RESPONSES OF HAWAIIAN ECOSYSTEMS TO REMOVAL OF FERAL PIGS AND GOATS

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ABSTRACT

Feral pigs (*Sus scrofa*) and goats (*Capra hircus*) damage a wide range of native ecosystems in Hawai'i, from dry to wet communities and from low to high elevations. Comparative studies suggest that once ungulate disturbance is curtailed, some communities recover better than others, depending on a number of interrelated variables. Remote and/or lightly disturbed rain forest, coastal strand, 'ōhi'a (*Metrosideros polymorpha*) and subalpine native shrub, and native bunchgrass/native shrub are among the least affected by long-term pig or goat disturbance, although most of these communities retain alien cover in the range of 10% or less. Lowland grasslands are less successfully reclaimed, retaining alien cover as high as 80% a decade or more after ungulate removal in some areas. Accessible (to humans, ungulates, and alien plant propagules) rain forests have a higher percentage of alien cover than remote rain forests after pigs are eliminated, but even remote and/or lightly disturbed areas can be invaded by aggressive alien species long after ungulate disturbance ceases. We conclude that because recovery depends on a number of variables and because some invasive plants can establish long after pig and goat removal, most disturbed sites require continual monitoring and specific alien plant management strategies after ungulates are eliminated. Even then, an enduring alien plant component will remain in near-natural areas.

INTRODUCTION

Removal of feral ungulates from areas managed for their values as native ecosystems in Hawai'i is a key step in reducing disturbance of native vegetation. Feral goats (*Capra hircus*) frequent dry to wet areas and consume native woody plants, although they also eat herbs and grasses (Yocum 1967; Baker and Reeser 1972; Spatz and Mueller-Dombois 1973; Mueller-Dombois and Spatz 1975). Goats may reduce many palatable native plant species to the point of extinction. Māmane (*Sophora chrysophylla*) is one example of a much-preferred or "ice cream" native species. Other native species such as pūkiawe (*Styphelia tameiameiae*)

seem less sought out and are usually eaten after other plants become unavailable. Goat diets can readily change to predominantly alien species where native plants are absent or scarce, and some alien grasses such as African dropseed (*Sporobolus africanus*) are favored in some Hawaiian habitats (T.J. Ohashi, pers. comm.). Through removal of plant cover, trampling of soil, and repeated use of trails, feral goats may increase erosion and encourage degeneration of watersheds (Yocum 1967).

Feral pigs (*Sus scrofa*) are omnivores that consume both plant and animal materials in wet to dry ecosystems. In Hawai'i, pigs consume or damage native tree ferns and small ferns; fragile native lilies, mints, and bryophytes; lobelioids, koa (*Acacia koa*) seedlings, and other woody plants (Giffin 1978; Diong 1983; Stone 1985). Pigs also expose considerable ground by "rototilling" soil for earthworms, rhizomes, and tubers. Their presence in rain forests is associated with decrease of numbers and diversity of small, native soil arthropods, such as collembola (Vtorov, in press), and with greater nitrogenous resources (Vitousek *et al.* 1987). The role of feral pigs in dispersal of alien plants such as strawberry guava (*Psidium cattleianum*) and banana poka (*Passiflora mollissima*) has been well established (LaRosa, this volume; Diong 1983; Warshauer *et al.* 1983; Smith 1985).

What follows reduction or removal of pigs and goats in natural areas in Hawai'i is of increasing concern. The cost of ungulate management is high, and some pig-inhabited areas have been so heavily invaded by alien plants as to appear beyond the point of recovery. Deterioration and subsequent recovery of a given area depend on a multitude of factors. These include: duration and intensity of ungulate disturbance; presence of aggressive alien plants able to outcompete native species; soil and climatic conditions that influence erosion; and native plant propagules available for revegetation. Generalizations are difficult, and a better understanding of these influences is needed. Determining vegetation characteristics after ungulate removal or in areas with few or no ungulates, however, enables the development of some hypotheses.

Loope and Scowcroft (1985) reported on studies of 51 small exclosures established to demonstrate and evaluate vegetation response after ungulate removal in Hawai'i. They concluded that native vegetation usually holds its own or increases after ungulate removal. However, the vegetation response was highly variable and seemed related to extent of degradation. Alien grasses seemed to thrive after ungulate disturbance and removal in some highly impacted dry areas. Loope and Scowcroft noted that few exclosures had been studied in rain forest. Williams (1990) reviewed studies of ecological effects of long-term pressure of ungulates on recovery of vegetation. Included were increased insect attacks on injured native plants and increased suckering as a response to ungulates. Competitive disadvantages to native plants caused by opening up of forest by ungulates, soil compaction, and other effects have been discussed elsewhere (*e.g.*, Mueller-Dombois *et al.* 1981).

In this paper, vegetation response after removal or reduction of pig or goat disturbance is summarized for a number of areas where feral animals

have been influences for long periods. Pig and goat exclosure and transect studies in large managed areas of rain forests and other vegetation types are also highlighted. A comparison of the vulnerability to invasion of different areas is considered to help provide better understandings of the recovery potential of different areas.

METHODS

Methods used in the studies summarized in this paper varied from site to site. Because of the number of uncontrolled and unmeasured variables affecting species composition and abundance in a given area, comparative methods were used. Vegetation differences were contrasted based on recent data and those collected several years before in the same area; from data taken inside and outside exclosures or from similar pig- and goat-inhabited and uninhabited areas; and from comparable areas of high and low animal density. Areas within communities of similar physiognomy (rain forests, grasslands, shrublands) are compared.

Point frequency measurements (with a 1-m tall point frame) and visual estimates were used to determine percent plant cover. Usually, 300 to 500 pin encounters comprised a point frequency sample in a given area. The Braun-Blanquet cover-abundance method was used to estimate percent cover for individual plant species and for other categories inside established relevés or plots. Plots were read by the same people to minimize observer error. Percent data from grouped 3 x 5 m Braun-Blanquet plots inside and outside exclosures were used for many rain forest comparisons. Cover was estimated (rather than directly measured) in one of seven or eight cover categories (Mueller-Dombois and Ellenberg 1974). Category means were transformed from percentage to arcsin values for analysis and reconverted to percentages for data presentation. Because mean category values were used, cover totals were not 100% in most cases, but those plots for which total cover did not total at least 70% were not analyzed. Braun-Blanquet plot data for the stratum from ground level to 0.5 m in height only are reported here because this stratum is most vulnerable to feral animals and most likely to respond quickly after their removal.

Native/alien species ratios and percent cover measurements for alien plants were used to estimate native species diversity and "intactness" of vegetation types in a number of areas. Responses of vegetation to ungulate removal or absence were partly a function of number of alien species that remained, although some invasive alien species were more important than others. Sampling strategy for, and sizes of, each of the areas discussed are briefly noted in the results and summary tables, for ease of association with data. Brief ungulate histories of study areas are presented in the results for the same reason.

RESULTS AND DISCUSSION

Feral Goats in Subalpine and Montane Parkland

Kahikinui Forest Reserve. Goats have likely been present in the subalpine shrub zone on the southern slope of Haleakalā, Maui, for 100-150 years, with populations similar to those present today. Year-round hunting and increased access since 1983 have resulted in reduction of goats on the southwestern part of the area, with most goats remaining in the southeastern portion, and intermediate densities between. A density of about 65 animals/km^2 was estimated in 1983 for the southeastern slopes. Two transects in each of eight equally spaced "bands" from west to east were used to measure percent cover by point frequency counts. Five hundred points were read in each band (T.J. Ohashi, pers. comm.).

