Pacific Science (1983), vol. 37, no. 2

Tree Cover Changes in *Māmane* (*Sophora chrysophylla*) Forests Grazed by Sheep and Cattle[1]

PAUL G. SCOWCROFT[2]

ABSTRACT: Using aerial photographs taken in 1954, 1965, and 1975, percentage of tree cover was determined for three sections of the sheep- and cattle-grazed *māmane* (*Sophora chrysophylla*) forest of Mauna Kea, Hawaii. In one section, the Ka'ohe Game Management Area, where grazing by sheep was judged light, tree cover increased slightly during the 21-yr period, and tree cover did not change significantly along an elevation gradient. This condition was probably the result of the predominance of *naio* (*Myoporum sandwicense*) trees, which are not as palatable as *māmane* and, therefore, are less sensitive to browsing. In the Mauna Kea Forest Reserve, the most heavily sheep browsed of the three sections, a significant loss of tree cover was observed between 1965 and 1975 near tree line where feral sheep tended to concentrate their browsing. Of the three sections examined, Parker Ranch, which was grazed mainly by cattle, sustained the greatest loss of tree cover during the 21-yr period, reflecting the more destructive nature of cattle browsing as compared to sheep browsing. Increases of tree cover in areas relatively free of sheep within the Mauna Kea Forest Reserve indicated that habitat for the *palila*, an endangered bird that depends on the *māmane* forest, will improve slowly after feral sheep are removed.

AT MAUNA KEA ON THE ISLAND of Hawaii the *māmane* (*Sophora chrysophylla*) forest has been adversely affected by feral sheep (*Ovis aries*) and other herbivores for more than 150 yr (Kramer 1971). Damage from sheep was so severe that an effort to eradicate them, begun in 1937 (Bryan 1937), was continued through 1949. As a result introduced and native herbaceous and woody vegetation became established and proliferated in many areas (Tomich 1969). At the same time, however, feral sheep became valued as a game species; consequently, the policy of eradication was replaced by sustained-yield game management in 1959 (Walker 1978). But in areas where the remaining sheep concentrated, especially near tree line, *māmane* and other vegetation did not regenerate (Warner 1960), a condition prevalent even as recently as 1980 (Scowcroft and Giffin, in press). Forest areas used by cattle (*Bos taurus*) for pasture also showed little evidence of successful *māmane* regeneration.

The continued decimation of the *māmane* overstory—from the death of old trees and from the failure to regenerate—was a significant threat to the *palila* (*Psittirostra bailleui*), an endangered endemic Hawaiian bird restricted to the *māmane* forest of Mauna Kea (Berger 1972). *Palila* depend on *māmane* and, to a lesser extent, on *naio* trees (*Myoporum sandwicense*) for food and nest sites (van Riper 1980*a*). Their breeding season coincides with the time of year when *māmane* bear seed pods (van Riper 1980*a*). *Palila* were found most abundant and in highest densities near tree line (van Riper, Scott, and Woodside 1978). The birds probably were attracted to this area because it contained a high proportion of large *māmane* trees capable of producing more food than smaller ones. If large trees are as necessary to the *palila* as these findings suggest, then death of such trees could further restrict the bird's acceptable habitat (van

[1] Manuscript accepted 30 December 1982.

[2] Institute of Pacific Islands Forestry, Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture, 1151 Punchbowl Street, Honolulu, Hawaii 96813.

Riper 1980*a*), especially if the forest failed to regenerate.

Because quantitative data were lacking, hunting advocates denied that tree cover had been lost. Some of those who acknowledged a loss suggested natural causes other than feral sheep. A study has shown that *māmane* regeneration is suppressed by feral sheep in the vicinity of tree line (Scowcroft and Giffin, in press). Because of this suppression and the abundance of dead trees in upper portions of the forest, I hypothesized that there should be a net loss of tree cover in the upper fringe of the forest.

This paper reports a study to determine changes in tree canopy cover from 1954 to 1975 within the Mauna Kea Forest Reserve (Mauna Kea FR), the Ka'ohe Game Management Area (Ka'ohe GMA), and adjacent Parker Ranch.

STUDY AREA

Site Description

The study area, totaling about 4280 ha, was located between 1750 m and 2900 m on the west flank of Mauna Kea (Figure 1). This area was chosen because aerial photos of it were available for 1954, 1965, and 1975. It was also an area where *palila* were found in high densities (van Riper, Scott, and Woodside 1978). Only forested land was included. Portions of the forest that were strip-bulldozed to enhance game-bird habitat were excluded.

Three land divisions are represented in the study area—the Mauna Kea FR (2360 ha), Ka'ohe GMA (890 ha), both owned and managed by the State of Hawaii, and Parker Ranch (1030 ha), which is privately owned. Cattle used the ranch land during winter months; feral sheep used the other areas year-round. For most of the period, sheep browsing was lighter (fewer sheep per hectare of utilized forest) in the Ka'ohe GMA than in the Mauna Kea FR (R. Walker, pers. comm.).

