

Feral Herbivores Suppress Mamane and Other Browse Species on Mauna Kea, Hawaii

PAUL G. SCOWCROFT AND JON G. GIFFIN

Abstract

Abundance, survival, and growth of mamane (*Sophora chrysophylla*) regeneration were determined inside and outside sheep exclosures located in heavily browsed portions of the mamane forest of Mauna Kea, Hawaii. Vegetational cover of other species was estimated. Mamane grew abundantly inside 16-year-old exclosures but was sparse outside. Height class distributions indicated that feral sheep prevented establishment of regeneration. Survival of seedlings and sprouts at 2-year-old exclosures was greater inside than outside. The largest difference between survival inside and outside was found where browsing pressure was greatest. Mamane reproduction exposed to browsing tended to be shorter than protected reproduction. Rate of height growth for protected mamane reproduction was significantly affected by exclosure location. Cover data for preferred browse species other than mamane indicated that 3 endemic grasses—Hawaiian bent (*Agrostis sandwicensis*), he'u-pueo (*Trisetum glomeratum*), and *Deschampsia australis*, an endemic shrub—aheaha (*Chenopodium oahuense*), and an introduced forb-gosmore (*Hypochoeris radicata*)—were susceptible to browsing. On the basis of these findings, vegetation recovery should be rapid in most areas where feral sheep are eliminated or reduced.

The mamane (*Sophora chrysophylla*) forest of Mauna Kea, island of Hawaii, occupies about 22,000 ha between 1,800- to 2,900-m elevation. The forest is open woodland of pure mamane, except along the southern flank where mamane and naio (*Myoporum sandwicense*) form dense stands to about 2,500-m elevation.

The xeric, high elevation forest is critical habitat for the Palila (*Psittirostra bailliei*), an endangered Hawaiian bird (Berger et al. 1977). Fifteen Hawaiian plant species growing within the forest have been recommended for inclusion in the list of threatened and endangered species of the United States (Ripley 1975).

These species are endangered partly because of the damage done by feral sheep (*Ovis aries*) during the last 150 years. Feral sheep became established on Mauna Kea in the 1820's. Lacking natural predators, except for the wild dog, the sheep population reached about 40,000 animals by the early 1930's, one for every 2 ha of habitat (Bryan 1937). They extensively suppressed mamane and other tree reproduction, stripped bark from tree stems, and consumed herbaceous vegetation, thereby leaving the soil exposed to accelerated erosion (Warner 1960). Because damage to the forest was severe, Hawaii Territorial foresters reduced the population through sheep drives and hunter-guide programs. Under sustained yield management for public hunting, which started in 1955, the population was kept below 5,000. During the 1970's, the population averaged 1,500 animals. Even at this relatively low level, mamane regenerated little or not at all in areas where sheep tended to concentrate, especially at tree line.

Cattle (*Bos taurus*), Mouflon sheep (*Ovis musimon*), and feral

goats (*Capra hircus*) also have contributed to destruction of native vegetation in this ecosystem. Cattle have done the most damage on the forest below 1,800-m elevation. Mouflon and goats are found primarily above 1,800 m, but damage has been limited because of their recent establishment in the forest and small populations (200 to 300 mouflon and 150 to 200 goats).

Because of continued forest degradation and the attendant threat to the Palila, the United States District Court for the District of Hawaii ordered the State of Hawaii to remove feral goats and sheep completely and permanently from those portions of the mamane forest designated as critical Palila habitat. Included were the Mauna Kea Forest Reserve up to an elevation of 3,000 m, the Kaohe Game Management area, and the upper Waikii parcel (U.S. Government Printing Office 1977). Eradication was completed in August 1981. But influx of feral sheep from areas adjacent to the critical habitat will require periodic hunts to comply with the court order.

This paper reports a study to evaluate changes in vegetative cover on high-use areas protected from grazing and browsing animals and to determine abundance, survival, and growth of mamane regeneration inside and outside animal exclosures. The results indicate the direction and speed that vegetation recovery should take once feral herbivores are removed.

Study Sites

Two sets of exclosures were examined. The Puu Nanaha, Puu Kole, and Kaluamakani exclosures were built in 1963 by the U.S. Soil Conservation Service and the Hawaii Division of Fish and Game. The Puu O Kauha, Hale Pohaku, and Wailuku exclosures were built in 1972 by the Forest Service, U.S. Department of Agriculture, in cooperation with the Hawaii Division of Forestry. All 6 exclosures were established at or near tree-line where browsing pressure was greatest (Fig. 1).

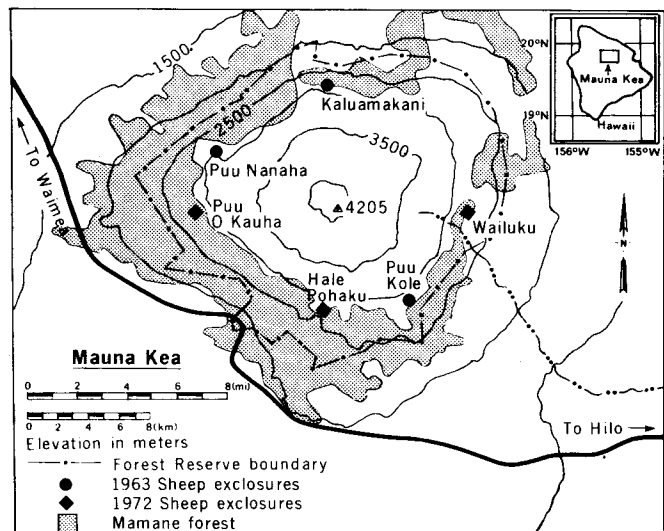


Fig. 1. Location of the 1962 (●) and 1973 (◆) sheep exclosure study sites within the Mauna Kea Forest Reserve, Island of Hawaii.

