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THE INFLUENCE OF FERAL GOATS ON THE LOWLAND
VEGETATION IN HAWAII VOLCANOES NATIONAL PARK

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TABLE OF CONTENTS

	Page
ABSTRACT	i
INTRODUCTION	1
THE COASTAL LOWLAND	2
Geography	2
Climate	2
Vegetation and substrate	3
The study area and the exclosures	4
METHODS	5
The Kukalauula exclosure	5
Measurement of plant cover	5
Check lists	5
The Puu Kaone exclosures	6
Point-frequency transects	6
Braun-Blanquet relevés	6
RESULTS	7
Changes in the annual grassland	7
Qualitative changes	8
Quantitative changes	12
Changes in the perennial grassland	16
Similarity comparison of exclosure A	16
Successional trends in exclosure A	21
Spatial and successional variations in exclosure B	23
DISCUSSION	29
Goats, seasonality and year-to-year rainfall as controls of vegetation dynamics	29

	Page
Plant life-form and species composition as an index of goat pressure and site degradation	31
The chances of native plant recovery after elimination of goats . .	33
CONCLUSIONS	37
ACKNOWLEDGEMENTS	40
APPENDIX: list of species by families	41
LITERATURE CITED	45

LIST OF TABLES

		Page
1	Species lists and per cent cover at four dates inside and outside the KUKALAUULA exclosure	9
2	Species lists and per cent cover at six dates inside and outside the PUU KAONE exclosure A	17
3	Spatial variations in species combinations and quantities inside the large KAONE exclosure (B) as assessed by four permanent relevés in March 1972 during the wet season	24
4	Cover change of species from August 1971 to August 1972 in four permanent relevés in KAONE exclosure B	27

LIST OF FIGURES

1	Map of Hawaiian Islands with study area in Hawaii Volcanoes National Park	2a
2	Outline of the KUKALAUULA goat exclosure and positions of the five point-frequency transects	5a
3	Outline of the two Puu Kaone goat exclosures with transect and relevé positions	6a
4	Photograph of Kukalauula exclosure soon after fence construction in August 1969	7a
5	The same exclosure 19 months later, in March 1971	7b
6	Succession scheme inside and outside Kukalauula exclosure	32a
7	Per cent cover changes of endemic, indigenous and exotic species inside and outside the KUKALAUULA exclosure for the period of one year	33a

ABSTRACT

The coastal lowland of Hawaii Volcanoes National Park, particularly its western part, is a concentration center of feral goats. Here, in a tropical seasonal climate, a widespread vegetation is an annual Eragrostis tenella grassland that occurs on lava rock substrates with thin layers of ash. Localized within this area occurs also a small area of deep-ash deposit (Puu Kaone) that is occupied by perennial introduced grass with scrub.

Experimental goat displacement in form of exclosures on these two grasslands has shown that both are entirely goat-derived vegetations. The response to displacement of goats was immediate in both areas. In the annual grassland, bunchgrasses, woody chamaephytes and an endemic legume vine (Canavalia kauensis) became established within less than two years, while the annuals are fast disappearing. In the perennial grassland, Melinis minutiflora enlarged its grass mat, woody plants became more abundant and exposed soil was partially covered within a year after exclosure construction.

The remarkable recovery of the endemic vine in the annual grassland shows that goat removal still holds hopes for at least a partial return of native vegetation. The effects of goats apart of their physical degradation of the lowland ecosystem has been primarily in the form of exhausting the seed supply of native plants by feeding on seedlings wherever they occurred in this territory. Total elimination of goats from this area can be expected to yield a partial return of native plants on these rockland surfaces.

INTRODUCTION

An earlier paper reported on the effect of goats on Acacia koa tree reproduction in the mountain parkland of Mauna Loa (Spatz and Mueller-Dombois 1972). It was shown that goat populations were capable in the past and present of totally disrupting the reproduction cycle of Acacia koa. But even in low numbers, their impact was seen to be manifested in strongly distorted distribution and density patterns of Acacia koa, which have altered the entire mountain parkland ecosystem.

This paper is concerned with vegetation changes that occurred in three recently constructed exclosures in two areas in the coastal lowland of Hawaii Volcanoes National Park. Here, quite unexpectedly, the impact of the goats on the existing vegetation proved even more dramatic.

Not much is known about the character of the lowland vegetation before introduction of the goats 200 years ago. But, the coastal strip was once highly populated by early Hawaiians (Ellis 1825). It is probable that the lowland area supported at that time a perennial bunch grass vegetation dominated by the pili grass (Heteropogon contortus) that the Hawaiians used for roof thatching. Heteropogon grassland is still found in this area, but it occurs mostly west of the present study area. Moreover, isolated trees of Metrosideros collina and Diospyros ferrea, which occur in certain places of the dry lowland, indicate that the area can support a woody vegetation as well.

Therefore, before going into detail, it seems necessary to describe the ecological setting within which the present study was done.

THE COASTAL LOWLAND

Geography

The Park includes a lowland area in the middle section along the SE coast of Hawaii. This section extends from Kalapana (near Black Sand Beach) in a SW direction to south of the Kau Desert over a distance of 37 km/. For most of this length, the coast is formed by lava rock that ends abruptly at the ocean, about 5 to 10 m above sea level. Inland the lava surface rises over a distance of about 5 km to 400 m (1300 feet). Here a steep rise, locally called "pali," forms the topographic boundary that separates the coastal lowland from the upland. For the most part, the coastal lowland forms a gently undulating plateau, which is disrupted only by a few faults and cliffs (or minor palis).

Climate

The climate is warm-tropical with a mean annual temperature ranging from 24°C at sea level to about 22°C at 400 m. The daily temperature range is within 10°C. There is no cold period. The mean January temperature is about 19°C. During the summer, particularly in September, it may become quite hot, but the mean monthly temperature does not exceed 27°C. (This and the following information on the coastal lowland climate is extracted from Doty and Mueller-Dombois 1966.)

There is a distinct rainfall gradient in the SW direction along the coastal lowland which ranges from about 2000 mm per year at Kalapana to about 800 mm south of the Kau Desert. The decrease in rainfall in the SW direction is related to the topographic sheltering of the coastal lowland from the NE tradewind rains. Rainfall is very unevenly distributed through the year. Concomitantly with the rainfall gradient, there is a drought-season gradient. At South Point the drought-season (defined as mean monthly rainfall of less than 40 mm = < 1.6 inches) lasts

FIG. 1. Map of Hawaiian Islands with study area in Hawaii Volcanoes National Park. 1 KUKALAUULA enclosure, 2 PUU KAONE enclosures. Shaded area shows approximate extent of *Eragrostis tenella* grassland.

for seven months, from April to October inclusive. In the park section, south of the Kau Desert, the drought season is probably not quite as long, lasting for approximately six months, from May through mid-October. At Kalapana there is no real drought season, only a short dry season in the summer, June through August, when the monthly rainfall drops below 100 mm. During the winter season, rainfall is usually high, i.e., in excess of 100 mm per month throughout the coastal lowland section in the Park.

Vegetation and substrate

The lowland vegetation has been mapped at 1 : 12,000 and described by four transects (Mueller-Dombois 1966). A coastal strip about 50 m wide shows spray-swept rock bluffs and pockets of beach communities. Inland, behind the salt-spray zone, there are several major communities that are well related to the rainfall and dry-season gradient. In the sequence from Kalapana SW to the area south of the Kau Desert, one can recognize a low-stature forest or tall-scrub with several native tree and shrub species. This woody vegetation gives way to the low-shrub savanna. Further southwest, the low shrubs become more and more scattered so that one can speak of a grassland. This perennial grassland, which is dominated by the pili grass (Heteropogon contortus), gives way to a primarily annual grassland, dominated by Eragrostis tenella in the area south of the Kau Desert.

The dominant substrate over this entire area is either massive or ropy pahoe-hoe lava (Doty and Mueller-Dombois 1966: 113) with a thin cover of ash, often restricted to pockets in the lava crevices. There is hardly any soil from weathered lava. The fine soil fraction is merely from ash (Cline et al 1955). The amount of ash overlay varies through the lowland, and with this varies also the density of the grass. Except for a local area at Puu Kaone, south of Hilina Pali, which is covered with deep, yellow, loess-like ash (the so-called pahala ash; Stearns ,

and Macdonald 1946, Macdonald and Abbott 1970), the ash overlay is usually less than 50 cm deep, so that rock outcrops occur throughout the lowland. Another important substrate variation is found in form of aa lava, the coarse, broken rock-rubble lava, which occurs in various bands within the pahoehoe matrix. These aa substrates are usually devoid of grasses and other herbaceous plants, but are instead stocked with widely scattered trees; mostly ^{with} two native species, Metrosideros collina var. polymorpha and Diospyros ferrea. In addition, the lava substrate ages vary from current and very recent to prehistoric (i.e., older than 200 years). The vegetation pattern described here relates only to that on the prehistoric flows. The most recent flows that in 1968 began to cover a considerable area (south of the Aloi-Alae Craters) in the mid-section of the lowland area of the Park are as yet practically devoid of plant growth.