Long-term goat foraging in the Forest Reserve has exposed soil (Table 1), especially in the southeastern portion, where goats have been abundant for long periods. Total percent cover of alien plants is also highest where goats are now abundant, but primarily because more alien grasses occur there with or without goats. Where goats are present, percent cover and diversity of native woody plants, especially the smaller (younger) individuals, is less. Pūkiawe masks this to some degree in the data set presented, since goats do not readily take this species, but the absence of kūkaenēnē (*Coprosma ernodeoides*), māmane, and ʻōhelo (*Vaccinium reticulatum*) in the higher goat density bands is apparent in tabulated data (Table 1).

Size class counts of kūkaenēnē and ʻōhelo showed little departure from J-shaped curves in the low goat density bands, but smaller size classes were missing in the high goat density bands (Ohashi 1984). However, the reduction in native woody species in the higher-density goat areas may, in fact, also be related to the influx of alien grasses in the eastern portion of the Reserve. Differences in microclimate between gulches and undissected slopes may have resulted in more woody plant habitat in some bands than in others in the low goat density areas.

Hawaii Volcanoes National Park. Goat populations below an exclosure fence at 6,600 ft (2,010 m) elevation were reduced considerably in the early 1970s when the fence was constructed, were controlled to remnant levels by 1982, and were eradicated by 1985. Above the fence, perhaps 20 goats remained in 1989. Forty paired 10 x 30 m plots were established in 1986, 20 above the fence where goats are still present and 20 below the fence (Tunison *et al.*, unpub. data). Plot elevations ranged from 5,740 to 6,740 ft (1,750-2,045 m), with 13 plot pairs in montane parkland and 7 in the subalpine zone. Point frequency counts were used to determine percent plant cover in two plant communities above and below the fence.

Only minor differences in cover of plants were found, although alien grasses and herbs comprised more cover in goat-inhabited areas in one plant community (Table 2) than where goats had been absent for six years. However, the big difference in the goat and goat-free areas in both plant communities was native tree abundance (Table 3), with māmane, the tree form of ʻaʻaliʻi (*Dodonaea viscosa*), and koa in goat-free areas showing

Table 1. Percent alien and native plant cover on southern slope of Haleakalā, 1983. Bands are subject to greater foraging pressure by goats from west to east (Band 1 to Band 8).*

Category and Species	Low Goat Densities (West) Band 1	Band 2	Medium Goat Densities Band 3	Band 4	Band 5	Band 6	High Goat Densities Band 7	(East) Band 8
Alien Grasses								
Danthonia pilosa	2.03	0.58	4.54	1.54	5.56	0.62		0.47
Holcus lanatus				0.19		0.62		
Sporobolus africanus				0.19	2.68	5.19	6.49	3.58
Subtotals	2.03	0.58	4.54	1.93	8.24	6.43	6.49	4.04
Alien Herbs								
Hypochoeris radicata		1.56	2.17	3.08	1.34	4.77	0.81	2.95
Subtotals		1.56	2.17	3.08	1.34	4.77	0.81	2.95
Native Ferns								
Asplenium trichomanes			0.20					
Pteridium aquilinum	1.62	1.75	3.55	8.09	3.83	0.41	8.32	8.09
Subtotals	1.62	1.75	3.75	8.09	3.83	0.41	8.32	8.09
Native Grasses, Sedges								
Carex wahuensis	10.55	11.31	10.06	3.85	6.51	3.11	1.62	0.62
Deschampsia nubigena	5.27	4.29	7.30	8.09	8.05	14.11	9.13	13.06
Subtotals	15.82	15.59	17.36	11.95	14.56	17.22	10.75	13.69
Native Woody Plants								
Coprosma ernodeoides	1.83	4.29	4.54	2.12	1.72			
Coprosma montana			0.59					
Dodonaea viscosa	1.62		1.18					
Metrosideros polymorpha			1.18					
Osteomeles anthyllidifolia			0.39					

Category and Species	Low Goat Densities (West) Band 1	Band 2	Medium Goat Densities Band 3	Band 4	Band 5	Band 6	High Goat Densities (East) Band 7	Band 8
Sophora chrysophylla	1.01							
Styphelia tameiameiae	9.33	17.54	10.85	18.50	14.75	26.14	16.43	20.53
Vaccinium reticulatum	12.37	5.26	14.60	15.99	11.69			
Subtotals	26.16	27.09	33.33	36.61	28.16	26.14	16.43	20.53
Moss	2.43		0.59	0.77	0.96			
Litter	18.46	15.40	19.13	15.99	18.97	10.37	13.39	9.80
Dead Branches	7.51	3.31	4.54	3.47	1.53	3.73	1.22	3.11
Soil	3.85	6.04	3.94	6.94	6.70	21.99	15.62	17.73
Rock	22.11	28.65	10.65	11.18	15.71	8.92	26.77	19.75
Goat Droppings							0.20	0.31
Number of Native Species	8	6	11	6	6	4	4	4
Number of Alien Species	1	2	2	4	3	4	2	3
Percent Native Cover	43.61	44.44	54.45	56.65	46.55	43.77	35.50	42.31
Percent Alien Cover	2.03	2.14	6.71	5.01	9.58	11.20	7.30	6.99
Total Points/Band	493	513	507	519	522	482	493	643

*As determined by point frequency transects.

Table 2. Percent cover of alien and native plants in two communities above and below goat fence at 5,800 to 6,600 ft elevation on Mauna Loa.*

Category and Species	Montane Parkland		Subalpine Scrub	
	Goats	No Goats	Goats	No Goats
Native Ferns				
Asplenium trichomanes		00.08		
Pellaea ternifolia			00.33	00.08
Pteridium aquilinum				00.17
Native Grasses, Sedges				
Agrostis avenacea				00.50
Carex wahuensis	01.08	03.50	00.42	
Deschampsia nubigena	23.00	22.08	03.83	09.42
Gahnia gahniiformis	01.08		02.75	02.08
Luzula hawaiiensis			00.17	00.08
Panicum tenuifolium	03.83	01.92		
Alien Grasses, Sedges				
Anthoxanthum odoratum	00.08			
Danthonia pilosa	01.08			
Ehrharta stipoides	00.50			
Holcus lanatus	02.00	01.50	00.08	00.75
Alien Herbs				
Gnaphalium japonicum	00.08			
Hypochoeris radicata	02.00	00.67	00.42	00.33
Rumex acetosella	00.17	00.50		
Native Woody Plants				
Coprosma ernodeoides			00.20	04.42
Coprosma montana			00.08	
Dodonaea viscosa		00.33	02.92	04.83
Metrosideros polymorpha			00.33	00.50
Sophora chrysophylla	00.08	00.83		00.33
Styphelia tameiameiae	44.83	41.17	18.92	18.83
Vaccinium reticulatum			12.58	08.83
Bryophytes	01.00	06.67	00.58	00.83
Lichens			00.17	00.08
Litter	11.58	17.42	15.75	12.33
Soil	02.83	02.25	12.42	06.83
Rock	04.75	07.08	26.25	28.75
Number of Native Species	6	7	10	10
Number of Alien Species	7	3	3	4
Percent Native Cover	73.91	69.83	44.00	49.50
Percent Alien Cover	5.92	2.67	0.83	1.66

*As determined by point frequency samples; 4 transects with 300 sample points each (n = 1,200) for each of the 4 areas.