Authors are research forester, Pacific Southwest Forest and Range Experiment Station, Forest Service, USDA, Honolulu, Hawaii, and wildlife biologist, Hawaii Department of Land and Natural Resources, Division of Forestry and Wildlife, Hilo, Hawaii.

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Table 1. Site attributes of the six exclosures established within the mamane forest of Mauna Kea, Island of Hawaii.

Site attributes	Puu Nanaha	Puu Kole	Kaluamakani	Puu O Kauha	Wailuku	Hale Pohaku
Year built	1963	1963	1963	1972	1972	1972
Size (ha)	0.4	0.4	0.4	0.3	0.9	0.3
Elevation (m)	2750	2860	2670	2750	2800	2770
Aspect	NW	SE	N	SW	E	S
Slope (%)	20	30	20	20	15	30
Annual rainfall (mm) ¹	380	700	500	380	700	700
Soil taxonomy ²	Very stony land	Cinder land	Typic vitrandept, medial over cindery, isomesic	Very stony land	Typic vitrandept, medial over cindery, isomesic	Cinder land
Sheep population size (animals/ha) ³	0.17/0.13	0.17/0.22	0.31/0.27	0.11/0.10	0.14/0.12	0.09/0.16
Dominant vegetation: Overstory Species	<i>Sophora chrysophylla</i>	Same	Same	<i>Sophora chrysophylla</i> <i>Myoporum sandwicense</i>	<i>Sophora chrysophylla</i>	Same
Understory species	<i>Hypochoeris radicata</i> <i>Holcus lanatus</i> <i>Rumex acetosella</i>	<i>Danthonia pilosa</i> <i>Holcus lanatus</i> <i>Trisetum glomerata</i>	<i>Deschampsia</i> spp. <i>Trisetum glomerata</i>	<i>Agrostis avenacea</i> <i>Festuca megalura</i> <i>Senecio sylvaticus</i>	<i>Danthonia pilosa</i> <i>Styphelia</i> spp <i>Anthoxanthum odoratum</i>	<i>Danthonia pilosa</i> <i>Verbascum thapsus</i> <i>Deschampsia</i> spp.

¹State of Hawaii 1970.

²Soil Conservation Service 1973.

³Data from Hawaii Division of Forestry and Wildlife, Honolulu, Hawaii 96813. Estimates are for 1962/1973 and indicate the number of sheep using the range around the exclosure sites.

The sites selected represent a diversity of soil, water, and browsing regimes (Table 1). The Puu Kole, Wailuku, and Hale Pohaku exclosures lie on the windward side of the mountain, and, therefore, receive more rainfall than the other exclosures that lie in the rainshadow of Mauna Kea. The latter receive the bulk of their rainfall during intense, nontrade-wind winter storms. Snow is rare at all 6 sites.

Three soil types are represented (Table 1). Differences found in soil of the same type were important. Puu Kole lies on the outside of a cinder cone and Hale Pokahu lies on the inside of a cone. Little soil development has occurred at Hale Pokahu. The Kaluamakani exclosure is located on unstable deep loamy sand with little vegetational cover. The same soil type at Wailuku is stable because of abundant herbaceous vegetation. Lava rock outcrops are found in the study areas at Puu Nanaha but not at Puu O Kauha. Of the 6 sites, Kaluamakani and Hale Pokahu appear to be harshest for plant growth, primarily because of unstable soil.

Methods

Mamane—1963 Exclosures

Although initial abundance and height data for mamane do not exist for these older exclosures, we did a comprehensive inventory in 1979. Height of each mamane plant inside and outside the Puu Nanaha and Puu Kole exclosures was measured to the nearest 0.1 m. The outside areas were located within 15 m of the exclosures and were the same size. Trees that were obviously living at the time the exclosures were built, were recorded separately. We made no attempt to distinguish plants of sprout origin from those of seed origin, but recorded separately the newly emerged plants in unprotected areas. We also noted the presence of browsing injury for unprotected mamane. We made similar measurements at the Kaluamakani exclosure in 1981.

Mamane—1972 Exclosures

At Puu O Kauha and Hale Pohaku, we measured the height of all mamane seedlings within protected and unprotected study boundaries 2 months and again 3 years after fencing. Similar data for sprout reproduction were not collected, except in the Puu O Kauha exclosure 2 months after fencing.

One year after the exclosures were built, we randomly selected

and tagged 25 sprouts and 25 seedlings inside and outside the Puu O Kauha and Wailuku exclosures. At Hale Pokahu where seedlings were scarce, the seedling sample consisted of all the seedlings found within plot boundaries—4 inside and 23 outside. Height and condition of these plants were determined at intervals for a 4-year period.

We examined the effect of site on rate of height growth of protected seedlings and sprouts by using a procedure described by Draper and Smith (1966). The procedure consists of constructing a joint 95% confidence region for the slope and intercept of each site. Lack of any overlap of regions was evidence for differences in growth rate. This procedure was chosen because it accounted for differences in the initial range of seedling and sprout height.

Other Species—1963 Exclosures

Because the 1963 exclosures were originally built to demonstrate the effect of browsing on vegetation by visual impact, quantitative data were not collected before or immediately after their construction. The early records consisted of sets of photographs taken in 1965 and 1966, and estimated aerial cover for species found in 2 permanent 1-m² quadrats inside and outside each exclosure.

About 12 years after construction, plant cover and height inside and outside the exclosures were estimated by using the line intercept method (Mueller-Dombois and Ellenberg 1979). Five 30-m long transects were systematically established inside and outside each exclosure. Intercepts for projected live crown area were recorded by species to the nearest 1 cm. Intercepts for bare soil, rock, and litter-logs were recorded also. The height of each intercepted live plant was measured. A Bonferroni *t*-test was used to test the hypothesis that protected plants were not taller than unprotected ones at a given exclosure site. This procedure used the Bonferroni inequality to adjust the Type I error for multiple comparisons (Miller 1966). The original 1-m² quadrats were relocated and cover was estimated for all species present.