The study area and the exclosures

Following the study of the Park's vegetation in 1965, the first author recommended to the Park Service the establishment of goat-and pig exclosures in various locations of the Park. One area was the coastal lowland in which feral goats are known to roam year-round in great numbers. In August 1968, a 7 by 100 m exclosure was built south of Kukalauula Pali (at 300 m elevation) in the predominantly annual grassland of Eragrostis tenella (love grass). Two more exclosures (a 10 by 90 m and a 100 by 100 m exclosure) were built in August 1971 on Puu Kaone, south of Hilina Pali (also at 300 m elevation) in a perennial grassland. In 1965, this area was dominated by stoloniferous mat-forming grasses Chrysopogon aciculatus (piipii) and Cynodon dactylon (Bermuda grass). This perennial grassland forms a local variation on the above mentioned deep ash deposit (Pahala ash) within the Eragrostis tenella grassland. It was

mapped as such in 1965, when it was noted that this grass cover remained green through the drought season. As a green 'oasis' within the otherwise yellow, dried-up and sparse annual grassland, Puu Kaone was seen to serve as a concentration center for goats during the summer-drought season (Mueller-Dombois 1966: 413).

METHODS

The Kukalauula exclosure

FIG. 2 shows an outline of this 7 by 100 m exclosure. A quantitative and qualitative analysis of the vegetation inside and outside was begun two years after its construction. The analysis was repeated four times over a yearly cycle, on July 6, 1971, December 23, March 29 and July 7, 1972.

Measurement of plant cover. - This was done with the point-frequency method, which allows one to express the result in percent cover by species (Levi and Madden 1933, Goodall 1953).

A one-meter long and one-meter high wooden frame was used with pointed steel rods. The rods were evenly spaced resulting in 5 points per meter (or 1 point every 20 cm). With this 5-point frame, five continuous 17 m long transects were run across the 7-m width of the exclosure as shown on FIG. 2. In this way, 10 m of the vegetation were sampled outside the exclosure along each transect, namely 5 m on either side. This resulted in a total sample of 250 points outside. Inside, the 7-m width was sampled 5 times resulting in a total sample of 175 points.

Check lists. - The above method enumerated only the more abundant and evenly distributed species. To get a total list of the species present, the whole area in and around the exclosure was searched each time for the species missed in

FIG. 2. Outline of KUKALAUULA goat enclosure and positions of the five point-frequency transects.

the point-frequency analysis.

The Puu Kaone exclosures

Point-frequency transects. - FIG. 3 shows the outline of the two exclosures. The 10 by 90 m exclosure (A) was sampled in the same way as the Kuka-lauula exclosure except, because of greater within variation, 10 transects were used instead of only 5. Each transect was 20 m long, sampling 10 m outside and 10 m inside the exclosure. This resulted in a total sample of 500 points each outside and inside.

Braun-Blanquet relevés. - In the 100 by 100 m exclosure (B), four permanent relevés were established, each 100 m² in size (FIG. 3) according to the method of Braun-Blanquet (1965). These were established to sample the more interesting variations in the Puu Kaone vegetation. Relevé 1 (10 x 10 m) was placed in the most prevalent grass community dominated by stoloniferous mat-forming grasses (Cynodon dactylon, Melinis minutiflora). Relevé 2 (10 x 10 m) was placed in a bunch grass community (Hyparrhenia rufa, Rhynchelytrum repens) on a steep, wind-exposed slope. Relevé 3 (10 x 10 m) was placed in a mixed matted bunchgrass community with a high cover of woody chamaephytes (Cassia leschenaultiana, Indigofera suffruticosa). Relevé 4 (5 x 20 m) was placed in a small scrub community dominated by Leucaena leucocephala.

Complete species lists were made for these four relevés during these repeated surveys done over an annual cycle; on August 14, 1971 on October 28, on December 14, on March 30, on June 19 and finally on August 13, 1972. Each time, the cover of the species present was estimated with the Domin-Krajina scale (Mueller-Dombois 1964). This admittedly is somewhat crude for the quantitative part of the relevé analyses. But this together with the quantitative analysis of the 10 by 90 m exclosure is the maximum one can do in the time :

FIG. 3. Outline of the two FUU KAOKE goat enclosures with transect and relevé positions.

during a day's visit to Puu Kaone. The changes took place so fast for some species, that the quantitatively variable species were easily distinguished from the quantitatively more stable ones. The important aspect to be shown, with the four relevés, is that the development in the large enclosure is quite variable depending on the plant life form that was the dominant one at the time the enclosure was established, i.e., in August 1971.

RESULTS

Changes in the annual grassland

When the writers, together with Park Naturalist Donald W. Reeser, visited the Kukalauula enclosure in July 1971, the enclosure was almost two years old. It stood out, from several kilometers distance, as a green "oasis" in the midst of the parched and dried-up grassland. It stood out similarly as the Puu Kaone grassland had stood out in the 1965 map-survey. FIG. 4 shows a photograph of the Kukalauula enclosure taken by Don Reeser right after construction of the enclosure in August 1969. FIG. 5 shows the same enclosure in March 1971, 19 months after construction. The appearance was almost identical in July 1971. The tall bunchgrasses in the foreground of FIG. 5 are Sporobolus africanus, Heteropogon contortus and Rhynchelytrum repens, the grassy matrix between the bunchgrass tufts is made up largely by 20-25 cm tall growing Cynodon dactylon. The thin woody stems belong to the shrub Waltheria indica and the broad-leaf mat occupying the greater part of the enclosure in the background is made up of Canavalia kauensis, a newly described endemic herbaceous vine. The surrounding short-grass cover is mostly of Eragrostis tenella and Cynodon dactylon.

FIG. 4. Photograph of Kukalauula exclosure soon after fence construction in August 1969. The short-grass cover inside and outside the exclosure is dominated by Eragrostis tenella and Cynodon dactylon. Photograph courtesy of Don Reeser. Note Pacific Ocean in background.

FIG. 5. The same exclosure 19 months later, in March 1971. A native leguminous vine (Canavalia kauensis) has become established covering much of the exclosure surface. The bunchgrasses in foreground (Sporobolus africanus, Rhynchelytrum repens) and the small shrub (Waltheria indica) do not occur outside. Photograph by Don Reeser.

TABLE 1 shows both the qualitative and the quantitative changes in species distribution inside and outside the exclosure.

Qualitative changes. - These refer to the presence-absence relations of the species. It is seen that a total of 10 grass species occurred inside the exclosure. Of these, five also occurred outside, while another five species occurred only inside, namely, Sporobolus africanus, Rhynchelytrum repens, Heteropogon contortus, Andropogon glomeratus and Hyparrhenia rufa. It is interesting that the latter five species are all perennial bunchgrasses, while the other five species that are common to the outside and inside vegetation are either annual grasses (Eragrostis tenella, Digitaria pruriens) or perennial stoloniferous (i.e., creeping or mat-forming) grasses (Cynodon dactylon, Chrysopogon aciculatus, Melinis minutiflora). This clearly shows that release of goat pressure favors invasion of bunchgrasses, while high goat pressure eliminates these entirely and instead allows only matted and annual grasses to prevail.

Three sedges also occurred in both inside and outside vegetations. Of these, Bulbostylis capillaris is an annual (like Eragrostis tenella), while Cyperus brevifolius and Cyperus compressus are perennial stoloniferous creepers (like Cynodon dactylon). Thus, the sedge life forms show the same pattern as the grasses with the exception that no bunch forming sedge had arrived in the exclosure.

The forbs (i.e., "normal" herbaceous plants) also show an interesting pattern. Except for Desmodium triflorum, they are all rare. None of the forbs was unique to the exclosure, and two forb species were found only outside (Oxalis corniculata and Desmodium uncinatum). This shows that forbs play a certain role as "fillers" in the heavily grazed environment, but they are unimportant in the succession following removal of goat pressure.

TABLE 1. Species lists and per cent cover at four dates inside and outside the KUKALAUULA exclosure. Dates 1 and 4 are in the dry season (July); dates 2 and 3 are in the wet season (December and March). Symbols are explained at the bottom of the table.