Table 3. Native tree abundance* in different size classes **in two communities above and below** goat fence (5,800-6,600 ft) on Mauna Loa, in 1986.**

Species and Size	Montane Parkland				Subalpine Scrub			
	Goats		No Goats		Goats		No Goats	
	#	%	#	%	#	%	#	%
Sophora chrysophylla (Māmane)								
<10 cm tall	13	21.31	16	10.06				
10 cm - 1 m	21	34.43	60	37.74	1	100	32	62.75
>1 m, <2cm dbh	18	29.51	57	35.85			16	31.37
2-5 cm dbh			21	13.21			3	5.88
6-10 cm dbh			2	1.26				
>10 cm dbh	9	14.75	3	1.89				
Subtotals	61		159		1		51	
Dodonaea viscosa ('A'ali'i)								
<10 cm tall	41	63.08	48	30.38				
10 cm - 1 m	12	18.46	55	34.81				
>1 m, <2 cm dbh	2	3.08	8	5.06				
2-5 cm dbh	4	6.15	7	4.43				
6-10 cm dbh			24	15.19			1	100
>10 cm dbh	6	9.23	16	10.13				
Subtotals	65		158				1	
Metrosideros polymorpha ('Ōhi'a)								
<10 cm tall								
10 cm - 1 m					1	6.67		

Table 3, continued.

Table 3, continued.

Species and Size	Montane Parkland				Subalpine Scrub			
	Goats		No Goats		Goats		No Goats	
	#	%	#	%	#	%	#	%
Metrosideros polymorpha ('Ōhi'a), cont.								
>1 m, <2 cm dbh					3	20.00	2	33.33
2-5 cm dbh					2	13.33		
6-10 cm dbh					2	13.33		
>10 cm dbh					7	46.67	4	66.67
Subtotals					15		6	
Acacia koa (Koa)								
<10 cm tall					5	83.33	18	12.77
10 cm - 1 m							80	56.74
>1 m, <2 cm dbh							38	26.95
2-5 cm dbh							4	2.84
6-10 cm dbh								
>10 cm dbh					1	16.67	1	0.71
Subtotals					6		141	
Total Native Trees	126		317		22		199	

*As determined by counts with 300 points per plot. Number of individuals and % of individuals of a species in particular size class.

**Area above or mauka with 100-200 goats at present; area below with few goats since early 1970s, no goats since 1985.

considerable regeneration. Significantly more (t test, p = <0.05) māmane, koa, and 'a'ali'i seedlings, saplings, and sprouts were found below the fence in both 1986 and 1988. No comparable differences in seedling and sapling numbers of 'ōhi'a (*Metrosideros polymorpha*) were found in areas where goats were present and where they had been at remnant levels since 1982 and eradicated since 1985.

In the same subalpine area on Mauna Loa, a transect (utilizing point frequency with 300 points) established in the *Deschampsia*/native shrub community in the goat-free area showed appreciable reduction in alien plant cover from 1978 to 1984 (Table 4), although decreased pig digging may also explain some of the change. Not much change in alien cover occurred along one transect (n = 300 points) in the 'ōhi'a/native shrub type in the low goat density area above the fence (goat densities <20/mi^2 or 8/km^2) (Table 4).

Table 4. Percent cover of native and alien plants in subalpine habitat (5,740-6,740 ft) on Mauna Loa in Hawaii Volcanoes National Park after goat removal.

	Open *Metrosideros* /Native Shrubs*		*Deschampsia* Grass /Native Shrubs**	
Category and species	11/78	04/84	11/78	04/84
Native Ferns	0.7			
Alien Ferns			0.3	
Native Grasses, Sedges	3.6	6.0	33.9	37.3
Alien Grasses, Sedges			11.4	5.3
Alien Herbs	0.3		5.6	1.7
Native Woody Plants	61.4	49.4	24.6	21.0
Lichen	1.0	0.3		1.6
Moss	1.0	0.6	2.0	2.0
Litter	5.7	8.3	5.0	6.7
Rock	19.7	18.0	14.3	21.7
Soil	6.0	17.3	3.0	2.7
Number of Native Species	9	9	6	5
Number of Alien Species	1	0	6	3
Percent Native Cover	65.7	55.4	58.5	58.3
Percent Alien Cover	0.3	0.00	17.3	7.0

* Transect 118, 6,800 ft.
** Transect 119, 6,200 ft.

Feral Goats in Coastal Lowlands

Hawaii Volcanoes National Park Lowlands. Feral goats were probably present in the lowlands (area below fault scarp at <1,500 ft or 500 m elevation) of Hawaii Volcanoes National Park for 150 years at densities of

about 170/mi^2 (60/km^2) (Stone and Keith 1986). Effective control of an estimated 15,000 animals began in 1971, with most goats gone (<200 left) by 1980, and populations in 1986 effectively zero. Lowland transects were established after initial goat reduction in the early 1970s. Results of point frequency studies (n = 300 points/transect) at that time in a number of lowland vegetation types (Tables 5a, b, and c) showed that current lowland vegetation was largely alien grasses. Percent alien cover values varied from 13 to 75% after six years at low goat densities for grasslands. Most of these areas had many more alien than native species, with only one native/alien species ratio reaching 1.0 (*Hyparrhenia* grassland in 1984). Changes in alien plant cover and native/alien ratios over a six-year period (1978-1984) were not great, and in many lowland grassland vegetation types, both alien and native cover declined somewhat, perhaps as a result of reduced precipitation levels and volcanic emissions from the current eruptive phase.

Lowland shrub systems (Table 5c) showed lower alien cover values and higher native/alien ratios than grasslands (Tables 5a and b), but change in these types after goat removal has also been slow. Alien cover values in lowland shrubland remained high (20.6-39.8%), but alien woody plants declined in cover over the six years. The native strand type showed a dramatic increase in percent native cover, largely as a result of increased naupaka kahakai (*Scaevola sericea*), a plant once browsed heavily by goats.

Native woody plant cover in a scrub ʻōhiʻa/native shrub community on ash substrate apparently decreased inside the Park and increased outside (where goats were not controlled) along one set of paired point frequency transects (n = 200 points/transect). However, native woody plants decreased outside the Park more than inside along another set of transects in a similar plant community on pāhoehoe substrate (Table 6). Variable goat browsing densities and distribution outside the Park, and weather, are again confounding factors. Small sample size and dramatic movement of ash with strong winds may also be important.

Two exclosures (Kaone and Kūkalauʻula) established in the lowlands of Hawaii Volcanoes National Park in 1969 and 1971 while goats were still abundant (Tables 7 and 8) showed low native/alien plant species ratios (0.28 to 0.50) after 13 to 15 years (1984) and high alien cover (over 70%). Alien plant cover (especially grasses) increased both inside and outside exclosures from 1971 to 1984. A previously undescribed jackbean (*Canavalia kauensis*, now included in *C. hawaiiensis*) appeared inside the Kūkalauʻula exclosure (St. John 1972; Mueller-Dombois 1981). A fire at the Kaone exclosure in 1980 probably encouraged increased cover of three alien perennial grasses, molasses grass (*Melinis minutiflora*), Natal red top (*Rhynchelytrum repens*), and *Hyparrhenia rufa* inside and outside exclosures. However, molasses grass and Natal red top also showed large increases inside and outside of the Kūkalauʻula exclosure, which did not burn. Mueller-Dombois (1981) noted the change over time from alien annual to alien perennial grasses. Native and alien cover may change gradually with time, or ratios may vary with succession, climatic trends, fires, or other variables.