Other Species—1972 Exclosures

We collected cover data for species inside and outside the Puu O Kauha and Hale Pohaku exclosures 2 months after fencing and again at about 3 years. The 2-month measurement was a 100% inventory inside. The exclosures were marked off in a 3.4-by 3.4-m grid with odd-sized cells located along two edges. Outside the

exclosures, we used 36 randomly selected 3.4- by 3.4-m cells located within a comparable size area adjacent to, but separated from, the fenced area by a 15-m buffer strip.

Vegetation was more abundant inside the exclosures 3 years after establishment, making a 100% inventory impractical. A subsample of interior plots, therefore, was used. At Puu O Kauha, 20 cells, and at Hale Pokaku, 25 cells were randomly selected. Border cells were excluded. Outside, 20 cells at Puu O Kauha and 25 cells at Hale Pokaku were randomly chosen from among the 36 established initially.

The basal area occupied by each plant was measured by using an air-list approach (Pearse 1935) for most herbaceous species. For Kentucky bluegrass (*Poa pratensis*), which spreads by rhizomes, we measured the ground area occupied by colonies instead of individuals. Because the canopy of aheahea (*Chenopodium oahuense*) bushes hugged the ground, preventing establishment of other plants, its basal area was defined by the outer boundary of the canopy at ground level. For rosette plants like turkey mullein (*Verbascum thapsus*), basal area was considered to be the area described by the leaf tips of the basal rosette. A value of 0.005 cm² was assigned to small grass seedlings. The total basal area for a species within a single sample cell was simply the sum of the individual plant basal areas. We also recorded the presence of species not tallied in the sample cells, but found within the study boundaries. The Bonferroni *t*-test was used to compare change in basal area inside with change outside for preferred browse species (Giffin 1976) and other perennials. Species lacking basal area estimates inside and outside at both measurement times could not be used in this comparison.

Results and Discussion

Mamane—1963 Exclosures

After 15 years, more mamane plants were growing inside the exclosures than outside. In 1979, 886 individual mamane plants were growing within the Puu Nanaha and 588 within the Puu Kole exclosure. Outside, the tallies were 24 mamane for Puu Nanaha and 93 for Puu Kole, excluding pre-exclosure trees. Of the mamane outside, 33% for Puu Nanaha and 71% for Puu Kole were recent emergents and never browsed.

Inside Puu Nanaha and Puu Kole, the mamane height class distributions displayed the characteristic reverse-J shape of an actively reproducing stand (Fig. 2). Outside, only two disjunct classes were represented—less than 0.6 m and greater than 2.6 m tall. The small size class included new emergents and suppressed plants hidden among rock rubble. The large size class included only old pre-exclosure trees.

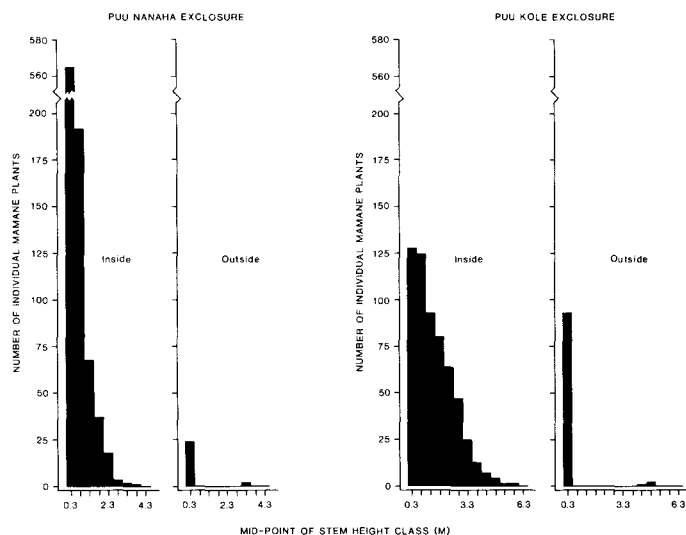


Fig. 2. Height class distribution of mamane trees inside and outside the Puu Nanaha and Puu Kole exclosures 16 years after their construction.

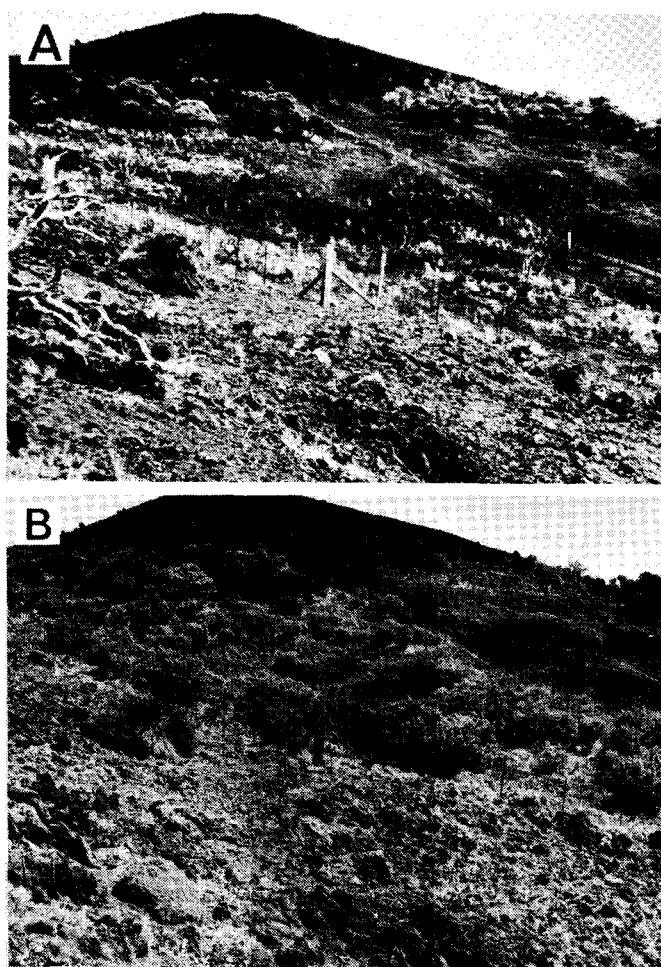


Fig. 3. Mamane regeneration in the Puu Kole exclosure was already visible in 1965 (A) 2 years after fencing. None was visible outside. In 1979 (B), mamane regeneration was flourishing inside with more than 580 individuals. The unprotected area (B-right center) supported 93 mamane, 70% of them newly emerged. Many pre-exclosure mamane outside died since 1965.