The forest overstory in the study area was chiefly *māmane* and *naio* with small stands of *Euphorbia olowaluana*, *na'ena'e* (*Railliardia arborea*), and coast sandalwood (*Santalum ellipticum*) scattered through portions at lower elevations. The relative abundance, density, and size of *māmane* and *naio* along the northern edge of the Ka'ohe GMA, as described by van Riper (1980*b*), apply to the entire GMA study area. On pasture lands the forest is pure, open *māmane* except near the boundary to the Ka'ohe GMA where *naio* grows together with *māmane*. The forest extends from about 2870 m down to about 1750 m elevation. The forest to the east of Pu'u Lā'au, and at upper elevations in the Mauna Kea FR, is also open woodland of pure *māmane*. Elsewhere in the Mauna Kea FR, *naio* grows mixed with *māmane*, with the proportion of *naio* decreasing with increasing elevation. Forest density decreases as elevation increases.

Climate in the study area is cool and dry (van Riper 1980*b*). Annual rainfall averages more than 500 mm, most of it falling between November and April. Temperature maximums rarely exceed 21°C, and the diurnal fluctuation is about 20°C. Fog frequently envelops the area by midafternoon.

Soils in the area are very fine sandy loams and loamy fine sands formed from volcanic ash, sand, and cinders (U.S. Department of Agriculture 1973). They are well drained to excessively drained, with rapid permeability (up to 50 cm/hr) and with little runoff or erosion.

Animal Populations

The only estimates for the size of sheep populations in the Mauna Kea portion of the study area are those made by the Hawaii Division of Fish and Game.[3] Sheep counts were obtained by aerial and ground surveys conducted by wildlife biologists. The counts were adjusted for duplicate sightings and for estimated number of animals missed due to

[3] Job Progress Reports on Statewide Game Research and Surveys compiled by the Hawaii Division of Fish and Game and on file with the Hawaii Division of Forestry and Wildlife (HDFW), 1151 Punchbowl St., Honolulu 96813. Reports are available for most years since 1953. Authors, job titles, and project numbers vary.