Table 5a. Percent native and alien plant cover in lowland grasslands and shrublands, Hawaii Volcanoes National Park.*

Category and Species	*Rhynchelytrum repens* Grassland**		*Heteropogon contortus/ Rhynchelytrum repens* Grassland***		*Melinis minutiflora/ Rhynchelytrum repens* Grassland#		*Schizachyrium condensatum* Grassland##	
	12/78	03/84	10/78	01/84	12/78	03/84	12/79	01/84
Alien Ferns								0.7
Native Grasses, Sedges				15.3	17.0			
Alien Grasses, Sedges	41.7	31.4	9.6	11.0	71.7	72.7	62.7	59.7
Alien Herbs	8.0		1.0	1.0	0.3			
Native Woody Plants	5.7	4.3	10.0	7.3	0.7	0.7	14.7	5.0
Alien Woody Plants		5.3	1.0	1.0	11.7	1.0	2.0	4.0
Lichen				0.3			0.3	
Moss	0.7						0.3	0.3
Litter	11.3	25.3	8.7	9.0	9.3	16.3	8.7	11.7
Rock	29.7	32.7	53.7	52.0	6.3	9.3	10.7	18.7
Soil	3.0	1.0	1.3	0.7			0.3	
Dead wood							0.3	
Number of Native Species	1	1	3	2	1	1	2	2
Number of Alien Species	5	6	8	7	6	6	4	6
Percent Native Cover	5.7	4.3	25.3	24.3	0.7	0.7	14.7	5.0
Percent Alien Cover	49.7	36.7	11.6	13.0	83.7	73.7	64.7	64.4

*n = 300 for each sample, point frequency transects.
**Transect 113, 800 ft elevation.
***Transect 106, 120 ft elevation.
#Transect 110, 1,240 ft elevation.
##Transect 121 (burned in 1981), 1,250 ft elevation.

Table 5b. Percent native and alien plant cover in lowland grasslands and shrublands, Hawaii Volcanoes National Park.*

Category and Species	*Hyparrhenia rufa* Grassland**		*Rhynchelytrum repens* Grassland***		Mixed Grassland#	
	12/78	03/84	10/78	03/84	10/78	01/84
Native Ferns					1.0	
Alien Ferns						1.0
Native Grasses, Sedges	0.7					5.7
Alien Grasses, Sedges	80.3	75.0	48.3	39.3	27.7	25.6
Native Herbs	2.0	3.7				
Alien Herbs	0.7		0.7	0.6	1.7	1.0
Alien Vines				1.7	0.3	
Native Woody Plants	1.0		9.0	7.7	9.7	7.4
Alien Woody Plants	1.0		10.0	3.7	4.0	1.6
Litter	9.7	13.7	11.3	28.7	8.3	12.7
Rock			20.3	18.3	40.0	45.0
Soil	4.7	7.7	0.3			
Sand						
Number of Native Species	3	1	1	1	4	3
Number of Alien Species	5	1	6	8	9	8
Percent Native Cover	3.7	3.7	9.0	7.7	18.0	13.1
Percent Alien Cover	82.0	75.0	59.0	45.3	33.7	29.2

*n = 300 for each sample, point frequency transects.
**Transect 109, 1,020 ft elevation.
***Transect 115, 80 ft elevation.
#Transect 105, 60 ft elevation.

Table 5c. Percent native and alien plant cover in lowland grasslands and shrublands, Hawaii Volcanoes National Park.*

Category and Species	Lowland Scrub** 09/78	Lowland Scrub** 01/84	Lowland Scrub*** 10/78	Lowland Scrub*** 01/84	*Scaevola sericea* Strand# 12/78	*Scaevola sericea* Strand# 03/84
Alien Ferns		0.6				
Native Grasses, Sedges	1.7	7.0	5.3	6.3	7.3	5.7
Alien Grasses, Sedges	35.7	37.0	18.3	15.3		
Native Herbs					18.0	4.0
Alien Herbs	1.0	0.3	2.0	1.3		
Native Woody Plants	17.7	23.0	47.0	43.4	47.9	94.0
Alien Woody Plants	6.7	1.7	7.9	4.0	0.7	
Moss		0.7				
Litter	20.0	17.7	9.7	20.7	7.7	2.0
Rock	17.3	12.7	9.0	9.0	3.7	
Sand					22.0	
Number of Native Species	5	5	7	7	5	4
Number of Alien Species	7	7	7	8	1	0
Percent Native Cover	19.4	30.0	52.3	49.7	65.9	98.0
Percent Alien Cover	43.4	39.6	28.2	20.6	0.7	0

*n = 300 for each sample, point frequency transects.
**Transect 103, 40 ft elevation.
***Transect 104, 70 ft elevation.
#Transect 116, 10 ft elevation.

Table 6. Percent cover of native and alien plants in *Metrosideros* shrubland inside and outside Hawaii Volcanoes National Park after goat removal program in the Park between 1971 and 1980 (for most animals).*

	Scrub *Metrosideros*/Native Shrubs**				Scrub *Metrosideros*/Native Shrubs ***			
	Inside		Outside		Inside		Outside	
Category and Species	01/79	01/84	01/79	01/84	01/79	01/84	01/79	01/84
Alien Grasses, Sedges	10.0	9.0	9.0	8.0	12.5	16.0	8.5	9.5
Native Woody Plants	4.0	1.0	4.5	6.0	6.0	5.0	4.5	2.0
Lichen	2.5	1.5		0.5	5.0	2.0	2.5	2.0
Moss				3.5	1.0	1.0		0.5
Litter	4.0	5.0	3.0	6.5	2.0	4.5	3.5	2.5
Rock	25.5	33.0	15.0	7.0	52.5	49.5	61.0	61.5
Ash	54.0	50.5	68.5	68.5	21.0	22.0	21.0	22.0
Number of Native Species	2	1	3	3	2	3	3	2
Number of Alien Species	4	3	4	4	5	4	4	3
Percent Native Cover	4.0	1.0	4.5	6.0	6.0	5.0	4.5	2.0
Percent Alien Cover	10.0	9.0	9.0	8.0	12.5	16.0	8.5	9.5

*n = 300 for each sample, point frequency transects.
**Transect 100 on ash substrate, 2,650 ft elevation.
***Transect 101 on pāhoehoe substrate, 2,650 ft elevation.

Table 7. Percent native and alien plant cover inside and outside Kaone Exclosure, Hawaii Volcanoes National Park.*

Category and Species	10/71		04/82		03/84	
	Inside	Outside	Inside	Outside	Inside	Outside
Alien Grasses, Sedges	15.8	9.6	42.4	51.2	61.0	68.0
Native Herbs				0.2	3.6	1.0
Alien Herbs	1.6	0.6	0.4	0.4		0.2
Alien Vines			0.4		1.3	
Native Woody Plants			1.4	1.0	0.6	0.6
Alien Woody Plants	11.2	10.8	38.2	33.4	15.1	13.4
Litter	50.4	58.2	2.2	4.0	6.3	6.6
Soil	21.0	20.4	15.0	9.2	12.2	10.0
Rock				0.6	12.2	0.2
Goat pellets		0.4				
Number of Native Species	0	0	1	2	2	2
Number of Alien Species	9	10	8	8	7	6
Percent Native Cover	0	0	1.4	1.2	4.2	1.6
Percent Alien Cover	28.6	21.0	81.4	85.0	77.4	81.6

*As determined by point frequency transects; n = 500 points/sample. The Kaone area burned in 1980.