Species	INSIDE				OUTSIDE			
	1	2	3	4	1	2	3	4
GRASSES								
<i>Eragrostis tenella</i>	10.7	0.6	0.5	(+)	30.0	20.0	34.0	19.6
<i>Cynodon dactylon</i>	26.4	18.8	14.2	21.7	31.4	18.8	28.4	32.8
<i>Chrysopogon aciculatus</i>	--	+	1.1	--	1.4	+	+	0.4
<i>Sporobolus africanus</i>	4.3	+	0.6	1.1	--	--	--	--
<i>Rhynchelytrum repens</i>	0.7	2.8	5.1	12.5	--	--	--	--
* <i>Heteropogon contortus</i>	+	1.2	+	+	--	--	--	--
<i>Melinis minutiflora</i>	--	+	+	+	--	1.6	+	0.8
* <i>Digitaria pruriens</i>	--	23.2	13.7	2.3	--	0.4	6.8	0.4
<i>Andropogon glomeratus</i>	--	--	+	+	--	--	--	--
<i>Hyparrhenia rufa</i>	--	--	--	+	--	--	--	--
SEDGES								
<i>Bulbostylis capillaris</i>	--	--	(+)	(+)	0.4	1.6	0.4	0.4
<i>Cyperus brevifolius</i>	--	+	2.4	(+)	1.3	4.4	+	1.2
<i>Cyperus compressus</i>	--	+	(+)	--	--	+	+	--

TABLE 1 Continued.

Species	INSIDE				OUTSIDE			
	1	2	3	4	1	2	3	4
FORBS								
Desmodium triflorum	8.6	1.2	1.1	0.4	7.3	0.4	+	0.8
Phyllanthus niruri	--	--	--	--	+	1.2	+	--
Euphorbia hirta	--	--	--	--	+	3.8	+	+
Portulaca oleracca	--	+	+	--	--	--	+	--
Gnaphalium purpureum	--	--	--	--	--	+	+	--
Linaria canadensis	--	--	(+)	--	--	--	+	--
Sisyrinchium micranthum	+	--	--	--	--	+	--	--
Oxalis corniculata	--	--	--	--	--	+	--	--
Desmodium uncinatum	--	--	--	--	--	+	--	--
Vernonia cinerea	--	--	--	--	+	--	+	+
Conyza sp.	--	--	--	--	--	--	+	--
*Portulaca cyanosperma	--	+	--	--	--	--	--	+
HERBACEOUS VINE								
*Canavalia kauensis	45.7	48.0	51.1	38.8	--	--	S	--

TABLE 1 Concluded.

Species	INSIDE				OUTSIDE			
	1	2	3	4	1	2	3	4
SHRUBS (0.5-1 m tall CHAMAEPHYTES)								
<i>Indigofera suffruticosa</i>	+	+	+	+	--	S	S	--
<i>Waltheria indica</i>	+	2.4	1.1	2.3	--	S	S	S
<i>Cassia leschenaultiana</i>	1.4	2.4	1.7	0.5	--	S	S	--
LITTER (%)	1.4	--	7.4	19.4	17.5	14.4	5.2	16.4
BARREN SOIL (%)		--	--	--		23.6	12.8	9.6
ROCK (%)	0.7	--	--	--	6.0	14.4	11.6	17.2
GOAT PELLETS (%)	--	--	--	--	0.4	--	--	0.4

* native species, + species present but not abundant enough to be intercepted by sampling points, (+) species growing near the fringe, -- species absent, S = seedlings

Dates 1 = July 6, 1971 Dry season
 2 = December 28, 1971 }
 3 = March 29, 1972 } Wet season
 4 = July 7, 1972 Dry season

Instead another herbaceous life form, the vine Canavalia kauensis showed an explosive dominance inside the exclosure, where it was almost unique, except for the occurrence of a few seedlings outside in the wet season (March 1972). However, these were all gone again in the dry season (July 1972). It is possible that the dominance of the Canavalia vine suppressed the appearance of other perennial forbs inside the exclosure.

The three chamaephytic shrub species (Indigofera suffruticosa, Waltheria indica, Cassia leschenaultiana) were not unique to the exclosure. But they occurred outside only temporarily as seedlings, like herbaceous annuals in the wet season. The most resistant among the three seems to be Waltheria indica of which a few seedlings still survived in the dry season (July 1972).

Quantitative changes. - These refer to the changes in species cover as shown by the figures in TABLE 1. Here we may first identify those species whose cover remained relatively stable, or that fluctuated quantitatively only with seasonal variations. We may assume (for the moment) that the outside vegetation remained under more or less the same goat pressure during the observation period, while we may expect that the inside vegetation would show more of a directional, i.e., a successional change.

By examining the outside trends, it can be seen that Eragrostis tenella decreased in quantity over the year, from 30 to 20%. As expected, however, it was present with a higher quantity during the latter part of the wet season in March, with 34%. Cynodon dactylon remained rather stable, showing nearly the same cover in July 1971 (31%) as in July 1972 (33%). Its cover was reduced during the wet season, when Eragrostis was more abundant. Thus, these two most dominant grass species seem to displace each other somewhat depending

on the season of the year. Chrysopogon aciculatus, though far less dominant than Cynodon, shows the same seasonal pattern, i.e., higher quantitative presence in the dry season and less in the wet season. The two other creeping grasses, Melinis minutiflora and Digitaria pruriens made their appearance only in the wet season (in December 1971), but remained in the following dry season.

Except for seasonal fluctuations, the sedges remained stable outside the exclosure. Both, the annual Bulbostylis and the perennial creeper Cyperus brevifolius showed their maximum quantity in the early part of the wet season, in December 1971.

Among the forbs, Desmodium triflorum showed a considerable quantitative decline in the second dry season (from 7.3% cover in July 1971 to 0.8% cover in July 1972). However, its decline was balanced somewhat by the appearance of Melinis and Digitaria as shown above. Thus, these quantitative shifts may merely be an expression of competitive displacements that vary from year to year with variations in rainfall (see under DISCUSSION). Of the other eleven forb species, eight were present only during the wet season (Phyllanthus niruri, Portulaca oleracea, Gnaphalium purpureum, Linaria canadensis, Sisyrinchium micranthum, Oxalis corniculata, Desmodium uncinatum, Conyza species). This shows that they are winter-annuals that appear only during the period with favorable soil moisture in this habitat. But even the other three species (Euphorbia hirta, Vernonia cinerea and Portulaca cyanosperma) are probably also winter-annuals with merely a somewhat greater dry-season survival capacity than the above eight species. Portulaca cyanosperma, the only native forb in the group, is a small succulent, that may be able to take advantage of its water storage capacity to survive longer through the dry

season.

As mentioned above the taller-growing life forms (the herbaceous vine and the shrubs) appeared merely as temporary seedling residents in the outside vegetation during the wet season. Thus, they behaved like annuals as "temporary fillers" in the grazed vegetation matrix when soil water was obviously more abundant. A "lag-effect" in response to the onset of the rainy season is shown in some temporary fillers, for example, in the Canavalia seedlings.

Much rock and barren soil was exposed outside the enclosure as can also be seen on FIGS. 3 and 4. The data in TABLE 1 (near bottom) show that 11.2% more rock was exposed during the dry season in 1972 than during the dry season in 1971. The latter difference may indicate a higher grazing pressure during the second dry season. That the percent barren soil was greater in the wet season was probably due to the fact that more litter covered the soil during the dry season. This relationship, together with the presence of goat pellets, detected only during the dry season, is probably merely a reflection of the decreased microbiological activity during the dry season. At that time, litter and goat pellets are not so readily decomposed because of drought.

Thus, it may be concluded that the exposure of 11.2% more rock surface in the dry season of 1972 as compared to 1971, the greater litter plus barren soil (25% in 1972 versus 17.5% in 1971), the 10.4% decline of Eragrostis and the 6.5% decline of Desmodium triflorum in the second dry season seem to show a certain degradation of the annual grassland that may have been caused by an increased goat pressure. This could be from a goat-concentration effect caused by the enclosure itself.