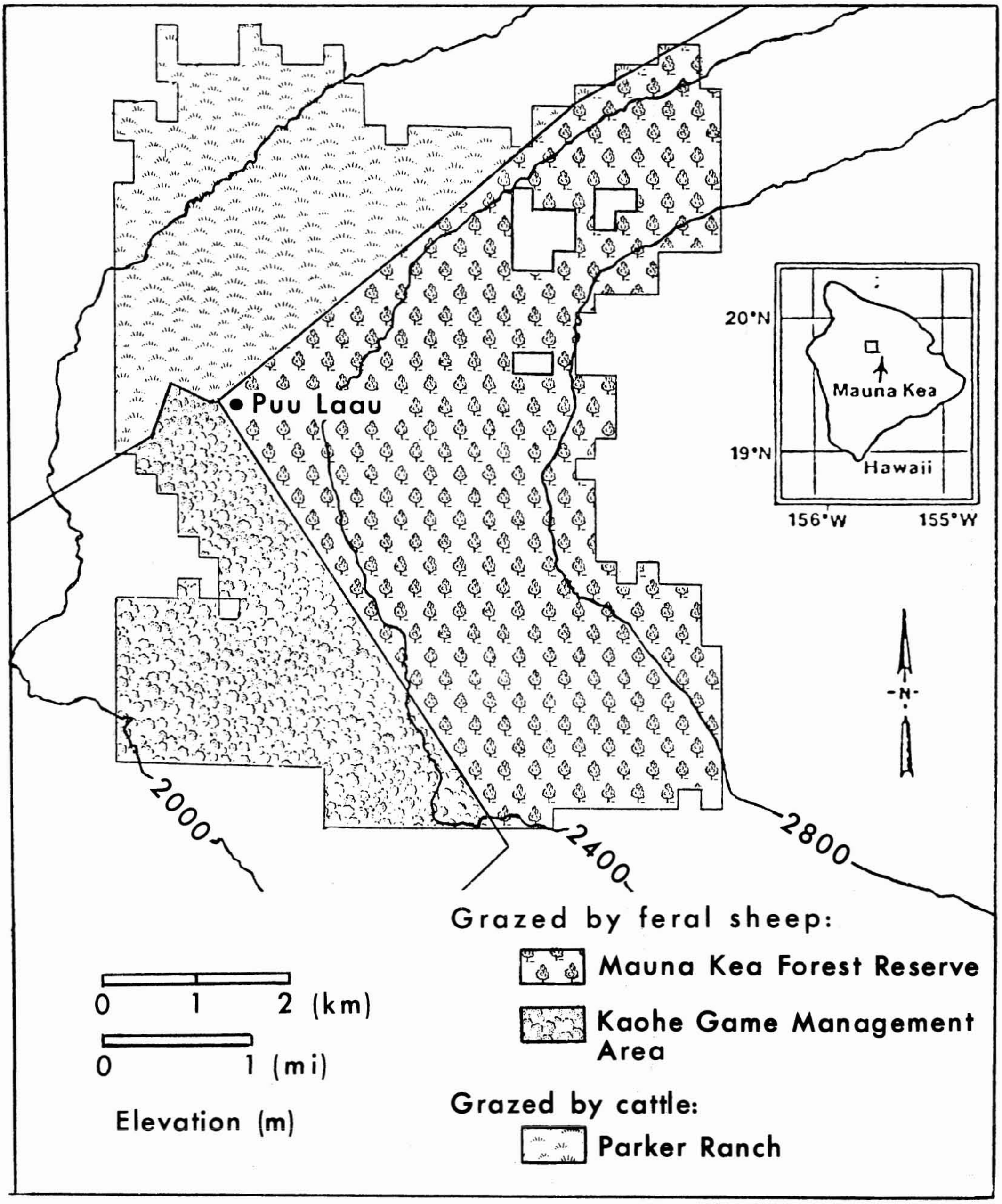

FIGURE 1. About 55 percent of the 4280-ha study area lay within the Mauna Kea Forest Reserve (FR), 21 percent within the Ka'ohe Game Management Area (GMA), and 24 percent within the Parker Ranch. Each is separated from the others by fences which converge near Pu'u Lā'au.

dense tree cover and fog. Estimates were reported separately for 6 to 10 topographically defined sections of the forest reserve. Thus, population estimates were available for the area between Pōhakuloa and Kemole gulches where my study area lay.

Sheep density was determined for the years 1954 through 1975 by dividing the estimated sheep population by the size of the forested area between Pōhakuloa and Kemole (4700 ha). I assumed that density within my 2360-ha study area was equal to the calculated density for the whole area between Pōhakuloa and Kemole.

Results showed that the feral sheep population varied from an estimated low of 0.10 animals/ha in 1954 to a high of 0.39 animals/ha of forest in 1968 (Table 1). In general, sheep densities were smaller during the first half of the period (1954–1965) than during the second half (1965–1975). A greater proportion of the total population of feral sheep in the Mauna Kea FR was found between Pōhakuloa and Kemole gulches after 1965 than occurred before that date.

The sheep were well distributed throughout the area before 1965 (R. Walker, pers. comm.). Even as late as the early 1960s it was common to find sheep grazing near the lower fence boundary at 2130 m elevation. This was the result of the maintenance of a relatively large number of feral sheep and of the game managers' deliberate husbandry of them to obtain a uniform spatial distribution.

About 1965, biologists realized that the large number of sheep in the Mauna Kea FR, although well distributed, were causing unacceptable damage to the vegetation. To reduce the population, the access road system was expanded and hunters were allowed to take both sexes instead of rams only. The increased hunting reduced the total sheep population in the Mauna Kea FR. In my study area, however, sheep populations were generally larger after hunting pressure increased.

Increased hunting pressure also caused the survivors to keep to higher elevations, generally above 2400 m. Before 1965, therefore, browsing pressure was evenly distributed throughout the forest, but after 1965 browsing pressure occurred mostly above 2400 m.

In the Ka'ohe GMA, census data on feral sheep existed only for 1961 (Walker 1961) and 1973 (J. Giffin, pers. comm.). These data and the recollections of the wildlife biologists on the Island of Hawaii during the 21-yr period (R. Walker, E. Kosaka, and J. Giffin, pers. comm.) indicated that the resident feral sheep population in Ka'ohe was less than one animal on 10 ha (0.09/ha) of forest through the 1960s, and possibly as high as 1.4 animals on 10 ha (0.14/ha) in the first half of the 1970s. Large concentrations of sheep were reported for 1965 in the upper, eastern quarter of Ka'ohe GMA where hunting pressure was low because of poor access (Bachman 1966). The sheep were more uniformly distributed throughout the area in the early 1970s (J. Giffin, pers. comm.). Additional browsing

TABLE 1

ESTIMATED DENSITY OF FERAL SHEEP IN THE STUDY AREA* AND THE ESTIMATED SIZE OF THE SHEEP POPULATION FOR THE ENTIRE FOREST RESERVE, 1954 THROUGH 1975

DATE OF CENSUS (mo/yr)	SHEEP DENSITY IN STUDY AREA (#/ha)†	ESTIMATED POPULATION IN MAUNA KEA FR‡
6/54	0.10	1560
3/55	0.11	2200
–/56	—	—
8/57	0.18	3200
10/58	0.19	3000
5/59	0.12	3500
5/60	0.20	4000
5/61	0.17	3500
3/62	0.13	2300
7/63	0.16	1250
7/64	0.17	1400
5/65	—	1840
5/66	0.34	2700
–/67	—	—
7/68	0.39	3250
7/69	0.35	2900
7/70	0.26	2500
7/71	0.19	2385
–/72	—	—
2/73	0.20	2125
5/74	0.13	1200
1/75	0.20	1735

* Within the Mauna Kea FR.

† Density was calculated by dividing the estimated number of sheep in the area between Pōhakuloa and Kemole gulches by the size of the forested area. This figure was assumed to represent animal density in the study area.

‡ From Giffin 1976.

pressure may have been exerted on less accessible areas when sheep from the Mauna Kea FR temporarily fled through broken fences into Ka'ohe GMA to escape hunters (R. Walker, pers. comm.).

In Parker Ranch, no estimate of cattle numbers was available. Use by cattle was seasonal, however. An unknown number of feral sheep lived on the ranch land year-round. The sheep population there was probably larger before 1965 than after (Walker 1961).