At Kaluamakani, 785 individual mamane were growing inside, but only 10 outside in 1981. All individuals outside were pre-exclosure trees. Of the mamane that had developed inside since fencing, 47% were seedlings <0.1 m tall. All of these seedlings were found in leaf litter under pre-exclosure trees. The height class distributions were similar to those at Puu Nanaha and Puu Kole.

In 1965, 2 years after the exclosure at Puu Kole was built, the old mamane trees outside were alive and healthy (Fig. 3A). But by 1979, many individuals had died and others were in the process of dying (Fig. 3B). The old mamane inside had not died, but instead, appeared vigorous. The browse line inside was gone by 1979, but that outside was still present.

Mamane—1972 Exclosures

Within 2 months of fence construction, mamane seedlings were already more numerous inside the Puu O Kauha exclosure than outside—45:1. The differences in number of seedlings at Hale Pokaku was less striking—3:1.

The difference in number of mamane seedlings found inside and outside the exclosures was probably not due to differences in seed abundance or viability. At Puu O Kauha 1.6 seeds/m² were found inside and 2.7 seeds/m² were found outside. At Hale Pokaku, 0.5 seeds/m² were found inside and 2.9 seeds/m² were found outside. The differences were not statistically significant (Wilcoxon 2-sample test, *p*>0.05). Too few seeds were recovered at these 2 sites to evaluate differences in seed viability, but limited data from Wailuku indicated no differences. About 67% of the buried seeds at

Puu O Kauha and 33% at Hale Pokaku were viable.

The average height of seedlings inside 2 exclosures and in adjacent unfenced areas of comparable size were about the same—all were less than 13 cm tall. At Puu O Kauha, the seedling height inside averaged 6.6 cm, outside, 7.6 cm; at Hale Pokaku, inside, height averaged 5.1 cm, outside, 2.5 cm. Protected and unprotected seedlings were unbrowsed. These findings indicated that all seedling were about the same age.

The seedlings at Puu O Kauha were tallied again in 1976. Inside, 41 seedlings were found, the same ones that were there initially. Outside, only 3 seedlings, all new emergents, were found. The seedlings averaged 52.6 cm tall inside, and 4.6 cm tall outside. The difference in height was statistically significant (2 sample *t*-test, $p \leq 0.05$).

exclosure 2 months after fencing. About 700 individual sprouts were tallied, averaging 18 cm tall (± 11 cm). More than 70% of the sprouts grew beneath a single old tree. In 1979, these sprouts ranged from 1.9 to 2.1 m tall. The other sprouts emerged from the roots of 3 other remnant mamane trees.

Two years after the seedlings were tagged in 1973, their survival inside the exclosures ranged from 42 to 100%, and sprout survival inside ranged from 84 to 100% (Fig. 4). None of the seedlings tagged outside the Puu O Kauha and Wailuku survived. About 92% survived outside the Hale Pokaku. Of the sprouts outside, survival ranged from 8 to 100%; the latter was recorded at Hale Pokaku where seedling survival outside was also high.

Differences in survival of tagged mamane seedlings and sprouts inside vs. outside exclosures were related to the relative browsing pressure at each site with the differences in survival (inside rate minus outside rate) increasing as browsing pressure increased (Fig. 4). As expected, the differences were larger for seedlings than for sprouts. Sprouts are supported by established root systems, whereas seedlings are developing theirs. Consequently, browsing is more likely to destroy a seedling.

The effect of browsing on mamane regeneration is illustrated further by differences in height growth inside and outside exclosures. Surviving sprouts at Puu O Kauha and Wailuku grew significantly more (2 sample *t*-test, $p \leq 0.05$) inside than outside. Height growth inside averaged 16.1 cm (± 8.3) at Puu O Kauha and 8.2 cm (± 6.5 cm) at Wailuku. Outside, mean growth was 1.5 cm (± 1.1 cm) at Puu O Kauha and -0.9 cm (± 2.0 cm) at Wailuku. Browsing by

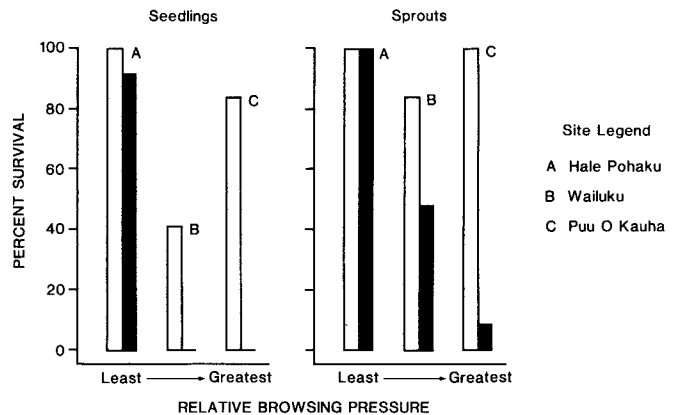


Fig. 4. Percent survival of tagged mamane seedlings and sprouts inside (□) and outside (■) The Puu O Kauha, Hale Pokaku, and Wailuku exclosures 2 years after their construction. Exclosure sites are ranked along a relative browsing pressure gradient.

feral sheep at Puu O Kauha, and by both feral and Mouflon sheep at Wailuku, was responsible for the reduced growth of unprotected sprouts. Similar comparisons for seedlings at these sites were not possible because none of the unprotected ones survived.

