitat for *Loxioides* as supplemental planting of *Sophora* combined with grass control.

We observed extensive browse damage on *Sophora* saplings and bark stripping on both *Sophora* and *Myoporum* in the vicinity of Puu Ulaula. Other native species with evidence of foliage browse damage include *Chenopodium oahuense*, *Rumex gigantea*, *Dubautia* spp., and *Stenogyne microphylla*. Native bunchgrass (*Eragrostis* sp.) clumps were also uprooted and flattened. The *Ovis* spp. population in this area has rebounded since the last major eradication effort in 1991. We regularly saw herds of 20–30 *Ovis* spp. at these two sites and herds of more than 50 on two occasions during this study. Both *Ovis aries* and *O. musimon* prefer *Sophora* (Giffin 1976, 1982), and there is currently a very large proportion of *Sophora* saplings and small young trees in this area that are within reach of browsing ungulates. Scowcroft and Conrad (1992) concluded that remaining *Ovis* spp. in Mauna Kea Forest Reserve could prevent the recovery of native species in areas where the animals concentrate.

Exotic species can irreversibly alter ecosystem processes such as fire regimes, change plant community composition, and cause faunal extinctions, not only on oceanic islands but also in continental areas (D'Antonio & Vitousek 1992). The Hawaiian Islands may be particularly susceptible to these perturbations because of the scale of exotic species invasions relative to the size of land mass, inability of native plants to tolerate browsing (Scowcroft & Giffin 1983), fire (Hughes *et al.* 1991, Smith & Tunison 1992), and loss of competitiveness (Carlquist 1970). Subalpine woodlands may be more capable of recovery after removal of browsing ungulates than submontane seasonally dry zones of Hawaii (Hughes *et al.* 1991). They, however, may require intensive management against alien grasses, which invade even relatively undisturbed areas of Hawaii and cause conversion from woodland to grassland (Hughes *et al.* 1991).

Invasive grasses in subalpine woodland have both competitive effects on establishment of native trees and ecosystem effects by altering fire frequen-

cy and intensity (D'Antonio & Vitousek 1992). After fires, germination of *Sophora* may be severely inhibited by grasses, which can recover quickly (Hughes *et al.* 1991, D'Antonio & Vitousek 1992). Although some *Sophora* may resprout after fires, aboveground cover is reduced for at least five years (Smith & Tunison 1992). *Loxioides* may require habitat that has recovered for a substantially longer time. More research is needed on the role of fire on Mauna Kea with respect to past and present levels of fuels and subalpine woodland regeneration.

The elimination of feral ungulates, as specified by the recovery plan (U.S. Fish and Wildlife Service 1986), will be necessary for reclamation of *Loxioides* habitat designated as critical. Supplemental plantings of *Sophora* saplings (Giffin 1982) may enhance habitat in areas of low density, but should not be attempted at all while large numbers of *Ovis* spp. persist on Mauna Kea. Grass control may be necessary in mid-elevation *Sophora* woodland to interrupt continuous fine fuels and to provide favorable germination and growth conditions for *Sophora*. It is not as important, however, in high elevation areas or in mixed species woodland, where grass cover is lower. Reduction of *Myoporum* is not likely to be as effective in enhancing habitat for *Loxioides* as the elimination of ungulates, supplemental planting of *Sophora*, reduction of grasses, and fire management.

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LITERATURE CITED

- AMARASEKARE, P. 1993. Potential impact of mammalian predators on endemic forest birds of western Mauna Kea, Hawaii. *Conserv. Biol.* 7: 316–324.
- BANKO, P. C. 1997. Palila restoration project. Final report (phases 1–3). Report to U.S. Army and U.S. Fish & Wildlife Service, Portland, Oregon.
- CARLQUIST, S. 1970. Hawaii: a natural history. The Natural History Press, Garden City, New York.
- COTTAM, G., AND J. T. CURTIS. 1956. The use of distance measurements in phytosociological sampling. *Ecology* 37: 451–460.
- CUDDIHY, L. W., AND C. P. STONE. 1990. Alteration of native Hawaiian vegetation: effects of humans, their activities and introductions. University of Hawai'i, Honolulu, Hawaii.