As expected, TABLE 1 shows mostly successional (rather than seasonal) trends inside the exclosure. Species showing a strong quantitative decline are: Eragrostis tenella and Desmodium triflorum. These two species are important components of the goat-grazed annual grassland. They will probably soon disappear entirely inside the exclosure. Cynodon dactylon displayed the same seasonal fluctuation inside as outside, but only a relatively small successional decline over the year, from 26.4% to 21.7%. This indicates a tremendous competitive capacity of this stoloniferous grass that it retains under varying conditions. Cynodon grew into 25 cm high mats inside the exclosure. It thus has a capacity to remain for a much longer period than for example, Eragrostis tenella or Desmodium triflorum in a community that becomes invaded with taller-growing life forms. It is interesting that the new-comer, Sporobolus africanus, already showed a decline over the year, from 4.3% to 1.1%. It will thus soon disappear, probably much sooner than Cynodon. Digitaria pruriens, a native (probably an annual) grass also showed a strong decline after an initial high quantitative presence during the early wet season (December 1971). Its strong seasonal fluctuation, shown also in the outside vegetation indicates, that it may resume a certain quantitative importance once again in the 1973 wet season. But it seems structurally on the way out in the exclosure, as are the three sedges which are disappearing. The Canavalia vine showed a certain increase in cover during the wet season. However, when compared in the first (July 1971) and last measurement (July 1972), it is shown that the vine has retreated (from 46% to 39% cover). It will probably persist for quite some time to come. This depends largely on the appearance and spread of the woody plants. The three chamaephytic shrub species now present do not seem to present a major threat to Canavalia. Their cover values are relatively small. Cassia

leschenaultiana is already on the decline, Indigofera suffruticosa so far has not become abundant, and Waltheria indica increased from a mere presence to 2.3% cover over the year. The latter is the only species in the exclosure that could compete successfully with Canavalia, but the two species rarely occur mixed together in the exclosure, but rather occupy different segments of it as shown on FIG. 5.

The only important "increaser" during the observation year was the bunchgrass Rhynchelytrum repens, which seemed to replace Sporobolus africanus. The native bunchgrass Heteropogon contortus indicates only a temporary appearance. It will probably be outgrown by one or more of the taller exotic grasses Andropogon glomeratus, Hyparrhenia rufa and Melinis minutiflora. The latter in particular which can form thick, up to one meter high mats under optimal conditions, may also form a potential threat to the Canavalia vine.

Changes in the perennial grassland

Similarity comparison of exclosure A. - Exclosure A is the 10 by 90 m exclosure (FIG. 3), which enclosed a representative sample of the Cynodon - Chrysopogon community on Puu Kaone.

The first analysis date (August 1971) followed right after construction of the exclosure. Therefore, the inside-outside comparison at date 1 in TABLE 2 offers a test of the similarity of species composition and species quantities in the two segments of the same community. TABLE 2 shows that at date 1 five grass species, one sedge, and one shrub species (= 7 species) were common to both segments. But outside were two additional grasses (Hyparrhenia rufa and Sporobolus africanus) and one additional forb (Desmodium triflorum), while inside there occurred one additional shrub (Indigofera suffruticosa). In applying

TABLE 2. Species lists and per cent cover at six dates inside and outside the PUU KAONE enclosure A. Dates and symbols are explained at bottom of the table. Sampling date 1 (August 1971) coincided with construction date of enclosure.

Species	INSIDE						OUTSIDE					
	1	2	3	4	5	6	1	2	3	4	5	6
GRASSES												
<i>Cynodon dactylon</i>	8.4	8.6	9.0	7.8	8.9	10.0	5.8	4.6	8.0	8.6	8.6	7.8
<i>Chrysopogon aciculatus</i>	2.8	2.2	0.8	2.0	1.3	0.6	3.0	2.0	2.4	2.4	2.4	2.8
<i>Melinis minutiflora</i>	0.2	1.6	1.6	11.8	19.4	22.8	0.6	0.4	1.2	6.4	14.8	18.0
* <i>Digitaria pruriens</i>	--	--	--	--	0.7	--	--	--	0.2	0.4	0.4	--
<i>Hyparrhenia rufa</i>	--	--	0.4	0.2	--	0.6	0.8	0.8	0.2	1.6	2.0	1.2
<i>Sporobolus africanus</i>	--	--	--	+	+	+	+	0.4	0.2	0.4	1.0	0.4
<i>Rhynchelytrum repens</i>	+	3.4	10.4	20.4	23.8	26.6	+	1.0	2.0	4.4	5.2	10.2
<i>Andropogon glomeratus</i>	+	+	+	+	+	+	0.2	0.2	0.2	0.4	0.2	0.4
* <i>Cenchrus echinatus</i> var. <i>hillebrandianus</i>	--	--	1.0	+	0.4	0.4	--	--	+	0.4	+	0.4
SEDGES												
<i>Cyperus brevifolius</i>	+	+	+	+	+	--	+	+	+	+	+	--
<i>Cyperus compressus</i>	--	--	+	--	--	--	--	+	+	--	--	--

TABLE 2 Continued.

Species	INSIDE						OUTSIDE					
	1	2	3	4	5	6	1	2	3	4	5	6
FORBS												
<i>Desmodium triflorum</i>	--	0.4	0.4	--	--	--	0.2	0.4	0.6	0.4	--	0.2
<i>Oxalis corniculata</i>	--	1.0	1.4	0.8	--	--	--	0.2	0.4	0.6	--	--
<i>Bidens pilosa</i>	--	--	--	--	--	--	--	--	0.2	--	--	--
<i>Emilia javanica</i>	--	0.2	3.2	3.4	2.9	1.8	--	0.2	0.4	0.6	--	--
<i>Ageratum conyzoides</i>	--	--	--	+	--	--	--	--	+	+	--	--
<i>Vernonia cinerea</i>	--	--	--	--	--	--	--	--	--	+	+	--
<i>Centaurea melitensis</i>	--	--	--	--	--	--	--	--	--	+	+	--
<i>Euphorbia hirta</i>	--	--	--	+	--	--	--	+	--	+	+	+
<i>Desmodium uncinatum</i>	--	+	+	+	+	+	--	--	--	+	--	--
<i>Solanum nigrum</i>	--	--	+	--	--	--	--	+	+	--	--	--
<i>Sonchus oleraceus</i>	--	--	--	+	--	--	--	--	--	--	--	--
<i>Chenopodium album</i>	--	--	--	+	--	--	--	--	--	--	--	--
<i>Conyza</i> sp.	--	--	--	--	--	--	--	--	--	+	+	--
<i>Erechtites valerianaeifolia</i>	--	--	--	--	+	+	--	--	--	--	--	--
* <i>Psilotum nudum</i>	--	--	--	--	+	+	--	--	--	--	--	--

TABLE 2 Concluded.

Species	INSIDE						OUTSIDE					
	1	2	3	4	5	6	1	2	3	4	5	6
HERBACEOUS VINE												
<i>Passiflora foetida</i>	--	--	+	+	+	+	--	--	--	--	--	--
SHRUBS												
<i>Cassia leschenaultiana</i>	3.6	9.4	11.4	11.2	8.3	6.0	4.8	9.6	16.2	14.0	9.6	6.4
<i>Indigofera suffruticosa</i>	0.2	1.2	3.8	12.2	10.1	7.1	--	0.6	0.6	0.6	1.0	0.8
<i>Waltheria indica</i>	--	--	+	+	+	+	--	--	+	+	+	--
<i>Sida rhombifolia</i>	--	+	+	+	+	+	--	--	--	--	+	--
<i>Malvastrum coromandelianum</i>	--	+	+	+	--	--	--	--	--	--	--	--
LITTER (% cover)	60.4	51.0	37.6	11.8	6.0	5.8	66.8	58.8	50.0	41.6	36.6	31.4
BARREN SOIL (%)	24.4	21.0	19.0	18.4	18.2	18.3	17.4	20.4	17.4	17.6	17.6	19.8
GOAT PELLETS (%)	--	--	--	--	--	--	0.4	0.4	--	--	--	0.2

*Native species, + species present but not abundant enough to be intercepted by sampling points,

-- species absent

Dates 1 = August 14, 1971	Height of drought season
2 = October 28, 1971	Beginning of wet season
3 = December 14, 1971	Wet season
4 = March 30, 1972	Wet season
5 = June 19, 1972	Beginning of drought season
6 = August 13, 1972	Height of drought season

this comparison to Sørensen's (1948) index of similarity (IS) we get:

$$IS = \frac{2c}{a + b} \times 100 = \frac{2 \times 7}{8 + 10} \times 100 = \underline{77.8\%}$$

where c = number of species common to both segments

a = total number of species inside the enclosure

b = total number of species outside

This value (77.8%) indeed shows a very high qualitative similarity. When we consider that the species common to both segments are also the quantitatively more important ones, the similarity is even higher. This is shown by applying the species quantities in the same similarity index (IS_Q) as follows:

$$IS_Q = \frac{2 \times w}{A + B} \times 100(\%)$$

where w = the lesser quantities of the species common to both segments

A = the sum of the quantities of all species inside

B = the sum of the quantities of all species outside

+ values are arbitrarily evaluated as 0.1% cover

$$IS_Q = \frac{2 \times 12.7}{15.5 + 15.7} \times 100 = \underline{79.2\%}$$

The same comparison at date 6, exactly one year later (August 1972), will provide an answer to just how much the qualitative and quantitative development inside the enclosure departed from that outside:

	August 71	August 72	Change
Qualitative IS	77.8%	70.0%	7.8%
Quantitative IS	79.2%	71.1%	8.1%

The similarity indices show a 7.8% increase in the qualitative difference and an 8.1% increase in the quantitative difference over this first year. This indicates only a small departure in vegetation development inside the enclosure from that outside. This can be explained by the fact that the Park Service removed more than 1,000 goats from Puu Kaone in December 1971. This radical reduction in the number of goats resulted in something of an "exclosure effect" also in the grassland

surrounding the enclosure.