Table 8. Percent native and alien plant cover inside and outside of Kūkalau'ula Exclosure, Hawaii Volcanoes National Park, 1971, 1982, and 1984.*

Category and Species	12/71		03/82		04/84	
	Inside	Outside	Inside	Outside	Inside	Outside
Native Grasses, Sedges	1.2		0.3		0.6	
Alien Grasses, Sedges	45.4	45.2	90.9	77.8	75.7	69.6
Native Herbs	45.0		6.0	13.2	8.9	17.2
Alien Herbs	1.2	0.4	2.3		1.7	
Native Woody Plants	2.4			1.4		1.0
Alien Woody Plants	2.4			5.2		1.4
Litter		14.4	0.6	1.6	13.1	9.6
Rock		38.0		0.8		1.2
Number of Native Species	3	0	2	2	2	2
Number of Alien Species	6	7	6	5	4	5
Percent Native Cover	47.4	0	6.3	14.6	9.5	18.2
Percent Alien Cover	49.0	45.6	93.2	83.0	77.4	71.0

*As determined by point frequency transects; n = 350 points inside, 500 outside. 1971 points were 270 and 140.

Feral Pigs in Subalpine and Montane Parkland Areas

Kalapawili Grasslands. Feral pigs have been present in the Kalapawili grasslands in Haleakala National Park since at least 1960 at low but unknown densities (probably $<10/km^2$). They were not effectively controlled until erection of fencing along the North Rim of the Crater and upper Kīpahulu Valley in 1985-1986. The native bunch grass *Deschampsia nubigena* is the dominant species, but velvet grass (*Holcus lanatus*) is a serious invader (Jacobi 1976, 1981).

Point frequency data (n = 500 points inside, 500 outside) from pig exclosures in the grasslands (J. Jacobi, pers. comm.) suggest that where disturbance by feral pigs continues, the percent cover of *Deschampsia* remains lower and the percent cover of velvet grass is somewhat higher than where disturbance by pigs ceases (Table 9). Estimates of plant cover from 100, 2 x 2 m plots along transects (Table 10), which cover a larger and more representative part of the grasslands, and where disturbance continued, show stable *Deschampsia* cover (57.3% in 1973 and 58.6% in 1986), but increasing *Holcus* (9.5% in 1973 to 15.3% in 1986) (J. Jacobi, pers. comm.). Pig control has been effective throughout the area since 1986. Blackberry (*Rubus argutus*) is gradually spreading at present.

Hawaii Volcanoes National Park. Three major intergrading plant communities were studied for recovery from feral pig damage in mountain parkland on Mauna Loa between elevations of 4,495 and 6,790 ft (1,370-2,070 m). Small stands of koa, shrublands dominated by pūkiawe and sometimes ʻaʻaliʻi, and grasslands dominated by native bunch grasses or alien grasses were sampled (Tunison *et al.*, in press). Twenty-seven 2 x 5-m plots were established in 1984 on sites recently (<30 days) disturbed by pigs. Plots in each of the three vegetation communities were each replicated nine times (clusters of three plots at three sites in each community). No disturbance by pigs occurred after plot establishment, since pig removal was nearly complete in 1984. Plots were sampled by the point intercept method from 1985 to 1988 with 10, 2-m long transects and 200 sample points per plot. Woody plants were counted in five height classes. Data from all 27 plots were pooled to give early successional trends.

Early results showed that bare soil and litter declined with increases in plant cover, as would be expected. Alien species cover increased at a faster rate than native species cover (Fig. 1), and alien grass cover accounted for most of the increase in total vegetative cover (Fig. 2). In lower-elevation parkland communities (4,400 ft or 1,340 m) dominated by alien grasses, especially sweet vernalgrass (*Anthoxanthum odoratum*) and velvet grass, these species increased in cover more rapidly than other native or alien grasses. At intermediate elevations (4,900 ft or 1,495 m) dominated by mixed alien and native grasses, dallis grass (*Paspalum dilatatum*) and sweet vernalgrass increased more rapidly than *Deschampsia*. At higher elevations (6,300 ft or 1,920 m) dominated largely by native grasses, velvet grass increased more rapidly than other species, but *Deschampsia* recovered nearly as rapidly. The total number of plant species increased slightly or remained the same for essentially all areas.

Table 9. Summary of percent cover of alien and native plants inside and outside Kalapawili Ridge Exclosure, Haleakala National Park, 1974 and 1985.*

	Transects 1-5				Transects 6-10			
	Inside		Outside		Inside		Outside	
Plant Species	'74	'85	'74	'85	'74	'85	'74	'85
Deschampsia nubigena	42	80	48	68	76	78	65	71
Holcus lanatus	1	16	2	22	7	16	5	21
Hypochoeris radicata	2	1	2	2	4		3	3
Rumex acetosella	9		4		1		4	
Other Species	3	3	5	3	4	4	4	3
Litter	36		32	4	8	2	17	2
Barren ground	7		7	1			2	

*As determined by point frequency sampling. Transects 1-5 received greater initial pig damage than 6-10 (from J. Jacobi, pers. comm.).

Table 10. Summary of percent cover of alien and native plants on Kalapawili grasslands transects, Haleakala National Park.*

	Transects	
Plant Species	1973	1986
Deschampsia nubigena	57.3	58.6
Holcus lanatus	9.5	15.3
Hypochoeris radicata	8.0	16.9
Rumex acetosella	0.9	0.1
Other Species	1.1	1.4
Rocks		0.8

*As determined by point frequency sampling (from J. Jacobi, pers. comm.).

Feral Pigs in Rain Forests

Feral pigs in rain forests in the Thurston and Puhimau areas of Hawaii Volcanoes National Park (Fig. 3) have probably been present for 60 years in densities of about 55/mi^2 (20 animals/km^2). In this very accessible area, hunting has been moderate to heavy for at least 20 years. The vegetation in the Thurston-Puhimau area is open to closed ʻōhiʻa with a native tree subcanopy, an open tree fern or hapuʻu (*Cibotium glaucum*) layer beneath, and ground cover composed of uluhe (*Dicranopteris linearis*), other native ferns, and both native and alien shrubs, herbs, and grasses.

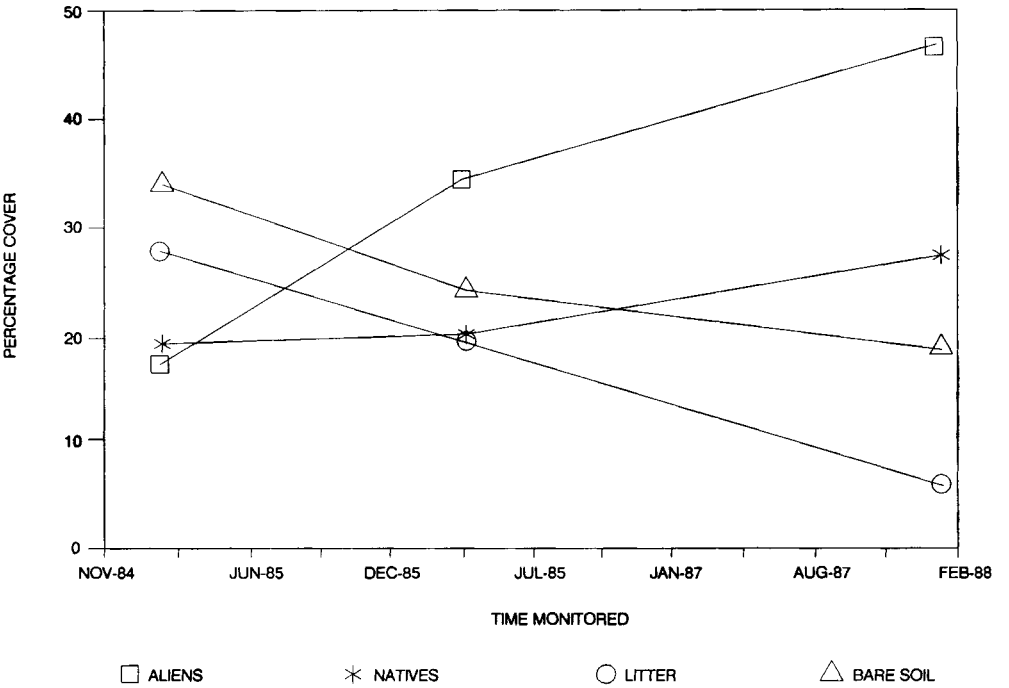

Figure 1. Changes in percentage cover (as determined by point intercept) in 27 plots in montane parkland area recently disturbed by pigs (elevation 4,495 to 6,790 ft) on Mauna Loa, Hawaii Volcanoes National Park, 1984-1985.