The growth of surviving seedlings and sprouts inside Hale Pokaku was greater than outside, but the differences was not significant. Seedling growth was 8.9 cm (± 8.4 cm) inside and 2.4 cm (± 3.1 cm) outside. Sprout growth was 6.7 cm (± 10.8 cm) inside and 6.0 cm (± 5.0 cm) outside.

Potential rates of height growth of mamane reproduction at the 3 sites in the absence of browsing were indicated by data for tagged plants inside the exclosures (Fig. 5). Puu O Kauha was the most favorable site for growth of both seedlings and sprouts. Wailuku was the least favorable site for seedling growth. Sprout growth was not significantly different ($p > 0.05$) at the Wailuku and Hale Pokaku sites.

The change in estimated basal area of mamane observed inside the Puu O Kauha exclosure (Table 2) needs to be explained, lest the reader conclude that protection does not enhance mamane growth. The loss of mamane basal area inside resulted from the death of 4

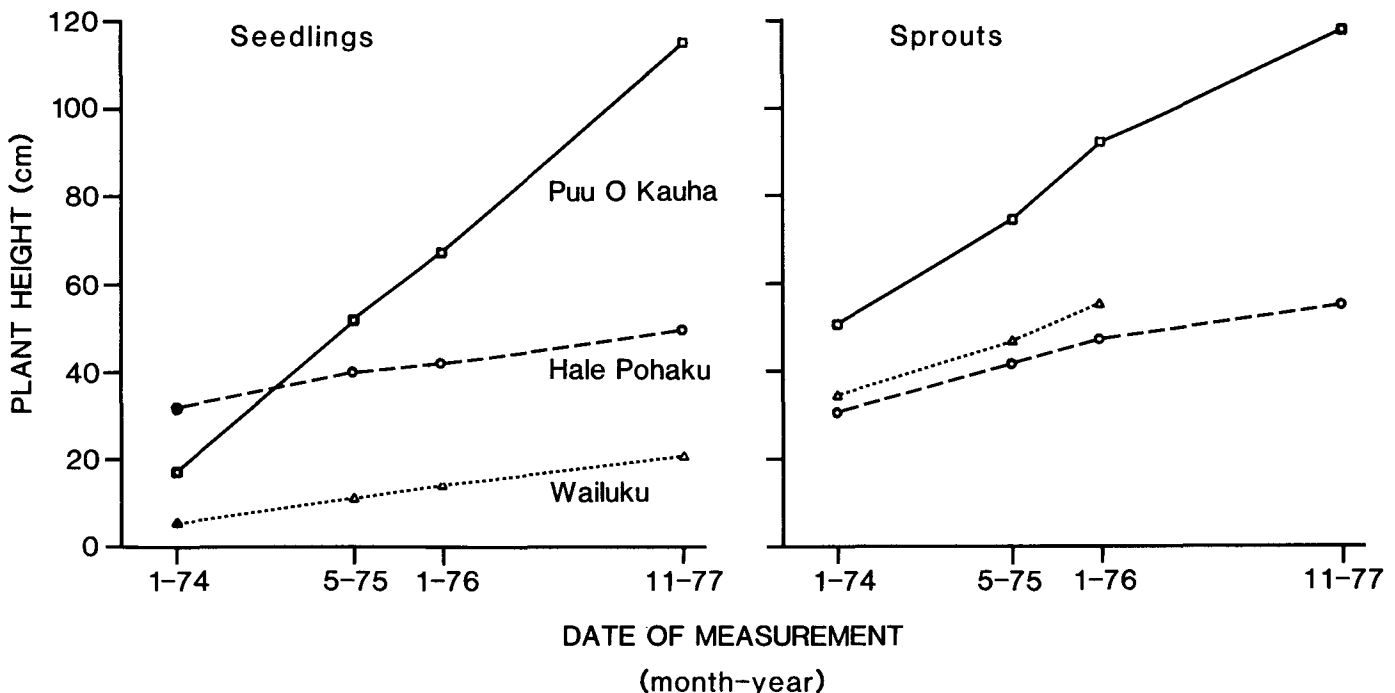


Fig. 5. Height growth of tagged mamane seedling and sprouts inside sheep exclosures built in 1972.

Table 2. Percent aerial plant cover and average live plant height based on line intercept measurements, by species inside and outside three sheep sites, exclosures 12 years after their construction.