MATERIALS AND METHODS

I estimated percentage of tree cover from aerial photographs taken in 1954, 1965, and 1975. These estimates allowed me to evaluate change in tree cover during a 21-yr period (1954–1975) and to look at the changes during the first (1954–1965) and second (1965–1975) halves of that period.

The 1954 and 1965 photos were black and white and the 1975 ones were color. The nominal photo scales were 1 : 40,000 for 1954, 1 : 24,000 for 1965, and 1 : 12,000 for 1975. Image resolution was poor for the 1954 photos but good for the other two sets.

The sample consisted of 870 circular sample plots: 480 plots lay within the Mauna Kea FR; 181 within the Ka'ohe GMA; and 209 within Parker Ranch. Plot centers were first established on a 1 : 24,000 U.S. Geological Survey quadrangle map with a uniform grid. Each center was transferred to the 1975 photos by matching the topographic features of the map and photos. The same plot centers were then carefully located on the 1954 and 1965 photos with the aid of the marked 1975 photos. Each plot circumscribed an area on the photo equivalent to 0.2 ha on the ground. Because of differences in photo scale, it was necessary to vary the diameter of the photo plots to assure that the same size ground area (0.2 ha) was examined in every case. This involved first determining the photo scales across each photo, and then using an acetate overlay inscribed with the appropriate size circle. The 870 plots represented a 4 percent sample of the study area.

Different scale grids of intersecting lines inscribed on a second clear acetate overlay were used to estimate cover. About 120 intersections fit within the smallest circle at the scale of 1 : 43,000, and more than 300 intersections fit within the largest at the scale of 1 : 11,000. The proportion of points that overlaid the image of tree canopies was determined under 8 × to 20 × magnification. This value, to the nearest whole percent, was recorded for each sample plot along with elevation and land use.

The change in percent tree cover for each of the 870 plots was calculated for each period by subtracting the percent cover at the start of the period from that at the end of the period. This difference was used in most of the analyses. Throughout the rest of the paper, I use the phrase *average change in percent tree cover* to mean the difference between cover at the start and end of a period averaged for all plots in the land-use category or elevation stratum under consideration.

Changes in percentage of tree cover between land uses were compared for each of the three periods by regressing cover at the end of the period on cover at the beginning (linear model) and then calculating a joint 95 percent confidence region for the slope and intercept (Draper and Smith 1966). This procedure allowed me to take into account differences in percent tree cover between land uses at the beginning of each period. Nonoverlapping confidence regions indicated that the change in cover was significantly different between the land uses being compared.

For each land use, I used the Bonferroni *t* test to compare the average change in tree cover between 150-m elevation strata and between periods (Miller 1966). The Bonferroni *t* test is a multiple pairwise comparison test applicable to data where the sample sizes of factor levels are equal or unequal.

RESULTS

Mauna Kea Forest Reserve

In 1954 the average percent tree cover for the sample area within the Mauna Kea FR, heavily grazed by sheep, was 27.3 percent. By 1965, average tree cover had declined slightly to 26.7 percent. A further decline to 25.6 percent occurred between 1965 and 1975.

These means were not significantly different (Bonferroni t test, $P \geq 0.05$). The loss of cover during the 21 yr represented about one-twentieth of the tree cover present in 1954.

I hypothesized that tree cover losses should be greater at higher elevations in the Mauna Kea FR where damage to vegetation, and, by inference, browsing pressure, had been reported as persistently high (Giffin 1976). This proved to be true when data were analyzed by 150-m elevation strata (Figure 2*A*). For the entire period, the two upper-elevation strata lost cover but the three lower strata gained cover. Only the loss in the uppermost stratum (8.5 percent), however, was statistically different (Bonferroni t test, $P < 0.01$) from the changes at lower elevations.

When the first half of the period was considered separately, average change in cover per plot was not statistically different among elevations (Figure 2*A*). During the second half, however, the changes in cover above 2590 m elevation were significantly different (Bonferroni t test, $P < 0.01$) from those below 2590 m. During the second half of the period, the net change in cover per plot for the five elevations followed the pattern I expected, with greatest gains at the lowest elevation and greatest losses at the highest elevation.

The mean change in tree cover during the first half of the period was not significantly different (Bonferroni t test, $P \geq 0.05$) from that during the second half (see Figure 2*A*, dashed lines).

Because errors in cover estimation may have resulted from poor image quality in the 1954 photos, I also compared changes in tree cover for only those plots that lost or gained at least 20 percent cover. When the entire 21-yr period was considered, 86 of the 480 plots in the Mauna Kea FR fell into this category: more than two-thirds of these lost cover. Analysis of the 86-plot subsample revealed that loss of tree cover increased at successively higher elevations, the same pattern I found when all plots were included in the analysis.

Ka'ohe Game Management Area

Tree cover in the Ka'ohe GMA averaged 54.5 percent in 1954, 52.3 percent in 1965, and 56.4 percent in 1975 (Table 2). Differences between these means were not significant (Bonferroni t test, $P \geq 0.05$). Losses incurred during the first 11 yr were compensated for during the last 10 yr.

The tendency for progressively greater losses of tree cover at higher elevations, which I observed in the Mauna Kea FR and which I attributed to increasing browsing pressure, was not evident in this dense portion of the forest (Figure 2*B*). If anything, the reverse was true: Cover losses became progressively greater at lower elevations. None of the differences between elevation strata were significant, however (Bonferroni t test, $P \geq 0.05$).