- D'ANTONIO, C. M., AND P. M. VITOUSEK. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annu. Rev. Ecol. Syst.* 23: 63–87.
- GIFFIN, J. G. 1976. Ecology of feral sheep on Mauna Kea. State of Hawaii, Dep. Land and Natu. Resour., Div. Forestry and Wildlife, Honolulu, Hawaii.
- . 1982. Ecology of mouflon sheep on Mauna Kea. State of Hawaii, Dep. Land and Natu. Resour., Div. Forestry and Wildlife, Honolulu, Hawaii.
- HARTT, C. E., AND M. C. NEAL. 1940. The plant ecology of Mauna Kea, Hawaii. *Ecology* 21: 237–266.
- HESS, S. C., P. C. BANKO, M. H. REYNOLDS, G. J. BRENNER, L. P. LANIAWE, AND J. D. JACOBI. In press. Drepanidae movements in relation to food resource availability in subalpine woodland on Mauna Kea, Hawaii. *Stud. Avian Biol.*
- HUGHES, F., P. M. VITOUSEK, AND T. TUNISON. 1991. Alien grass invasion and fire in the seasonal submontane zone of Hawaii. *Ecology* 72: 743–746.
- JACOBI, J. D., S. G. FANCY, J. G. GIFFIN, AND J. M. SCOTT. 1996. Long-term population variability in the palila, an endangered species. *Pac. Sci.* 50: 363–370.
- JUVIK, J. O., AND S. P. JUVIK. 1984. Mauna Kea and the myth of multiple use: endangered species and mountain management in Hawaii. *Mountain Res. and Dev.* 4: 191–202.
- , AND D. NULLET. 1993. Relationships between rainfall, cloud-water interception, and canopy throughfall in a Hawaiian montane forest. In L. S. Hamilton, J. O. Juvik, and F. N. Scatena (Eds.). *Tropical montane cloud forests*, pp. 102–113. East-West Center, Honolulu, Hawaii.
- , D. NULLET, P. C. BANKO, AND K. HUGHES. 1993. Forest climatology near the tree line in Hawaii. *Agric. and For. Meteorol.* 66: 159–172.
- LINDSEY, G. D., S. G. FANCY, M. H. REYNOLDS, T. K. PRATT, K. A. WILSON, P. C. BANKO, AND J. D. JACOBI. 1995. Population structure and survival of palila. *Condor* 97: 528–535.
- MOUNTAINSPRING, S., J. G. GIFFIN, C. B. KEPLER, R. T. SUGIHARA, J. E. WILLIAMS, AND T. W. SUTTERFIELD. 1987. Regeneration of the subalpine woodland on Mauna Kea. U.S. Fish and Wildlife Service Report, Portland, Oregon.
- MUELLER-DOMBOIS, D., AND H. ELLENBERG. 1974. *Aims and methods of vegetation ecology*. John Wiley & Sons, Inc., New York, New York.
- MURPHY, P. G., AND A. E. LUGO. 1986. Ecology of tropical dry forest. *Annu. Rev. Ecol. Syst.* 17: 67–88.
- OLSON, S. L., AND H. F. JAMES. 1982. Prodrum of the fossil avifauna of Hawaiian Islands. *Smithsonian Contrib. Zool.* 365.
- POLLARD, J. H. 1971. On distance estimators of density in randomly distributed forests. *Biometrics* 27: 991–1002.
- SAS INSTITUTE INC. 1985. *SAS user's guide*, version 5 edition. SAS Institute Inc., Cary, North Carolina.
- SCOTT, J. M., S. MOUNTAINSPRING, F. L. RAMSEY, AND C. B. KEPLER. 1986. Forest bird communities of the Hawaiian Islands: their dynamics, Ecology and Conservation. *Stud. Avian Biol.* 9: 1–431.
- , S. MOUNTAINSPRING, C. VAN RIPER III, C. B. KEPLER, J. D. JACOBI, T. A. BURR, AND J. G. GIFFIN. 1984. Annual variation in the distribution, abundance, and habitat response of the palila (*Loxioides bailleui*). *Auk* 101: 647–664.
- SCOWCROFT, P. G. 1983. Tree cover changes in mamane (*Sophora chrysophylla*) forests grazed by sheep and cattle. *Pac. Sci.* 37: 109–119.
- , AND C. E. CONRAD. 1992. Alien and native plant response to release from feral sheep browsing on Mauna Kea. In C. P. Stone, C. W. Smith, J. T. Tunison (Eds.). *Alien plant invasion in Hawaii: management and research in native ecosystems*, pp. 625–665. University of Hawai'i Press, Honolulu, Hawaii.
- , AND J. G. GIFFIN. 1983. Feral herbivores suppress mamane (*Sophora chrysophylla*) and other browse species on Mauna Kea, Hawaii. *J. Range Manage.* 36: 638–645.
- , AND H. F. SAKAL. 1983. Impact of feral herbivores on mamane forests of Mauna Kea, Hawaii: bark stripping and diameter class structure. *J. Range Manage.* 36: 495–498.
- SMITH, C. W., AND T. TUNISON. 1992. Fire and alien plants in Hawaii: research and management implications for native ecosystems. In C. P. Stone, C. W. Smith, and J. T. Tunison (Eds.). *Alien plant invasion in Hawaii: management and research in native ecosystems*, pp. 394–408. University of Hawai'i Press, Honolulu, Hawaii.
- STOTZ, D. E., J. W. FITZPATRICK, T. A. PARKER III, AND D. K. MOSKOVITS. 1996. *Neotropical birds: ecology and conservation*. University of Chicago Press, Chicago, Illinois.
- U.S. FISH AND WILDLIFE SERVICE. 1986. *Recovery plan for the palila*. U. S. Fish and Wildlife Service, Portland, Oregon.
- VAN RIPER, C., III. 1980a. Observations on the breeding of the palila *Pittitirostra bailleui* of Hawaii. *Ibis* 122: 462–475.
- . 1980b. The phenology of dryland forests of Mauna Kea, Hawaii, and the impact of recent environmental perturbations. *Biotropica* 12: 282–291.
- WARNER, R. E. 1960. A forest dies on Mauna Kea. *Pac. Discovery* 13: 6–14.
- WILLIAMS, A. C. 1994. *Effects of non-native grasses on a dry subalpine forest native to Hawaii and a discussion of effects of canopy on understory productivity*. M.S. Thesis, University of California, Berkeley, California.
- WOLFE, E. W., AND J. MORRIS. 1996. *Geologic map of the island of Hawaii*. U.S. Department of the Interior. U.S.G.S. Misc. Investigations Series, Reston, Virginia.