Species	Percent aerial cover						Average plant height (cm)/# of plants examined					
	Puu Nanaha		Puu Kole		Kaluamakani		Puu Nanaha		Puu Kole		Kaluamakani	
	Inside	Outside	Inside	Outside	Inside	Outside	Inside	Outside	Inside	Outside	Inside	Outside
Grasses												
→ ¹ <i>Agrostis sandwicense</i> (E) ²	— ³	—	—	—	0.3	—	—	—	—	—	25/2	—
<i>Anthoxanthum odoratum</i>	2.2	1.3	4.1	0.3	—	—	43/25	24/25	24/20	27/4	—	—
<i>Bromus rigidus</i>	+ ⁴	+	—	—	—	—	+	+	—	—	—	—
→ <i>Danthonia pilosa</i>	+	+	8.7	4.2	—	—	+	+	17/59	13/37	—	—
<i>Deschampsia australis</i> (E)	—	—	—	—	0.9	—	—	—	—	—	42/2	—
→ <i>Holcus lanatus</i>	6.8	1.7	+	+	+	—	27/75	11/30	+	+	+	—
→ <i>Poa pratensis</i>	0.5	3.6	+	0.2	—	—	25/1	2/10	+	11/2	—	—
→ <i>Trisetum glomeratum</i> (E)	1.4	—	3.9	—	—	—	47/11	—	62/19	—	—	—
Sedges and rushes												
<i>Carex macloviana</i> (E)	0.2	0.1	0.6	—	—	—	12/1	7/1	23/1	—	—	—
<i>Luzula hawaiiensis</i> (E)	0.3	+	+	+	—	—	24/3	+	+	—	—	—
Ferns												
<i>Asplenium</i> spp.	0.1	0.1	+	+	+	+	17/1	2/1	+	+	+	+
<i>Pellaea ternifolia</i>	0.1	+	+	+	+	+	18/2	+	+	+	+	+
<i>Pteridium aquilinum</i>	+	+	0.1	0.1	+	+	+	+	32/1	18/1	+	+
Herbs and forbs												
<i>Centaureum umbellatum</i>	+	+	—	—	—	—	+	+	—	—	—	—
<i>Cirsium vulgare</i>	+	+	+	+	+	+	+	+	+	+	+	+
<i>Crepis pulchra</i>	—	—	+	—	—	—	—	—	+	—	—	—
→ <i>Epilobium cinereum</i>	0.5	0.3	0.1	—	+	—	8/4	1/4	1/2	—	+	—
→ <i>Hypochoeris radicata</i>	8.2	3.1	0.3	+	+	+	12/69	3/55	13/1	+	+	+
<i>Medicago lupulina</i>	0.9	0.2	—	—	—	—	2/10	1/1	—	—	—	—
<i>Rumex acetosella</i>	3.3	1.8	3.4	0.8	—	—	11/35	7/36	17/29	9/17	—	—
<i>Senecio sylvaticus</i>	+	+	—	—	+	+	+	+	—	—	+	+
<i>Solanum nigrum</i>	—	—	—	—	+	+	—	—	—	—	+	+
→ <i>Sonchus oleraceus</i>	+	+	—	—	+	+	+	+	—	—	+	+
<i>Stenogyne</i> sp.	—	—	+	—	—	—	—	—	+	—	—	—
<i>Taraxacum officinale</i>	+	+	—	—	+	+	+	+	—	—	+	+
<i>Verbascum thapsus</i>	—	—	0.3	1.6	—	—	—	—	68/1	13/12	—	—
Shrubs												
<i>Styphelia tameiameia</i> (E)	0.6	0.1	+	+	—	—	29/3	5/1	+	+	—	—
Trees												
→ <i>Sophora chrysophylla</i> (E)	6.2	3.2	25.1	+	20.6	+	102/11	700/1	235/14	+	268/7	+
Nonplant												
Bare soil	12.5	26.5	67.4	84.2	84.0	95.7						
Rock	55.4	57.2	2.4	7.1	4.6	4.3						
Litter and logs	7.0	4.0	8.6	1.5	10.2	0.0						
Totals												
Live plants	31.3	15.5	46.6	7.2	21.8	0.0	21.8 (19.3) ⁵	8.6 (11.9)	23.8 (19.6)	12.6 (8.0)	33.2 (9.9)	— (—)
Bare soil, rock litter	74.9	87.7	78.4	92.8	96.9	100.0						

¹→ = preferred browse species

²E = endemic species

³— = species not found within the study boundaries

⁴ + = species present within study boundaries, but not encountered along the line transects

⁵Standard deviations are shown in parentheses for average heights of all plants taken together, excluding mamane

of the 5 seedlings in the 1972 sample. The 4 were the only seedlings that died in the exclosure and, therefore, our data greatly overestimates loss of basal area. Also, because the 41 surviving seedlings were growing vigorously, as were the sprouts, we suspect that actual mamane basal area increased. But basal area was measured only within sample quadrats.

Other Species—1963 Exclosures

Before the 1963 exclosures were fenced, species composition and cover of protected and unprotected areas at each site were similar (Pers. comm., R. Walker). Recovery inside the exclosures were already evident by 1965. For example, mamane seedlings and sprouts, *Deschampsia australis*, *Conyza* sp., bracken fern (*Pteridium aquilinum*), spear thistle (*Cirsium vulgare*), dandelion (*Taraxacum officinale*), and sheep sorrel (*Rumex acetosella*), were growing well inside the Kaluamakani exclosure, but outside the area was denuded except for large mamane trees. Even mamane sprouts were lacking outside, a condition that persisted through 1980.

The limited cover data for the 1-m² quadrats did not bear out the

narrative account that vegetation recovery had begun inside the exclosures. Probably, the lack of evidence of recovery was because the sample was too small—only 2 quadrats inside and 2 outside. By using the same quadrats, however, we found that recovery was evident in 1979, 16 years after fencing. Cover inside the Puu Nanaha exclosure increased 17.5%; cover outside did not change. Inside Puu Kole, quadrat cover increased 44% compared with only 5% outside. The increases inside at both sites were largely because of the growth of mamane seedlings and not because of the establishment of herbaceous species.

Results of the 12-year measurements indicated that total crown cover inside was greater than outside the exclosures (Table 2). Plants other than mamane accounted for 81% of the differences in cover between inside and outside at Puu Nanaha, 36% at Puu Kole, and 6% at Kaluamakani. Although the differences were not large, cover of preferred browse species—and most others as well—were greater inside than outside. Heu-pueo (*Trisetum glomeratum*) and Hawaiian bent (*Agrostis sandwicense*), both endemic grasses, appeared particularly vulnerable to grazing because they were only

Table 3. Average basal area cover (cm²/ha) (± standard error) by species inside and outside two sheep exclosures 2 months after construction and 3 years later.