The maintenance of a close similarity of the grassland inside and outside over this first year, therefore, does not imply stagnation in vegetation development.

Successional trends in enclosure A. - TABLE 2 shows two grass species that increased considerably in quantity over the year. These are Melinis minutiflora (from 0.2% cover to 22.8% inside; from 0.6% to 18.0% outside) and Rhynchelytrum repens (from mere sporadic presence to 26.6% cover inside; and from + to 10.2% outside). Other important "increasers" were the grasses Hyparrhenia rufa and Cenchrus echinatus, the forb Emilia sonchifolia and the shrubs Cassia leschenaultiana and Indigofera suffruticosa. This shows a development towards a greater importance of tall-growing grasses (the thick mat-former Melinis and bunchgrasses Rhynchelytrum, Hyparrhenia and Cenchrus) and shrubs. It may be noted also that the quantitative increase in most of these "increasers" was greater inside the enclosure than outside. This indicates that there was still a certain goat pressure even after removal of the more than 1,000 goats in December 1971. A much greater increase occurred, for example, for Indigofera suffruticosa inside the enclosure than outside. This shows that goats, under low pressure, become more selective and feed on this shrub preferentially over, for example, the second legume shrub, Cassia leschenaultiana. A similar relationship is shown for the two important "increasers" among the grasses. While Rhynchelytrum increased inside to 26.6% cover, it increased outside to only 10.2%. In contrast, the increase of Melinis was similar inside (to 22.8%) and outside (to 18%). Thus, Rhynchelytrum is preferred by the goats, while Melinis can develop almost unhindered under low goat feeding pressure. This gives Melinis a considerable competitive advantage under such conditions.

The creeping grass Chrysopogon aciculatus decreased inside the enclosure and Desmodium triflorum disappeared, while both these species remained rather stable

outside. This indicates that the small plants or low-growing creepers (i.e. Chrysopogon) are eliminated by competition from taller-growing plants upon release of goat pressure, while their presence in greater quantities indicates a certain goat pressure.

Cynodon dactylon remained rather stable over the year. It increased only slightly in quantity. This indicates again the capacity of this grass (as shown for the Kukalauula enclosure) to adapt to a release of goat pressure by a considerable upgrowth of its shoot-mat. It also has a great resistance to increasing goat pressure by surviving as a thin sparse mat flat on the ground (as seen outside the Kukalauula enclosure). A species somewhat similar in adaptive capacity is Cyperus brevifolius. However, this species is quantitatively less important.

Pronounced seasonal fluctuations were shown again among several of the forbs (Oxalis corniculata, Bidens pilosa, Emilia javanica, Vernonia cinerea, Centaurea melitensis) which appeared only during the wet season. The same thing applied also to the native grass Digitaria pruriens.

Remarkable was the high area of barren soil (TABLE 2, near the bottom) both inside and outside the enclosure. This relates to the trail-making and trampling effect caused by the high numbers of goats that roamed Puu Kaone until establishment of the enclosure and the December 1971 goat drive and to a greater exposure of soil on the wind-exposed and sloping seaward (makai) side of Puu Kaone. Inside the enclosure the barren soil area decreased by 6.1%, while outside it even increased by 2.4%. This shows the tremendous soil-erosion potential correlated to the high goat pressure.

Also of interest is the change in exposed dry litter. Inside the enclosure, exposed litter decreased by 54.6% from overgrowth with green shoot material. Outside, it decreased only by 35.4%. This shows that the goats outside, even though

they were reduced considerably in number by the December goat drive, kept the ground relatively open by not allowing the grass mat to close-in over the barren soil, or over much of the litter-strewn surface. The high amount of litter, which covered more than 60% of the surface both inside and outside the exclosure in August 1971, was largely from Melinis minutiflora. It is not clear yet what caused the "collapse" of large sections of this otherwise vigorous exotic thick mat-forming grass. It may simply be seasonality, but such a seasonal behavior is not supported by the data. These litter masses could also be the result of accumulation due to an inhibition in microbial decomposition. Melinis, wherever established in this climatic zone in the Hawaiian Islands, seems to outgrow nearly all other herbaceous plants (Kartawinata and Mueller-Dombois 1972), thereby reducing the diversity and the stability of such herbaceous covers.

Spatial and successional variations in exclosure B. - TABLE 3 shows the contents of the four permanent relevés established in the large one hectare exclosure. The species lists and quantitative values are for March 1972, when most of the annuals were present.

In spite of the fact that the four relevés were established to evaluate the major spatial variations in floristics and structure within the exclosure, the comparison shows that the exclosure contains one general community. It can be described as a Rhynchelytrum-Melinis grass community with a high shrub component of Cassia leschenaultiana and Indigofera suffruticosa. A comparison with the March 1972 analysis in TABLE 2 (date 4) shows that exclosure A is also part of that general grass-scrub community. Relevé 1 and 3 are most similar, because both contain a large quantity of Cynodon dactylon. These two relevés are more broadly representative of the Puu Kaone grassland than the other two relevés. Relevé 2 is quite unique by its absence of Cynodon and its high cover of the bunchgrass Hyparrhenia rufa. Ecologically it falls somewhat out of line, because it occurred on a steep

TABLE 3. Spatial variation in species combinations and quantities inside the large KAONE enclosure (B) as assessed by four permanent relevés in March 1972 during the wet season. Explanation of numerical values at bottom of table.

Species	Releve no.			
	1	2	3	4
TREE				
<i>Leucaena leucocephala</i>	--	--	--	6
SHRUBS				
<i>Cassia leschenaultiana</i>	4	2	4	3
<i>Indigofera suffruticosa</i>	3	2	5	2
<i>Waltheria indica</i>	1	--	+	4
<i>Leucaena leucocephala</i>	3	--	5	5
<i>Sida rhombifolia</i>	1	--	3	5
<i>Malvastrum coromandelianum</i>	--	--	1	3
* <i>Sida fallax</i>	--	--	--	7
VINES				
* <i>Ipomoea indica</i>	--	--	--	2
<i>Merremia aegyptia</i>	--	--	+	--
FORBS				
<i>Salvia occidentalis</i>	1	--	1	3
<i>Desmodium triflorum</i>	--	3	--	--
<i>Emilia javanica</i>	--	1	--	--
<i>Ageratum conyzoides</i>	--	+	--	--
<i>Bidens pilosa</i>	--	1	--	--
<i>Oxalis corniculata</i>	--	1	1	2
<i>Solanum nigrum</i>	--	--	--	3

Table 3 Concluded.