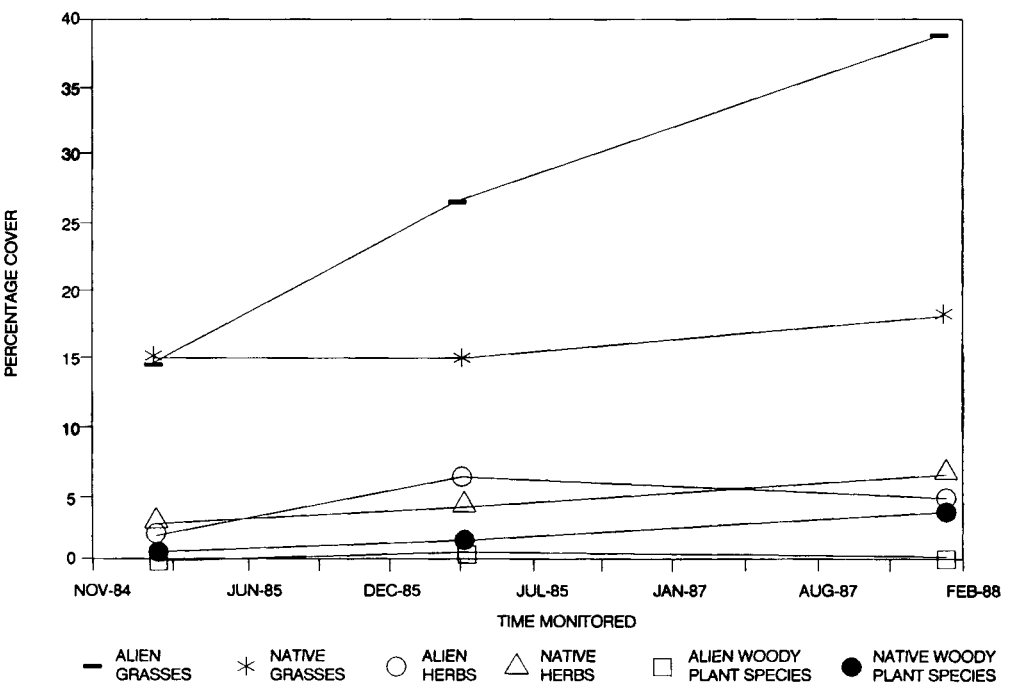

Figure 2. Changes in percentage cover of native and alien plants (as determined by point intercept) in 27 plots in montane parkland area recently disturbed by pigs (elevation 4,495 to 6,790 ft) on Mauna Loa, Hawaii Volcanoes National Park, 1984-1985.

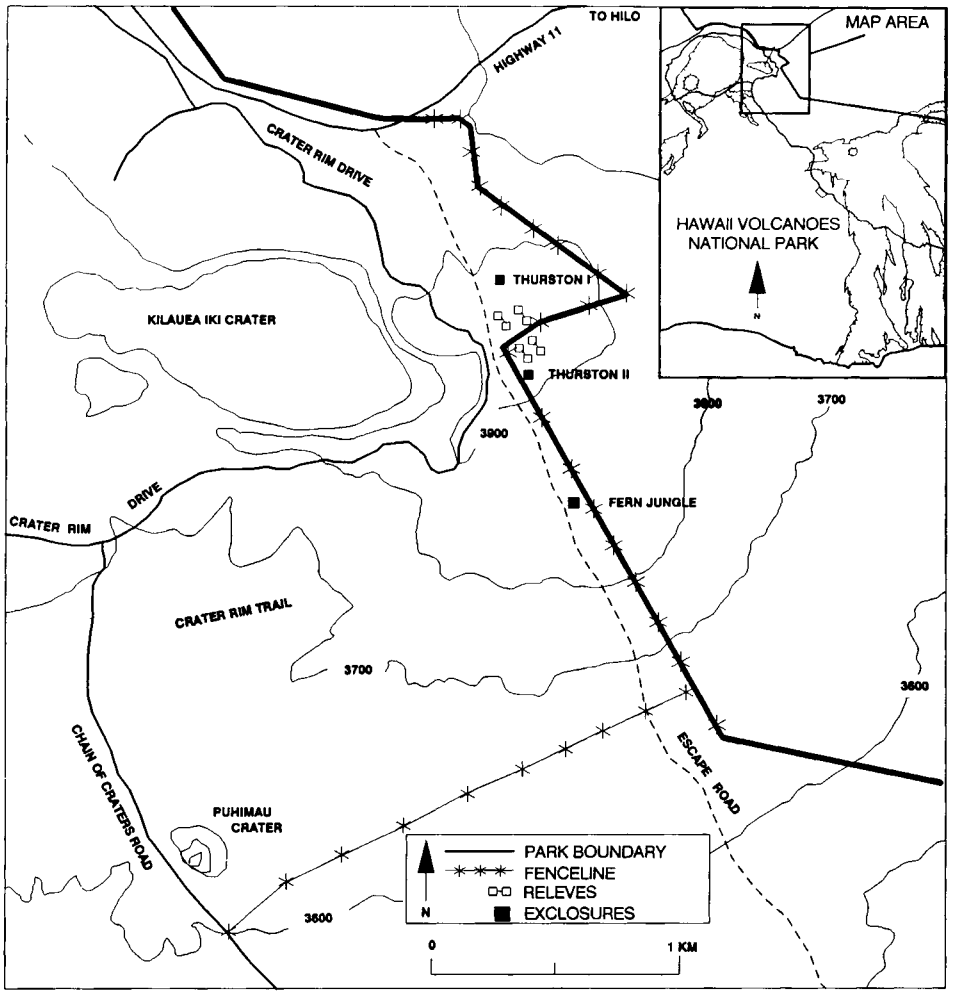

Figure 3. Locations of rain forest exclosures and relevés in Thurston area of Hawaii Volcanoes National Park.

One feral pig exclosure (Fern Jungle) was established in 1968 and two (Thurston I and II) in 1981. The enclosed 4.6 km^2 Thurston Lava Tube Management Area, which contains the Thurston I exclosure, has been pig-free since the fence was finished in December 1980. Another fence enclosing approximately 5.2 km^2, including the Fern Jungle Exclosure, Puhimau Crater, and part of the Crater Rim Trail, was finished in August 1984. Transects were established at that time to monitor alien plants and feral pig activity in the Thurston area and in an adjacent area on private (now State-owned) land still inhabited by pigs. Braun-Blanquet percentage cover estimates were obtained from 3- x 5-m plots. Unfortunately, data from many plots could not be included for the Thurston area analyses because cover

totals did not exceed 70 percent. As indicated previously, sample sizes are given in tables for each area.