Species	Puu O Kauha				Hale Pohaku			
	Inside		Outside		Inside		Outside	
	1972	1975	1972	1975	1972	1975	1972	1975
Grasses								
<i>Agrostis avenacea</i>	7983(3565)	88467(32340)	1142(620)	101824(28194)	—	—	—	—
→ ¹ <i>Agrostis sandwicense</i> (E) ²	122(78)	1238(943)	— ³	16(16)	+ ⁴	—	—	—
→ <i>Bromus rigidus</i>	241(230)	1165(1089)	—	* ⁵	1621(460)	1(1)	165(99)	*
<i>Dactylis glomerata</i>	—	+	—	—	—	—	—	—
→ <i>Danthonia pilosa</i>	—	—	—	—	110165(59968)	17310(8494)	28972(15529)	29991(19488)
<i>Deschampsia australis</i> (E)	—	—	—	—	+	+	—	+
<i>Festuca megalura</i>	+	214(90)	+	11(6)	—	—	—	—
→ <i>Holcus lanatus</i>	—	+	—	—	—	—	—	—
<i>Hordeum leporinum</i>	+	8(5)	—	—	—	—	—	—
→ <i>Poa pratensis</i>	+	307(213)	—	54350(47932)	—	—	—	—
<i>Stipa cernua</i>	+	7872(7687)	—	—	5008(4514)	1391(1254)	—	—
→ <i>Trisetum glomeratum</i> (E)	30(28)	85783(35595)	—	*	—	—	—	—
Sedges and rushes								
<i>Carex macloviana</i>	1733(1628)	47633(45374)	—	—	—	—	—	—
Ferns								
<i>Asplenium adiantum-nigrum</i>	+	—	+	—	—	—	—	+
<i>Asplenium trichomanes</i>	+	+	+	+	8852(3051)	5077(2158)	3895(2056)	3895(2056)
<i>Pellaea ternifolia</i> (E)	1890(1772)	+	698(652)	394(367)	17388(5488)	2436(754)	4932(1347)	4932(1347)
Herbs and forbs								
<i>Achillea millefolium</i>	—	—	—	—	—	+	—	—
<i>Argemone glauca</i> (E)	328(302)	*	—	—	—	—	—	—
<i>Cirsium vulgare</i>	61(37)	—	44(41)	*	445(401)	—	220(209)	+
<i>Conyza</i> sp	—	+	—	1049(776)	28(26)	105(52)	—	2(1)
→ <i>Epilobium cernua</i>	—	+	—	—	2913(2529)	+	508(299)	2(1)
<i>Erodium cicutarium</i>	30(28)	296(147)	+	548(385)	1528(993)	154(75)	522(311)	123(117)
<i>Gnaphalium purpureum</i> (E)	8791(1376)	22(9)	590(197)	75(43)	390(237)	—	—	—
<i>Gnaphalium sandwicensium</i> (E)	30(28)	10949(4890)	+	66(63)	984(704)	656(273)	—	2(1)
<i>Heterotheca grandiflora</i>	30(28)	2950(2222)	—	*	—	10(7)	—	+
→ <i>Hypochoeris radicata</i>	+	—	+	44(41)	57(34)	1296(494)	—	170(89)
<i>Medicago lupulina</i>	+	—	—	—	—	—	—	—
<i>Polycarpon tetraphyllum</i>	+	—	—	—	—	76(52)	—	252(155)
<i>Rumex acetosella</i>	—	—	—	—	—	563(530)	—	151(138)
<i>Senecio sylvaticus</i>	13821(4709)	*	969(332)	10(7)	+	—	32(29)	—
→ <i>Sonchus oleraceus</i>	30(28)	1095(848)	66(63)	+	—	—	—	—
<i>Taraxacum officinale</i>	1615(1353)	23(15)	616(441)	85(64)	—	7(6)	—	—
<i>Urtica urens</i>	+	+	—	*	—	—	—	—
<i>Verbascum thapsus</i>	626(454)	147(100)	259(247)	6(6)	28(25)	71543(29190)	—	22950(12316)
<i>Veronica plebia</i>	—	+	—	+	—	—	—	—
Shrubs								
→ <i>Chenopodium oahuense</i> (E)	295(229)	4004279 (3126191)	—	—	—	—	—	—
<i>Dodonea</i> sp (E)	61(58)	+	—	—	—	—	—	—
Trees								
→ <i>Sophora chrysophylla</i> (E)	446(240)	34(28)	5(5)	3(3)	211478(188975)	7631(6653)	12393(8556)	6134(5600)
Total basal area cover	38163(6699)	4252482(3126905)	4389(1105)	158481(55617)	360885 (198433)	108256 (31239)	51639(17906)	68594(23852)
Native spp. except <i>S. chrysophylla</i>	13280(2800)	4149904(3126727)	1288(681)	551(375)	18762(5538)	3092(802)	4932(1347)	4932(1347)
Exotic spp.	24437(6081)	102544(33345)	3096(869)	157927(55616)	130645(60279)	97533(30512)	34314(15672)	57528(23146)
Number of species								
Total	29	29	15	22	17	18	9	17
Common to inside	15	20	15	20	9	15	9	15

¹→ = preferred browse species

²E = endemic species

³— = species not found within the study boundaries

+⁴ = species present within study boundaries, but not tallied in the sample quadrats

*⁵ = basal area <1 cm²/ha

found inside the exclosures. At Kaluamakani, *Deschampsia*, another endemic grass, was also completely suppressed outside.

The relatively slight difference in mamane over inside and outside the Puu Nanaha exclosure is misleading. The outside value (3.2%) represented only one large-crowned tree. Cover inside (6.2%) was based on 11 intercepted mamane that became established after the exclosure was built. A more intensive sample may have resulted in a much larger difference.

The proportion of bare ground and rock was lower inside than outside exclosures but the reverse was true for the total of litter and log percentages. Even inside, however, bare ground and rock made up a high proportion of the area—68 to 89% (Table 2).