From 1954 to 1965 tree cover in Ka'ohe declined an average of 2.2 percent (Figure 2*B*, dashed line). From 1965 to 1975 cover increased an average of 4.1 percent. These mean changes were significantly different (Bonferroni t test, $P < 0.01$).

Compared with the heavily browsed Mauna Kea FR, only 9 percent of the 181 plots in the lightly browsed Ka'ohe GMA changed cover more than 20 percent during the 21-yr period. More than one-half of such plots gained cover while the rest lost cover. Analysis of the 16-plot subsample revealed that average change in tree cover was not significantly different between elevation strata.

Parker Ranch

The remnant *māmane* forest on Parker Ranch, grazed by cattle, lost one-fifth of its tree cover during the 21-yr period (Table 2). This loss was the greatest of those measured for the three land divisions. Almost all of this cover was lost before 1965 when the average percent tree cover fell from 18.9 percent in 1954 to 15.1 percent in 1965. The difference between cover in 1954 and 1965 was significant (Bonferroni t test, $P < 0.05$). Average tree cover in 1975 was 15.0 percent.

During the first half of the period, net losses were observed in all strata below 2290 m elevation (Figure 2*C*). But during the second half, net losses were noted only in the two strata between 1831 to 2130 m. The highest stratum (2291 to 2440 m) gained cover in both the first and second halves of the period. Some of the

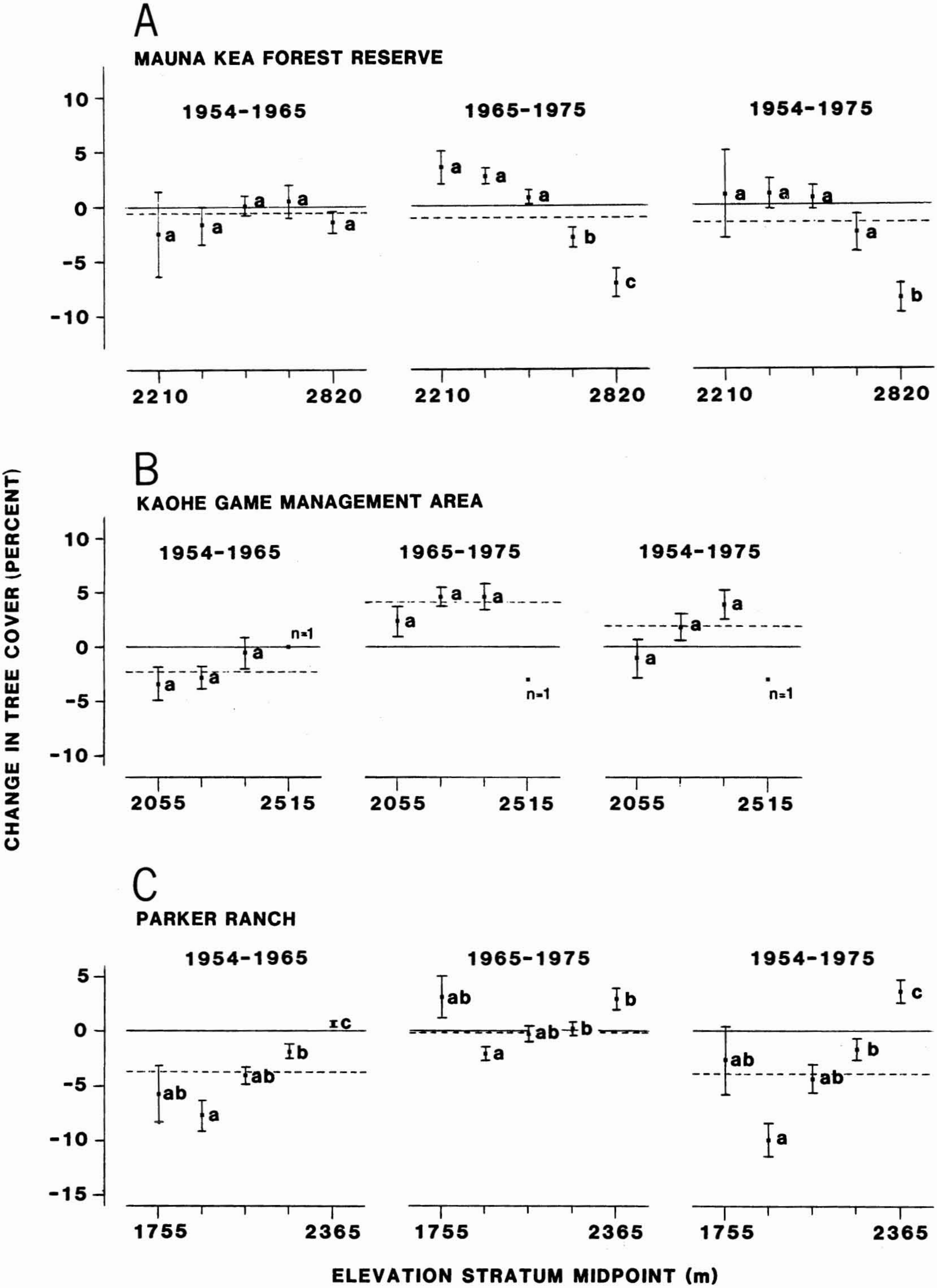

FIGURE 2. Average change in percent tree cover per plot ($\pm s_{\bar{x}}$) within the Mauna Kea FR (A), the Ka'ohe GMA (B), and the Parker Ranch (C), by 150-m-wide elevation strata and period. Elevation means for a given period and land division followed by a common letter are not significantly different (Bonferroni t test, $P \geq 0.05$). The dotted lines indicate the average change per plot for all strata combined for the given period. The uppermost elevation stratum in the Ka'ohe GMA had only one sample plot.