Species	1	2	3	4
SHRUB SEEDLINGS				
<i>Leucaena leucocephala</i>	2	--	2	3
<i>Waltheria indica</i>	--	--	--	--
<i>Cassia leschenaultiana</i>	2	2	--	2
<i>Indigofera suffruticosa</i>	--	1	--	
<i>Sida rhombifolia</i>	2	--	--	
<i>Sida fallax</i>	--	--	--	2
<i>Malvastrum coromandelianum</i>	--	--	--	2
GRASSES				
<i>Cynodon dactylon</i>	9	--	8	--
<i>Chrysopogon aciculatus</i>	--	3	--	--
<i>Melinis minutiflora</i>	4	2	1	5
<i>Rhynchelytrum repens</i>	4	3	5	4
* <i>Digitaria pruriens</i>	--	--	1	2
<i>Hyparrhenia rufa</i>	--	7	--	--
<i>Andropogon glomeratus</i>	--	--	--	--
* <i>Cenchrus echinatus</i> var. <i>hillebrandianus</i>	--	--	--	+

* native species

Meaning of Domin-Krajina scale values:

+ = solidary with small cover; 1 = seldom, with small cover;

2 = very scattered, with small cover; 3 = scattered, with cover

< 5%; 4 = any number, with 5-10% cover; 5 = 10-20% cover; 6 = 20-33%

cover; 7 = 33-50% cover; 8 = 50-75% cover; 9 = 75-95% cover (from

Mueller-Dombois 1972: 41).

slope with goat-trails and signs of strong soil erosion. However, its presence of Chrysopogon aciculatus forms a similarity link to enclosure A. Relevé 4 is the most unique because it encompasses a low-stature Leucaena leucocephala forest that shows a high shrub component of Sida fallax. The Leucaena trees were apparently planted in that locale before Puu Kaone was included in the National Park in 1916. However, the spread of Leucaena was checked by heavy goat browsing. Relevé 1 is, among the four, the one that compares closest to enclosure A, because it has a smaller shrub component than relevé 2. But relevé 1 lacks Chrysopogon aciculatus, which is still important in enclosure A. The spatial variation suggests an approximate developmental sequence from enclosure A (being the least successively advanced grassland form) to relevé 1 → relevé 3 → relevé 4 with relevé 2 forming a special case. This order is used for the arrangement of the four relevés in TABLE 4.

TABLE 4 shows the changes that took place in the four relevés over the year, from August 1971 to August 1972. The four intermediate analyses are omitted from the table. It can be seen that Melinis minutiflora increased greatly in all four relevés, while Cynodon dactylon (in relevés 1 and 2) either declined or remained relatively stable. Rhynchelytrum repens increased in relevés 1 and 3. So far the trends coincide with those in enclosure A. In relevé 2, Rhynchelytrum declined. The reason for this is not clear, but it could be competitive displacement from Melinis. In the tall-scrub relevé 4, Rhynchelytrum was only a temporary resident during the rainy season (compare TABLE 4 with TABLE 3). Hyparrhenia rufa remained stable in relevé 2, while another bunchgrass, Andropogon glomeratus made its appearance.

The shrub component increased greatly in both relevés 1 and 3 (e.g. Indigofera suffruticosa, Leucaena leucocephala and Sida rhombifolia). In relevé 2 there was

TABLE 4. Cover change of species from August 1971 to August 1972 in four permanent relevés in KAONE enclosure B. For explanation of numerical values see TABLE 2, bottom.

Species	Relevé August	1		3		4		2	
		71	72	71	72	71	72	71	72
GRASSES									
Cynodon dactylon		9	8	8	8	--	--	--	--
Melinis minutiflora		3	5	2	6	--	5	3	4
Rhynchelytrum repens		3	4	3	4	--	--	5	3
Chrysopogon aciculatus		--	--	--	--	--	--	3	3
Hyparrhenia rufa		--	--	--	--	--	--	7	7
Andropogon glomeratus		--	--	--	--	--	--	--	1
*Cenchrus echinatus var. hillebrandianus		--	--	--	+	--	--	--	--
SHRUBS									
Cassia leschenaultiana		4	4	7	5	2	--	--	2
Indigofera suffruticosa		--	4	3	6	--	--	3	3
Waltheria indica		2 *	3	--	--	3	2	--	--
Leucaena leucocephala		1	5	--	5	3	6	--	--
Sida rhombifolia		--	3	--	4	--	2	--	--
Malvastrum coromandelianum		--	--	--	1	--	3	--	--
*Sida fallax		--	--	--	--	--	7	--	--

TABLE 4 Concluded.

Species	Relevé	1		3		4		2	
	August	71	72	71	72	71	72	71	72
FORBS									
Salvia occidentalis		1	2	2	2	3	2	--	--
Desmodium triflorum		--	--	--	--	--	--	1	2
Solanum nigrum		--	--	--	--	--	1	--	--
Emilia javanica		--	--	--	--	--	--	--	1
VINES									
Merremia aegyptia		--	--	--	1	--	--	--	--
*Ipomoea indica		--	--	--	--	--	2	--	--
SHRUB SEEDLINGS									
Cassia leschenaultiana		--	2	--	--	3	--	3	2
Leucaena leucocephala		--	2	1	--	3	--	--	--
Waltheria indica		--	--	--	--	3	--	--	--
TREE									
Leucaena leucocephala		--	--	3	--	8	6	--	--

* native species

no such increase in shrubs, except for an increase in the small, usually grass-associated legume shrub Cassia leschenaultiana. The lack of woody plant invasion in relevé 2 may be related to its slope position and to its greater exposure of bare soil, on which seeds are washed away during the rainy season. Here, the mat-forming grass Melinis and also the bunchgrasses seem to have a competitive advantage over woody plants. The tall-scrub relevé 4 showed Indigofera only as a temporary wet-season resident (TABLE 3). Instead, here the shrub Sida fallax (not yet found in any other relevé) exploded into an abundant presence in the undergrowth of Leucaena trees. The smaller Leucaena trees expanded their crowns (see under SHRUBS, TABLE 4, from 3 to 6), which before were badly chewed up and narrowed by goat browsing. Also, many Leucaena seedlings occurred (see TABLE 4, bottom). The decline of Leucaena trees (see under TREE, TABLE 4, from 8 to 6) was caused by cutting the weed trees down from about 70% to less than 30% cover, an operation done by the Park Service after establishment of exclosure B. Yet, as can be seen from TABLE 4, this operation encouraged establishment of a thick shrubby undergrowth in which Leucaena again becomes abundant.

DISCUSSION

Goats, seasonality and year-to-year rainfall as controls of vegetation dynamics

The exclosure study results show that the lowland vegetation is surprisingly dynamic. There are pronounced seasonal changes in species composition and quantities, and successional changes in the early stages after release of goat pressure occur at a fast rate in both the annual and the perennial grassland. It is clear from this that the goats exert a remarkable control on the present floristic composition and structure of these grasslands. However, there is still the possibility that some of the directional changes in vegetation development observed may

be caused by a third variable, namely the year-to-year variation in rainfall.

Unfortunately, there are no current rainfall records from the study area, since the area is so remote to access by vehicle. The formerly given information on mean rainfall (800 mm) was extracted from the Taliaferro rain-isohyet map and the climate-diagram map in Doty and Mueller-Dombois (1966: 41 and 87). We may assume that the year-to-year rainfall in the study area south of the Kau Desert corresponds reasonably close with the year-to-year fluctuation in the upper Kau Desert at Halemaumau Crater. Here, the rainfall during the year preceding the study (August 1970 through July 1971) was 1.55 times that of the 30-year norm; in the year during the study (August 1971 through July 1972) it was 1.08 times that of the norm. Expressed in rainfall figures this means that the year preceding the study was extremely moist with approximately 1240 mm falling in the study area, while the study year itself had rainfall close to the 30-year norm, about 860 mm. The excess rainfall in the preceding year occurred in December and January, when it rained about 3 times as heavily as usual. Such high rainfall-years occur about once every 5 years (Doty and Mueller-Dombois 1966: 61), and a rainfall of 1.6 times the normal annual amount corresponds to the maximum ever recorded in 30 years at Halemaumau. On the other hand, low rainfall years, with about 60% the normal amount occur about 4 times in 30 years, but rarely do two dry or two moist years follow in succession.

This analysis shows that the changes observed during the study year are probably quite representative, since the study-year had a near-normal rainfall. However, certain distribution and growth effects may have been in part still a response to the preceding, extremely wet year. For example, the explosive presence of the Canavalia vine in the Kukalauula enclosure (FIG. 5) may have been in part a response to unusually favorable soil moisture conditions in that year. However,

this native vine would have probably developed also in a normal rainfall year, except that it would then not have assumed such a dominance in cover. Similarly, Melinis minutiflora and some of the bunchgrasses (Hyparrhenia and Rhynchelytrum) and shrubs may have received a "boost" during that wet year in the Puu Kaone grassland. Thus, their successional advance may not be as rapid in the next years to come as during the observation year.

Plant life form and species composition as an index
of goat pressure and site degradation

The foregoing analysis allows one to some extent to read the degree of goat pressure and site degradation in the western coastal lowland from existing plant life form and species compositions.

However, this can only be done within the limits of each site. It is, of course true, that the species compositions at Kukalauula and Puu Kaone show a considerable overlap. For example, Cynodon dactylon, Desmodium triflorum, Rhynchelytrum repens, Melinis minutiflora, Cassia leschenaultiana, Waltheria indica, Indigofera suffruticosa and others were recorded at both sites. Yet, some important plants were unique to either area, notably Canavalia kauensis to the Kukalauula site and Leucaena leucocephala to the Puu Kaone site. Furthermore, the quantitative relations among the species common to both areas varied greatly.