Plants inside the Puu Nanaha and Puu Kole exclosures were taller than those outside (Table 2). Statistical tests of differences were possible only for five species: Hairy oatgrass (*Danthonia pilosa*), velvet grass (*Holcus lanatus*), gosmore (*Hypochoeris radicata*), sweet vernal (*Anthoxanthum odoratum*), and sheep sorrel, the first 3 of which are preferred browse species. Each was significantly taller ($p \leq 0.05$) inside than outside the exclosures. The mean height of all plants excluding mamane was significantly greater inside than outside the Puu Nanaha and Puu Kole exclosures. Similar tests for Kaluamakani were not needed because so few plants grew outside.

Other Species—1972 Exclosures

More species were represented inside the Puu O Kauha and Hale Pokaku exclosures than outside (Table 3). The differences were less pronounced 3 years after fencing. At Hale Pokaku, the 3rd-year difference was small, possibly because of low browsing pressure outside.

At Puu O Kauha, 15 species were common to both protected and unprotected areas in 1972. Three years later, 20 species were common to both. At Hale Pokaku, 9 were common in 1972 and 15 in 1975. The species common to fenced and exposed areas accounted for more than 90% of the cover in 1972 at both sites. By 1975, the common species made up less than 5% of the cover inside Puu O Kauha, but more than 98% outside. This difference was because of large aheahea bushes inside—they accounted for 94% of the cover—but not outside. At Hale Pokaku, common species accounted for more than 95% of the cover inside and outside in 1975. These data indicate that species composition is not greatly different, except for some native species like aheahea, heu-pueo, and Hawaiian bent, which are completely suppressed by heavy browsing.

Total basal area cover was small (<0.4%) at both sites even 3 years after fencing (Table 3), but fenced areas always had more cover than unprotected ones. Total cover increased with time both inside and outside the Puu O Kauha exclosure. The increase inside (11,000%) was primarily because of growth of aheahea bushes that were not found outside. Outside cover increased 350%, possibly because of lower sheep use occasioned by our visits to the site.

At Hale Pokaku, total basal area cover decreased over time inside and outside. The losses may not be real, however, because of differences in the very mamane, which accounted for a large proportion of the total cover in 1972, was measured. Diameters of clumps were measured the first time and diameters of the individual stems making up the clumps were recorded the second. A great deal of bare ground was thus tallied as mamane basal area the first time, yielding an inflated basal area estimate. The lack of mamane mortality at Hale Pokaku also indicated that loss of mamane cover and, therefore, a decrease in total cover, may be an artifact of measurement techniques. Excluding mamane, total basal area decreased only slightly inside and increased slightly outside. None of these changes in total plant cover with time inside was significantly different from those outside (Bonferroni t -test, $p \leq 0.05$). The same was true at Puu O Kauha.

The effect of protection on recovery of native species other than mamane was different at the two exclosure sites (Table 3). At Puu O Kauha immediately after fencing, native species comprised about 35% of the estimated plant basal area inside and 29% out-

side. Three years later, native species accounted for 98% of the basal area inside (mostly because of aheahea), but less than 1% outside. At Hale Pokaku, native species other than mamane comprised 13% of the basal area both inside and outside the exclosure just after fencing. But in contrast to Puu O Kauha, 3 years later, the proportion of native plants inside dropped to 3%. The proportion of native plants outside also dropped, but only to 8%. We expect this differential response will show-up elsewhere around the mountain.

Data were sufficient on only 4 preferred browse species at Puu O Kauha to statistically compare changes inside against changes outside: Hawaiian bent, heu-pueo, aheahea, and mamane, all endemic plants. Cover for both heu-pueo and aheahea increased significantly ($p \leq 0.05$) more inside than outside. The absence of aheahea outside indicated that sheep completely suppressed it, at least in this tree-line zone. Aheahea and heu-pueo should be considered sensitive indicators of vegetation recovery. For mamane and Hawaiian bent, the change inside was not significantly different from that outside.

At Hale Pokaku, cover estimates were complete for only 2 preferred browse species: hairy oatgrass and gosmore. Statistical comparisons of change in cover inside vs. outside showed that gosmore increased significantly more inside than outside ($p \leq 0.05$). A similar comparison for hairy oatgrass revealed no significant difference.

Conclusion

Results indicate that feral sheep browsing suppresses regeneration of mamane. Three other endemic species, Hawaiian bent, heu-pueo, and aheahea, are also suppressed. Other preferred browse species were either not significantly affected by browsing or the data for them were inadequate to evaluate.

Now that feral sheep and goats have been eradicated, we expect recovery of mamane to be rapid in most tree-line areas. Because mamane seeds remain viable in the soil for years, even barren areas supporting only skeletal remains may once again give rise to mamane regeneration. Site conditions on some areas like that represented by Kaluamakani will prevent rapid plant regrowth. Forest decline in general, however, will be checked, thereby removing one of the threats to Palila and other endemic flora and fauna.

Another threat may interfere with the ultimate recovery of the mamane forest—Mouflon sheep and feral-Mouflon hybrids. These animals are being retained as a game species on Mauna Kea. Their food preferences are similar to those of feral sheep, with mamane being one of the most important items in their diet (Giffin 1981). The 2 species are also alike in their herding, behavior, and habitat use patterns. The Mouflon population density has increased to a point where mamane reproduction is being severely suppressed, especially in the area of tree-line. This problem can only be alleviated by drastically reducing herd size. The number of Mouflon that can be managed without habitat damage has yet to be determined.

Our data support the observation that profound changes can occur following introduction of grazing and browsing animals (Spurr and Barnes 1980). Island ecosystems are especially susceptible to damage (i.e., Coblenz 1978), because the animals often find themselves in a favorable habitat rich in plants lacking defensive mechanisms and without natural enemies (Mueller-Dombois 1981). Introduced grazing and browsing animals can also damage continental ecosystems (Wodzicki 1950). Endemic fauna ultimately suffer. Preventing the introduction of exotic animals and reducing or eliminating established populations are steps managers must take to maintain or restore the integrity of native ecosystems.

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