TABLE 2

AVERAGE PERCENT TREE COVER PER PLOT FOR THREE GRAZED PORTIONS OF THE MĀMANE FOREST OF MAUNA KEA IN 1954, 1965 AND 1975

ELEVATION STRATUM (m)	SAMPLE SIZE	PERCENT TREE COVER PER PLOT*		
		1954	1965	1975
			Mauna Kea FR	
2131–2290	6	24.2 (4.0)†	21.7 (4.2)	25.2 (3.7)
2291–2440	121	33.0 (2.0)	31.3 (1.8)	33.9 (1.8)
2441–2590	148	29.3 (1.9)	29.3 (1.8)	30.0 (1.8)
2591–2740	111	24.9 (2.1)	25.3 (2.3)	22.4 (2.2)
2740	94	20.1 (2.2) a	18.7 (2.1) a	11.6 (1.6) b
All	480	27.3 (1.0)	26.7 (1.0)	25.6 (1.0)
			Ka'ohe GMA	
1981–2130	33	56.6 (3.8)	53.2 (3.8)	55.4 (3.8)
2131–2290	93	52.3 (1.8)	49.5 (1.8)	54.0 (1.9)
2291–2440	54	56.5 (3.3)	55.9 (3.2)	60.5 (3.0)
2441–2590	1	89.0 (—)	89.0 (—)	86.0 (—)
All	181	54.5 (0.9)	52.3 (0.6)	56.4 (0.7)
			Parker Ranch	
1831	10	18.1 (3.6)	12.3 (1.8)	15.4 (3.5)
1831–1980	42	23.1 (2.6) a	15.4 (1.7) b	13.2 (1.6) b
1981–2130	73	18.8 (1.4)	14.7 (1.1)	14.4 (1.4)
2131–2290	68	17.8 (1.1)	15.9 (0.8)	16.1 (0.8)
2291–2440	16	13.7 (1.4)	14.5 (1.3)	17.4 (1.6)
All	207	18.9 (1.5) a	15.1 (1.5)b	15.0 (1.5) b

*Values within a row followed by the same letter do not differ significantly (Bonferroni procedure for pairwise comparisons, $P \geq 0.05$). No significant differences exist in rows where letters do not appear.

† Values in parentheses are standard errors of the mean.

average changes in tree cover for the elevation strata were significantly different (Figure 2*C*).

Areawide changes in cover for the first and second halves of the study period are shown in Figure 2*C* (dashed lines). The mean change during the first half ($\bar{x} = -3.8$ percent, $SE = 0.5$) was significantly different (Bonferroni t test, $P < 0.01$) from that during the second half ($\bar{x} = -0.1$, $SE = 0.4$).

Like the Ka'ohe GMA, 9 percent of the 209 pasture plots underwent a change in cover of 20 percent or more during the 21-yr period. Fifteen of the 16 plots lost cover. No trend was apparent in net cover change with elevation.

All Three Land Uses

I also compared the average change in tree cover per plot among the three land uses. The statistical analysis involved first regressing cover at the end of the period on cover at the beginning and then calculating a joint 95 percent confidence region for the slope and intercept. Differences in the change of cover were significant if confidence regions did not overlap.

Before 1965, all three land divisions suffered a net loss of cover, but the loss for the forest grazed by cattle was significantly greater ($P < 0.05$) than the losses in the other areas (Table 3). After 1965, net losses continued in the Mauna Kea FR and in Parker Ranch, both heavily grazed, but the Ka'ohe GMA, lightly grazed, gained cover. Considering the entire 21-yr period, the greatest net loss occurred in cattle-grazed areas ($\bar{x} = -3.9$ percent/plot). A smaller loss was observed for areas heavily grazed by sheep ($\bar{x} = -1.7$ percent/plot). The lightly sheep-browsed forest actually gained cover ($\bar{x} = +1.9$ percent/plot). Each of these changes was significantly different from the others ($P < 0.05$).