The two sites were differentiated as predominantly annual grassland (Kukalauula) and as perennial grassland (Puu Kaone). While the grassland stage in both cases is undoubtedly goat induced, the differences between the two grasslands are not caused by goat pressure, but by the fundamental site differences. If either of the two sites had a greater goat-feeding and -trampling pressure, it was the perennial grassland of the Puu Kaone site rather than the annual grassland.

As mentioned above, the Puu Kaone site differs fundamentally from the Kukalauula site in spite of both sites being in the same drought-season climate. The

fundamental difference is in the substrate. The Puu Kaone site has a deep, fine-textured silt-loam soil of high water holding capacity, while the Kukalauula site has a pahoehoe lava outcrop substrate with only pockets of soil, which is also coarser (i.e. mostly of sand-grain-sized ash). The substrate of the Kukalauula site is the more widespread kind in the western lowland area, while the Puu Kaone site is a localized exception.

These basic environmental differences must be kept in mind when trying to evaluate the degree of goat pressure from the present vegetation or when trying to predict the course of retrogressive or progressive succession.

The trends observed at the Kukalauula site in the annual grassland can be summarized in a simplified succession scheme (FIG. 6).

The five dominant life form groups indentified on the scheme all coexisted still inside the enclosure in year 3 after construction, but the dominance had shifted to the life form on the right side. Three life forms were unique to the enclosure (bunchgrasses, chamaephytic shrubs and the vine). On the outside a slight shift towards further degradation was recorded during the observation year.

It would be a little premature to draw a similar scheme for the Puu Kaone enclosures as the observation period there was only one year.

It is, for example, entirely possible that an increased goat pressure on Puu Kaone would by-pass the annual grassland stage. Soil erosion from wind and water already occurs heavily in the perennial bunchgrass and stoloniferous (= creeper) grass stage. Under those conditions the seeds of annuals are as easily removed as is the surface soil. Thus, site differences are important. They may produce deviations in the succession sequence even where access to the same set of species is not a factor.

In 1965, Puu Kaone was mapped as a Chrysopogon-Cynodon grassland. When the

FIG. 6. Succession scheme inside and outside Kukalauula enclosure applying to a period of 3 years. Horizontal lines show present coexistence of life forms including exposed substrate. A progressive successional displacement was indicated towards the right, inside, a regressive displacement towards the left, outside, and seasonal fluctuations in vegetation cover increase towards the left. *native species

senior author investigated it at that time, Chrysopogon was clearly the more dominant of the two. Indigofera suffruticosa and Leucaena were locally present, but not widespread over Puu Kaone. The bunchgrasses Rhynchelytrum, Andropogon glomeratus and Hyparrhenia and the mat-former Melinis were not obvious at that time. This indicates that the goat pressure on Puu Kaone was stronger in 1965 than in 1971. In 1965 over 5,000 goats were eliminated, largely from the lowland (Baker and Reeser 1972: 10), which also shows that they were very abundant at that time.

The present data on Puu Kaone indicate that the bunchgrasses will subsist together with the chamaephytic shrubs, such as Cassia leschenaultiana, Waltheria and Indigofera. Another creeper, the thick-mat former Melinis, seems to threaten the bunchgrass-chamaephytic community with overgrowth of its thick, dense shoot-mat. Among the three chamaephytic shrubs, Indigofera appears to be best equipped to survive with Melinis. However, Leucaena, which is an abundantly seeding weed-tree, will compete well with Melinis, and the grass may eventually disappear under the Leucaena canopy. Thus, the general pattern of succession without goats up to a Leucaena low-stature forest, seems quite predictable from this study.

The chances of native plant recovery after elimination of goats

The recovery of the Kukalauula enclosure with a dominance of native plant species within two-years time is truly a remarkable phenomenon. It is shown on FIG. 7 in some detail. The upper part of FIG. 7 portrays the cover-dominance of native and exotic plant species during the observation period inside the enclosure. It can be seen that exotic species covered a little over 50% of the surface in July 1971, at which time endemic species covered 46%. During the wet season in March 1972, endemics covered 50% while exotics covered 27% only. In the following dry season (July 1972) endemics and exotics had an equal cover of about 38% each.

FIG. 7. Percent cover changes of endemic, indigenous and exotic species inside and outside the KUKALAUULA enclosure for the period of one year.

The endemic species were only two, the vine Canavalia kauensis and the small succulent Portulaca cyanosperma. The high cover of endemics is entirely due to the vine. Portulaca occurred only singly and temporarily, in December 1971. The cover of exotics is produced by four grass species, one forb (Desmodium triflorum) and two shrubs (TABLE 1). The balance is tipped still further in favor of native plants by the second group of native species, the grasses Heteropogon contortus and Digitaria pruriens, which are considered indigenous according to Fosberg's checklist (in Doty and Mueller-Dombois 1966). Thus, in the two years after the elimination of goat pressure there appeared to be a relatively stable balance established between 4 native and 7 exotic plant species. In contrast, outside the fence the native Digitaria pruriens assumed a temporary cover of 7% only in the wet season, while exotics remained the sole dominants. In addition, they never reached 100% cover, because the goats prevented the closure of the grass mat, which left a considerable amount of rock and barren soil exposed (FIG. 7).

One may extrapolate from these results that native plants may become dominant after elimination of the goats. However, a prediction of further vegetation development is not that simple. For example, the Puu Kaone exclosure results give evidence to the contrary. Here only two native species participated in the recovery of exclosure A so far, the grass Digitaria pruriens and the primitive vascular chamaephyte Psilotum nudum. The appearance of Psilotum is perhaps remarkable, but it occurred only solitarily. The species seems to have a limited potential for spreading. Digitaria thrives during the wet season also under goat pressure. It is thus not a species that was eliminated by the goats. On the Puu Kaone site, the plant species participating significantly in the exclosure succession were mostly exotics, and it is highly questionable whether native plants will ever play a dominant role on this site. Here, the trend may be irreversible. However,

Sida fallax, an indigenous species arose from absence to near 50% cover, under the Leucaena canopy in relevé 4 of enclosure B (see TABLE 4).

The key to predicting successional development among lowland species does not lie in the alternatives offered by their origin, i.e. whether they are natives or exotics. It lies rather in the ecological properties of the species (i.e. their life forms, competitive capacities and physiological requirements) in their ability to reach the site in question and, in the specific set of habitat factors and in their competitors.

A reasonably accurate prediction of development on a specific site needs much further study. What this study has shown, however, is that native species can be strong competitors if they are given a chance.

The most remarkable fact is that the vine Canavalia kauensis was found to be an undescribed endemic species that has only recently been described from the Kukalauula enclosure as a new species (St. John 1972). Seeds were found around the enclosure and at some distance into the wider surroundings. It is significant that a few sporadic seedlings were observed during the wet season (TABLE 1 date 3). This indicates that the seeds were probably not dormant for 100 years as suggested by Baker and Reeser (1972). The reason why the plant remained unnoticed may be related to its site relationship. It is possible that Canavalia kauensis became established in sufficient quantity to reach maturity for seed production only in extremely wet years. In addition, its survival was probably depending on low goat pressure during such periods. In that case it may have been absent from the area (except for its seed) as long as 5 to 10 years at a time. The periodic cropping of goats by the Park Service may have helped to prevent the exhaustion of the seed supply. It is of interest here that a few stumps of Canavalia (of 2-3 cm diameter) were found in the vicinity outside the enclosure.

An island species that can maintain itself in a goat-infested area by quick growth to maturity and production of abundant seed during rare favorable years and by a seed that respire slowly enough to retain viability over several years, can be called highly competitive and resistant by any standard.

A prediction that can be made from this study is that removal of an artificial stress factor (in this case the goats) may still offer unexpected recoveries of native island plant species. Furthermore, it appears that the regeneration chance with native plants is greater on rocky soils than on deep fine-textured soils as shown by the Puu Kaone example. It is very doubtful that native plants will ever play an important role on this site in spite of goat exclusion. The succession here will progress probably rather soon (within 5 to 10 years) to a Leucaena leucocephala forest, similarly as they exist in many parts of the lowland elsewhere on the Hawaiian Islands. However, here we can expect a high percentage of the indigenous Sida fallax in the understory. Leucaena thrives in these other lowland areas also on rocky soils, so that it is rather likely that it would spread from Puu Kaone over the lava rock habitats with shallow ash soil, now occupied by the annual grass cover. However, as stated above, the chance for native plant recovery on these rocky habitats in the Park lowland seems to be better than on deep, fine soil. One reason seems to be the less aggressive invasion of exotic woody plants, ^{the} another, evolutionary adaptation of native woody species to cope successfully with unweathered volcanic substrates (Smathers and Mueller-Dombois 1972). Lava rock substrates with and without ash pockets form the prevalent substrates throughout the coastal lowland of the Park. On these native trees, though occurring in widely scattered groups or as individuals, are still the dominant phanerophytes. Metrosideros collina and Diospyros ferrea occur within the territory of the present annual Eragrostis grassland. This shows that the dry-season climate with 800 mm

mean rainfall can support an open woodland, which may form the end-phase of a progressive succession after goat removal from this area of the lowland.