Fern Jungle Exclosure. Alien plant species cover inside the Fern Jungle Exclosure (0-0.5 m stratum) in 1981 was considerably less after 14 years without pigs than that outside, where disturbance continued (Table 11). Alien grasses, especially meadow ricegrass (*Ehrharta stipoides*), and the native ʻōhiʻa tree accounted for much more cover outside. In contrast, a native grass, ʻohe (*Isachne distichophylla*), and native bryophytes provided more cover inside the exclosure (Higashino and Stone 1982). Litter, especially that of uluhe, was greater inside the exclosure, and exposed ground was greater outside. Unfortunately, we were unable to directly compare 1968 data with 1981 data inside the exclosure, and no monitoring was done outside in 1968.

Table 11. Mean percent cover of alien and native plants in 3 x 5 m Braun-Blanquet relevés inside and outside Fern Jungle Exclosure, Hawaii Volcanoes National Park, 1981 (ground-0.5 m stratum).*

Category and Species	Inside**	Outside
Native Ferns, Clubmosses	0.5	0.3
Native Grasses, Sedges	5.0	2.8
Alien Grasses, Sedges	0.6	5.8
Alien Herbs	0.2	0.7
Native Woody Plants	1.3	4.8
Native Bryophytes	9.3	4.5
Litter	68.0	57.5
Exposed Ground		5.2
Total Cover***	84.9	81.6
Percent Native Cover	16.1	12.4
Percent Alien Cover	0.8	6.5
Number of Native Species	15	15
Number of Alien Species	9	12

*Sample size = 15 plots inside and 18 outside exclosure.
**Feral pigs excluded for 14 years.
***Because Braun-Blanquet cover estimates rely on category midpoints, percent cover does not necessarily add to 100.

Thurston I Exclosure. An increase in bryophyte cover outside the exclosure was the most significant change noted in the Thurston I exclosure study (0-0.5 m stratum) over four years (Table 12). Native grasses appeared to increase inside and outside the exclosure, and native woody plants appeared to decrease inside and outside the exclosure. Alien grasses, especially meadow ricegrass, showed some increase inside the exclosure. Litter appeared to decrease outside the exclosure, but the 1981 readings were taken in October, and the 1985, in July, perhaps accounting for some of the difference. Disturbed ground decreased inside and outside the exclosure. Since pigs have not been present outside Thurston I exclosure (established in 1981) since 1980, it was not surprising that similar vegetation responses occurred inside and outside.

Table 12. Mean percent cover of native and alien plants in 3 x 5 m Braun-Blanquet relevés inside and outside Thurston I Exclosure, Hawaii Volcanoes National Park, 1981 and 1985 (ground-0.5 m stratum).*

	1981		1985	
Category and Species	Inside	Outside	Inside	Outside
Native Ferns	0.2	1.4	0.5	2.4
Alien Ferns	**	**	**	
Native Grasses, Sedges	3.0	3.7	4.9	4.7
Alien Grasses	3.4	0.5	5.2	0.3
Native Herbs	**	**		0.1
Alien Herbs	0.8	0.3	0.1	0.1
Native Woody Plants	5.7	3.5	3.6	1.7
Alien Woody Plants	**	**	**	**
Native Bryophytes	8.1	1.9	8.1	15.9
Litter	47.6	69.6	47.6	50.0
Logs			2.5	
Exposed Ground	6.2	1.5		
Total Cover***	75.0	82.4	72.5	75.2
Percent Native Cover	17.0	10.5	17.1	24.8
Percent Alien Cover	4.2	0.8	5.3	0.4
Number of Native Species	14	13	17	15
Number of Alien Species	9	7	9	8

*Sample size = 8 plots outside, and 7 inside exclosure.
**Measurable cover but <0.1% mean.
***Because Braun-Blanquet cover estimates rely on category midpoints, percent cover does not necessarily add to 100.

Thurston II Exclosure. Insufficient plots were available with adequate cover estimates outside the exclosure, but obvious changes occurred inside over the four years (Table 13). Exposed ground decreased inside the exclosure, and the alien plant cover, especially the shade-tolerant meadow ricegrass, showed a great increase. Exposed ground available for ricegrass invasion was greater prior to construction of this exclosure, largely because pigs were not being controlled in the Thurston II area, as was the case in the Thurston I area. New alien plants in the plots in 1985 included strawberry guava (*Psidium cattleianum*), blackberry, broomsedge (*Andropogon virginicus*), and Hāmākua pāmakani (*Ageratina riparia*). Glenwood grass (*Sacciolepis indica*) was present in 1981 but not 1985.

Table 13. Mean percent cover of alien and native plants in 3 x 5 m Braun-Blanquet relevés inside Thurston II Exclosure, Hawaii Volcanoes National Park, 1981 and 1985. (ground - 0.5 m stratum).*

Category and Species	1981	1985
Native Ferns	0.4	0.4
Native Grasses, Sedges	2.1	2.0
Alien Grasses, Sedges	2.7	22.7
Alien Herbs	0.2	0.1
Native Woody Plants	1.3	2.4
Alien Woody Plants	**	**
Native Bryophytes	3.3	2.0
Exposed Ground	11.1	**
Litter	41.5	35.8
Total Cover***	62.6	65.4
Percent Native Cover	7.1	6.8
Percent Alien Cover	2.9	22.8
Number of Native Species	12	11
Number of Alien Species	3	6

*Sample size = 5 plots; sample size outside exclosure not adequate.
**Measurable cover, but <0.1% mean.
***Because Braun-Blanquet cover estimates rely on category midpoints, percent cover does not necessarily add to 100. Although all plots totalled >70%, means for the two years were somewhat lower after conversion from arcsin.

Thurston Relevés. Percent alien plant cover and number of alien species in plots in a pig-inhabited area near the Thurston II exclosure showed an increase in 1985, compared to 1981 (Table 14). Among the new invaders in the plots over the four-year period were kāhili ginger (*Hedychium gardnerianum*), strawberry guava, and firetree (*Myrica faya*), three of the most invasive species in the area. Meadow ricegrass continued to increase, although exposed ground from feral pig disturbance was higher in 1985 than 1981. A more extensive area was covered in this comparison than in plots limited to inside and immediately outside exclosures.

Table 14. Percent cover of alien and native plants in 3 x 5 m Braun-Blanquet relevés in pig-inhabited area of Thurston Lava Tube area, Hawaii Volcanoes National Park, 1981 and 1985 (ground-0.5 m stratum).*

Category and Species	1981	1985
Native Ferns	0.9	**
Native Grasses, Sedges	2.4	4.6
Alien Grasses, Sedges	11.5	18.9
Alien Herbs	0.1	0.3
Native Woody Plants	1.5	1.7
Alien Woody Plants	**	0.3
Native Bryophytes	2.8	4.9
Exposed Ground	0.4	4.2
Litter	58.5	36.6
Total Cover***	78.1	71.5
Percent Native Cover	7.6	11.2
Percent Alien cover	11.6	19.5
Number of Native Species	8	9
Number of Alien Species	3	11

*Sample size = 5 plots.
**Measurable cover, but <0.1% mean.
***Because Braun-Blanquet cover estimates rely on category midpoints, percent cover does not necessarily add to 100.