TABLE 3

AVERAGE CHANGE IN PERCENT TREE COVER PER PLOT FOR THE FIRST HALF (1954–1965), SECOND HALF (1965–1975), AND ENTIRE STUDY PERIOD (1954–1975) ON GRAZED PORTIONS OF THE MĀMANE FOREST OF MAUNA KEA

LAND USE	SAMPLE SIZE	PERCENT CHANGE IN TREE COVER PER PLOT* FIRST HALF (1954–1965)	SECOND HALF (1965–1975)	ENTIRE PERIOD (1954–1975)
Heavily grazed by sheep (Mauna Kea FR)	480	−0.6 (0.6)† a	−1.1 (0.4) a	−1.7 (0.7) a
Lightly grazed by sheep (Ka'ohe GMA)	181	−2.2 (0.7) a	4.1 (0.6) a	1.9 (0.8) b
Grazed by cattle (Parker Ranch)	207	−3.8 (0.5) b	−0.1 (0.4) a	−3.9 (0.7) c

* Values within a column followed by the same letter do not differ significantly ($P \geq 0.05$). See text for description of statistical test.
† Values in parentheses are standard errors of the mean.

DISCUSSION

I suspect that the small scale and poor resolution of 1954 photos introduced some error into the data. Small-crowned trees may have been missed, with the result that cover was underestimated. This situation most likely was true for areas of low to moderate tree cover where plant competition was low enough to permit establishment of trees during the late 1940s and early 1950s when sheep numbers were low. Underestimates of initial cover would have resulted in the overestimation of gains and the underestimation of losses in tree cover over time. Such errors probably affected data for those parts of the Mauna Kea FR where initial tree cover was low to moderate and browsing pressure was nil for a time. I do not believe such errors affected the significance of differences (Figure 2*A*). This view was supported when only plots that changed by 20 percent or more were compared.

In areas with dense tree cover in 1954, shadows may have been viewed as tree canopy, leading to an overestimate of cover. The effect on cover change over time would have been an overestimate of losses and an underestimate of gains in cover. This type of error probably affected data of the Ka'ohe GMA and those areas of the Mauna Kea FR where stand density was high. Such errors would not have affected the outcome of the statistical tests, however. For instance, in Ka'ohe cover was uniformly dense, in general, and the means for all elevations would have been equally affected. So differences among means would still have been nonsignificant (Figure 2*B*). Supporting this view was the lack of any statistical differences between elevation strata when the analysis included only plots that changed by 20 percent or more.

The average changes in percent tree cover per plot were generally on the order of 1 to 4 percent in the Mauna Kea FR and can be attributed to photo interpretation error. But in the uppermost tree-line stratum, tree cover declined 8.5 percent from 20.1 percent in 1954 to 11.6 percent in 1975 (Table 2). If 5 percent of this change is attributed to interpretation error, then the actual loss was 3.5 percent in 21 years. This was a large loss considering that tree cover was initially sparse. Sustained losses of this magnitude in future years could result in a lowering of tree line, such as that alluded to by Berger (1972).

In the ranch statistical differences in the average change in percent tree cover were detected, but they too were generally on the order of 1 to 5 percent. The exception was the stratum between 1830 to 1980 m where cover declined from 23 to 13 percent in 21 yr (Table 2). If 5 percent of this change is attributed to interpretation error, then actual loss was 5 percent in 21 yr. As at tree line in the Mauna Kea FR, such a loss was large relative to the amount of cover present initially.

Evidence from other studies (Scowcroft and Giffin, in press, Scowcroft and Sakai 1983) implicate feral sheep as a factor that could explain the reduction of tree cover near tree line in the Mauna Kea FR. These studies show that sheep suppressed *māmane* regeneration in areas they used frequently. And because they used the upper fringe of the forest most (Giffin 1976), replacement of dying overmature *māmane* could not occur. The predictable outcome was an increase of *māmane* tree cover in lower areas and a decrease in upper areas.

While the main effect of sheep browsing is suppression of *māmane* regeneration, sheep can reduce tree cover directly by consuming foliage and twigs of established *māmane* trees. Such losses are probably small because the browse height of sheep is less than 2 m. Similarly, sheep probably do not reduce tree cover by directly causing whole tree mortality. Indeed, mortality would occur even without browsing pressure. But in a stable forest ecosystem, one would expect replacement of dead trees and reestablishment of lost leaf area. One would not expect significant losses of tree cover in the absence of browsing pressure and catastrophic events. Thus, browsing damage and decline in tree cover in the Mauna Kea FR are linked by the fate of *māmane* reproduction.

In the Ka'ohe GMA, the lack of change in tree cover during the 21-yr period beyond what could be attributed to interpretation error was not surprising. The area already supported dense stands of *naio* and *māmane* in 1954, making large increases in cover unlikely. Large decreases in cover were also unlikely, if we assume that the principal factors causing a decrease were sheep browsing and old *māmane* tree mortality. The sheep population was relatively small and spatially well distributed during most of the 21-yr period (Walker, pers. comm.). And more importantly, *naio*, which is less palatable than *māmane* and comprises but a small fraction of the diet of sheep (Giffin 1976), dominates the forest in this area. The regeneration of *naio* in openings and the expansion of crowns of larger trees, therefore, would be uninhibited by feral sheep. Furthermore, preferential browsing of any *māmane* regeneration would give *naio* a competitive advantage (van Riper 1980*b*). Sheep browsing in the Ka'ohe GMA, therefore, even if heavy, would probably not be reflected in large losses of tree cover.