In the eastern lowland near Kalapana there still occur large numbers of Canthium odoratum, Wikstroemia ?phillyraefolia and Diospyros ferrea, these grow there in form of a tall-scrub vegetation mixed with a few exotics such as Schinus terebinthifolius, Eugenia cumini and Psidium guajava. Leucaena leucocephala has not assumed any quantitative importance in this vegetation.

Thus, there is a definite chance of native plant recovery in the coastal lowland similarly as shown for the mountain parkland (Spatz and Mueller-Dombois 1972). However, one can certainly not expect a total reestablishment of what may have been the original species composition before introduction of the goats. For this, degradation by "seed exhaustion" may have already gone too far and exotic species will necessarily participate in any future progressive succession. Nevertheless, much is accomplished in the way of keeping the Park vegetation natural; if the goats be removed totally.

CONCLUSIONS

The exclosure study has clearly shown that the widespread annual Eragrostis tenella grassland in the western coastal lowland and the more localized exotic, perennial grassland at Puu Kaone, are goat-derived vegetations. This means that they are not natural, but artificial grasslands, since the goats are a non-evolutionary, man-induced, artificial stress-factor in the island environment. Cover measurements in both grasslands revealed that these derived vegetations are not stable, but that they fluctuate in relation to the degree of goat pressure. In the grassland Eragrostis at Kukalauula, the percentage of exposed rock increased by 11.2% over a yearly cycle. In the Puu Kaone grassland, exposed barren soil increased from 17.4 to 19.8% in spite of the removal of more than 1,000 goats from that area during the

same time. This shows that goats can degrade the lowland ecosystem even beyond the annual grassland stage to a rock skeleton if allowed to increase even further in number. Parts of the lowland area in the range of the Eragrostis tenella grassland are today a lava rock-skeleton and these are not necessarily more recent lava flows. By comparison, the study site at Kukalauula is still one of the less extreme variations of degraded Eragrostis tenella grassland in the coastal lowland today.

However, what is much more important in terms of degradation of the Park vegetation is the "seed exhaustion effect" caused by the goats. The study of the small exclosure at Kukalauula has shown that a recovery is still possible even with native plants that are no longer in sight in the vicinity of the area. A "spontaneous" regeneration occurred here with bunchgrasses, woody chamaephytes and an endemic vine (Canavalia kauensis). The regeneration was "spontaneous" in the sense that these three life forms are not found in the vicinity of the exclosure. Seed of the bunchgrass (Heteropogon contortus, Sporobolus africanus, Rhynchelytrum repens) may have been blown to the site during the three years of existence of the exclosure. Seed of the woody chamaephytes (Cassia leschenaultiana, Waltheria indica, Indigofera suffruticosa) were probably still present on the site from an earlier stage of less intense goat pressure in the recent past. This is almost certain for the endemic Canavalia vine. It did not arrive from any neighboring or even more distant seed source. Its seed was on the site; this shows that it survived from an earlier stage of reduced goat pressure. Its supply had not yet been exhausted from respiration or seasonal germination with unsuccessful survival.

Spontaneous recovery of this sort shows that not all is lost in terms of native plant recovery in spite of 200 years of goat degradation. Moreover, while goats are excluded, plants may arrive from neighboring seed sources of native plants.

The potential for tree growth is indicated by remnant stands in the same climatic zone. This may eventually result in an open woodland or savanna-type of vegetation.

On rocky soils there is still hope for native shrubs and trees to revegetate the coastal lowland in the Park, because native species are still available in the vicinity and they appear to be more competitive on these substrates than on deep, fine soil. On the latter, such as found at Puu Kaone, it is doubtful that native plants will play a major role in any goat exclosure succession. However, this is a localized area in the Park lowland.

Thus, a program to eliminate goats totally is extremely urgent and important if a partially native ecosystem is to be saved. Recent steps taken in this direction, the goat displacement program by systematic fencing, as outlined by Baker and Reeser (1972) appears to be an excellent and highly recommendable plan. If successful, it will result in the elimination of a man-induced, artificial stress-factor that was never part of the evolutionary stress factors in the island ecosystems. Elimination of such man-induced stress factors without introducing new ones through, for example, a well-intentioned, but artificial rehabilitation program, should be the aim of Park management. For example, eradication of the Leucaena seed source at Puu Kaone would seem a positive next step, but planting of native trees would be against the concept of maintaining a natural environment. Man has become so dominant a factor, that this concept can at best be only a compromise, but it is important that the Park is not changed into a botanical garden. If endemic species are to be saved, small, fenced botanic gardens may be set aside in the Park environment at different locations. But these must be designated as what they are, i.e. botanical gardens for endangered species and not natural areas.

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APPENDIX: list of species by families^a

^a Citation of plant names follows Fosberg (1966, revised 1972).
X = exotic, I = indigenous, E = endemic species.

PSILOTACEAE

- I Psilotum nudum (L.) Beauv.

GRAMINEAE

- X Andropogon glomeratus (Walt) BSP
I Cenchrus echinatus var. hillebrandianus (Hitchc.) F. Br.
X Chrysopogon aciculatus (Retz.) Trin.
X Cynodon dactylon (L.) Pers.
I Digitaria pruriens (Trin.) Buese
X Eragrostis tenella (L.) Beauv.
I Heteropogon contortus (L.) Beauv.
X Hyparrhenia rufa (Nees) Stapf
X Melinis minutiflora Beauv.
X Sporobolus africanus (Poir.) Rob & Tourn.
X Rhynchelytrum repens (Willd.) CE
(= Tricholaena rosea Nees = T. repens Hawaiian authors)

CYPERACEAE

- X Bulbostylis capillaris (L.) C.B. CL.
X Cyperus brevifolius (Rottb.) Hassk.
(= Kyllingia brevifolia Rottb.)
X Cyperus compressus L.

IRIDACEAE

- X Sisyrinchium micranthum Gav.

CHENOPODIACEAE

- X Chenopodium album L.

PORTULACACEAE

- E Portulaca cyanosperma Egler
X Portulaca oleracea L.

LEGUMINOSAE

- E Acacia koa var. hawaiiensis Rock
X Cassia leschenaultiana DC.
X Desmodium triflorum (L.) DC.
X Desmodium uncinatum (Jacq.) DC.
 (= D. sandwicense E. Mey.)
E Erythrina sandwicensis Deq.
X Indigofera suffruticosa Mill.
X Leucaena leucocephala (Lam.) de Wit

OXALIDACEAE

- X Oxalis corniculata L.

EUPHORBIACEAE

- X Euphorbia hirta L.
X Phyllanthus niruri L.

ANACARDIACEAE

- X Schinus terebinthifolius Raddi

MALVACEAE

- X Malvastrum coromandelianum (L.) Garcke

I Sida fallax Walp

(= S. cordifolia sensu Hawaiian authors)

X Sida rhombifolia L.

STERCULIACEAE

X Waltheria indica L.

(= W. americana L.)

PASSIFLORACEAE

X Passiflora foetida L.

THYMELEACEAE

E Wikstroemia phillyraefolia Gray

MYRTACEAE

E Metrosideros collina var. incana (Levl.) Rock

CONVOLVULACEAE

I Ipomoea indica (Burm.) Merr.

X Merremia aegyptia (L.) Urb.

LABIATAE

X Salvia occidentalis Sw.

SOLANACEAE

X Solanum nigrum L.

SCROPHULARIACEAE

X Linaria canadensis var. texana (Scheele) Pennell

RUBIACEAE

- I Canthium odoratum (Forst.) Seem.

COMPOSITAE

- X Ageratum conyzoides L.
X Bidens pilosa L.
X Centaurea melitensis L.
X Conyza sp.
X Emilia javanica (Burm. f.) C.B. Rob.
X Erechtites valerianaefolia D.C.
X Gnaphalium purpureum
X Sonchus oleraceus L.
X Vernonia cinerea var. parviflora (Bl.) D.C.

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