The small changes of tree cover in the cattle-grazed area was surprising. Cattle are known to destroy vegetation by trampling and snapping twigs and branches as they maneuver in the vegetation, as well as by eating large quantities of plant material. Even established trees can be affected adversely. The relative youthfulness of a large portion of the *māmane* trees in the ranch and the wide spacing of individuals may account for the small changes in cover—that is, even though regeneration may be suppressed, few established trees would die.

This study showed that the *māmane* component of the *palila*'s habitat (perhaps the most critical component) has been decreasing in the tree-line area of the Mauna Kea FR (Figure 2*A*, Table 2). Because the *palila* depends on the *māmane* forest of Mauna Kea, the continued but gradual loss of *māmane* tree cover can only affect this endangered species adversely. The remnant *māmane* forest in the ranch apparently is not used by the *palila*, possibly because the surviving large trees are too widely scattered to support the bird. The *palila* apparently can not reoccupy the ranch as long as the food producing capacity of the *māmane* forest remains low. And although tree cover increased slightly in the Ka'ohe GMA, the increase probably resulted from regeneration and growth of *naio*, a species of much less value to *palila*.

In 1979, the State of Hawaii was ordered by a federal judge to eliminate feral sheep and feral goats from the *palila*'s critical habitat to comply with the Endangered Species Act of 1973. The Mauna Kea FR and Ka'ohe GMA are part of the critical habitat. That effort has been completed. I expect *māmane* to recover quickly in the higher elevations. Perhaps the losses sustained in the past will be erased and the forest secured for the *palila*. But *māmane* grows slowly in the Mauna Kea FR, and, because large trees are necessary to *palila*, many years will pass before degraded areas again reach their full potential for supporting the bird.

LITERATURE CITED

BACHMAN, R. E. 1966. Mauna Kea feral sheep survey, job completion report. Pittman-Robertson Proj. No. W-5-R-16, Job No. 46(16), July 1964–June 1965 Unpubl. rept. Hawaii Dept. Land and Nat. Res., Div. of Fish and Game, Honolulu.

BERGER, A. J. 1972. Hawaiian birdlife. Univ. Press of Hawaii, Honolulu, 270 pp.

BRYAN, L. W. 1937. Wild sheep in Hawaii. Pac. Para. 49:19, 31.

DRAPER, N. R., and H. SMITH. 1966. Applied regression analysis. John Wiley and Sons, New York. 407 pp.

GIFFIN, J. G. 1976. Ecology of the feral sheep on Mauna Kea, final report. Pittman-Robertson Proj. No. W-15-5, Study No. IX, 1972–1975. Unpubl. rept. Hawaii Dept. Land and Nat. Res., Div. of Fish and Game, Honolulu.

KRAMER, R. J. 1971. Hawaiian land mammals. Charles E. Tuttle Co., Tokyo, Japan. 347 pp.

MILLER, R. G. 1966. Simultaneous statistical inference. McGraw-Hill Book Co., New York. 272 pp.

SCOWCROFT, P. G., and J. G. GIFFIN. In press. Feral herbivores suppress mamane and other browse species on Mauna Kea, Hawaii. J. Range Mgt.

SCOWCROFT, P. G., and H. F. SAKAI. 1983. Impact of feral herbivores on mamane forests of Mauna Kea, Hawaii: Bark stripping and diameter class structure. J. Range Mgt. 36(4):495–498.

TOMICH, P. Q. 1969. Mammals in Hawaii: A synopsis and notational bibliography. Bernice P. Bishop Museum Spec. Pub. 57, Bishop Museum Press, Honolulu. 238 pp.

U.S. DEPARTMENT OF AGRICULTURE, SOIL CONSERVATION SERVICE. 1973. Soil survey of island of Hawaii, State of Hawaii. Soil Cons. Ser. in cooperation with the Univ. of Hawaii Agr. Exp. Sta. U.S. Govt. Printing Office, Washington, D.C. 115 pp.

VAN RIPER, C., III. 1980*a*. Observations on the breeding of the Palila *Psittirostra bailleui* of Hawaii. Ibis 122:462–474.

———. 1980*b*. The phenology of the dryland forest of Mauna Kea, Hawaii, and the impact of recent environmental perturbations. Biotropica 12:282–291.

VAN RIPER, C., III, J. M. SCOTT, and D. M. WOODSIDE. 1978. Patterns in the distribution and abundance of the Palila on Mauna Kea, Hawaii. Auk 95:518–527.

WALKER, R. L. 1961. A brief report on the present status of game populations in the horse pasture game management area and recommendations for management and hunting. Unpubl. rept. Hawaii Dept. Agr. and Conserv., Div. of Fish and Game, Honolulu. 2 pp.

———. 1978. A history of the Division of Fish and Game. Paper presented at the 20th Annual Hawaii Forestry Conference: Habitats, Energy, and Other Good Things, Kona, Hawaii, September 1978.

WARNER, R. E. 1960. A forest dies on Mauna Kea. Pac. Dis. 13:6–14.

ACKNOWLEDGMENTS

The author thanks Carl Masaki for interpreting the aerial photos; C. W. Smith, R. A. Merriam, R. L. Walker, J. A. Baldwin, C. J. Ralph, C. van Riper, and J. G. Giffin for their critical reviews of earlier drafts of this manuscript; and J. A. Baldwin for his invaluable statistical guidance.