Preliminary population data for firetree and kāhili ginger in the Thurston area of Hawaii Volcanoes National Park five years after feral pig removal showed strong inverse J-curves indicative of stable or, more likely, expanding populations since removal (Figs. 4 and 5). Population expansion of these and probably other species subsequent to feral animal removal is likely to occur in some areas without aggressive alien plant

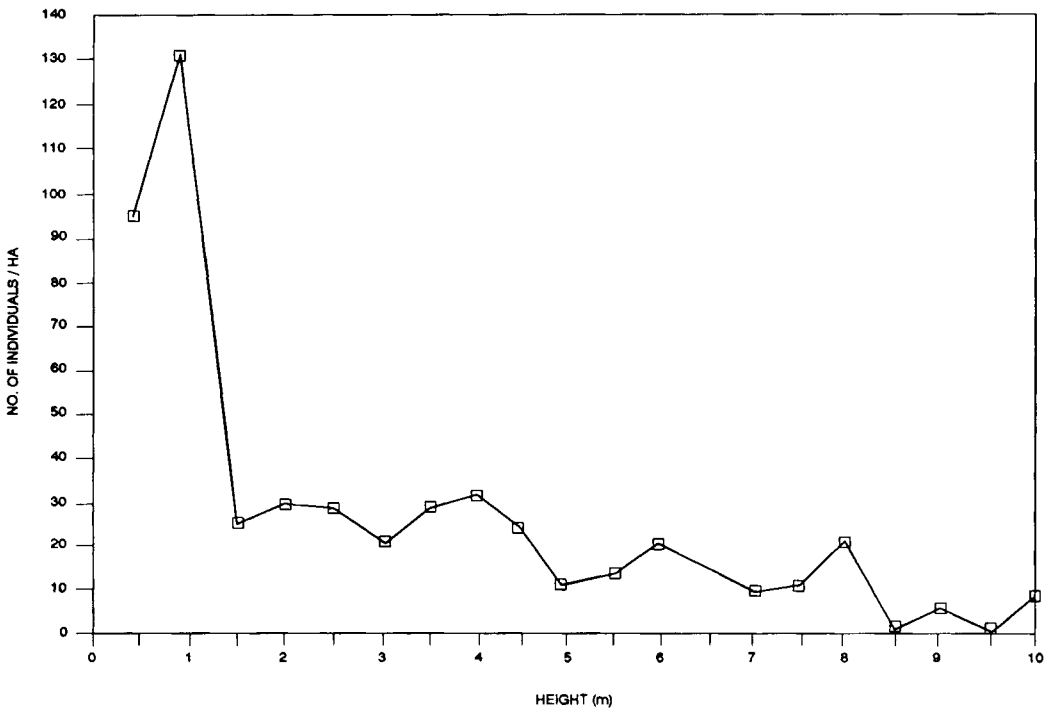

Figure 4. Population structure of firetree in Thurston area of Hawaii Volcanoes National Park, five years after feral pig removal.

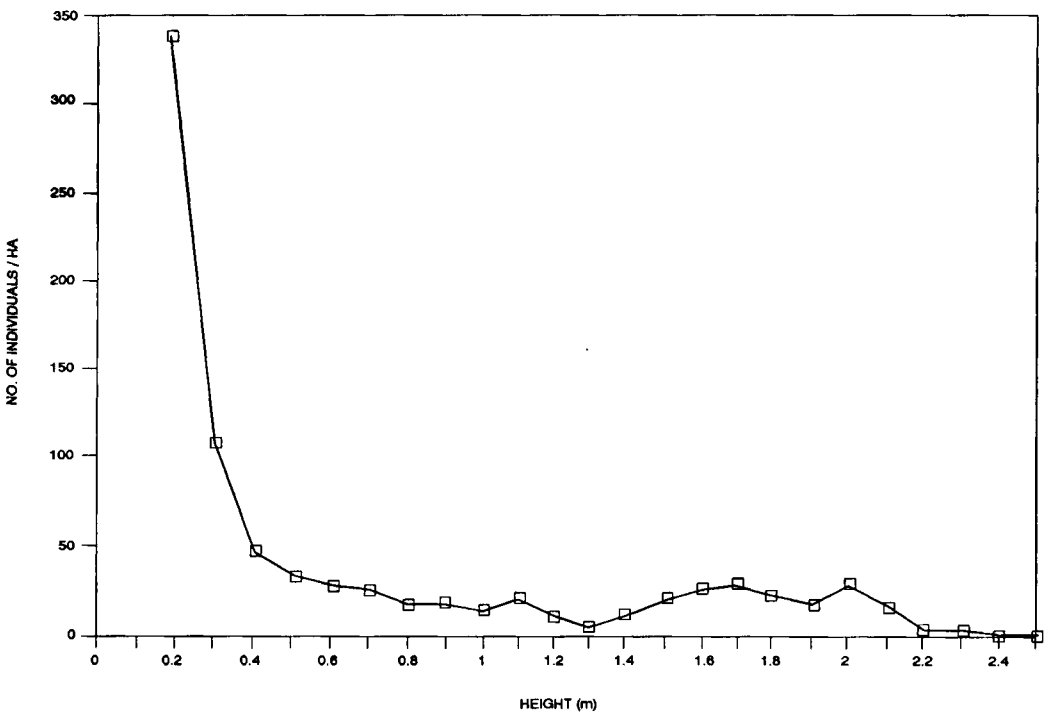

Figure 5. Population structure of kāhili ginger in Thurston area of Hawaii Volcanoes National Park, five years after feral pig removal.

management programs. Yellow Himalayan raspberry (*Rubus ellipticus*), Hilo grass (*Paspalum conjugatum*), meadow ricegrass, strawberry guava, kāhili ginger, firetree, banana poka (*Passiflora mollissima*), and palm grass (*Setaria palmifolia*) are the rain forest invaders of most concern in the Park, once feral pigs are gone.

Nāpau. Nāpau Exclosure, located a little over 0.3 mi (0.5 km) south-southeast of Nāpau Crater in Hawaii Volcanoes National Park, provided information on a remote rain forest area from which pigs had been excluded for 11 years when data were collected. The exclosure was built in 1975, and results to 1980 were reported by Katahira (1980) (based on 9 Braun-Blanquet plots established inside and 12 outside the exclosure). The rain forest in the area is closed-canopy ʻōhiʻa with tree fern (hapuʻu) understory. The exclosure is located in an area that is far removed from many of the plant propagules produced by aggressive alien species in Hawaii Volcanoes National Park.

Although measurable alien plant cover was not recorded inside or outside the exclosure in 1981, it was considerably higher by 1986, especially outside (Table 15). Exposed ground was much greater outside the exclosure in 1981 and 1983, but by 1986 tephra outfall from the ongoing volcanic eruption at Puʻu ʻŌʻō covered a large area inside and outside. Tephra probably was the overriding cause of vegetation changes both inside and outside the exclosure by 1986, including the invasion of Hilo grass, which accounted for most of the alien plant increase. Bryophytes that had begun to recover inside and outside the exclosure by 1983 decreased over the next three years, perhaps as a result of proximity to volcanic emissions. Alien species seemed to play a minor role in this remote area until the tephra outfall, and native species cover that had been slowly increasing seemed to decline over the same period.

Boundary Kīpuka. A natural feral pig exclosure on the East Rift of Hawaii Volcanoes National Park, located less than 0.3 mi (0.5 km) from the top of Puʻu Kamoamoa, was destroyed in 1983 by lava flow and cinder fall from the Puʻu ʻŌʻō eruption series. Unofficially called the Boundary Kīpuka, it probably had experienced only occasional pig use prior to that time because of isolation by rough lava flows and a pig fence that partially protected it. The Kīpuka was a 175-a (71-ha) closed canopy ʻōhiʻa rain forest. Percent cover values from 24 Braun-Blanquet releves in the Kīpuka and 24 in adjacent forest inhabited by pigs indicated that total native species cover was higher in the pig-inhabited forest than in the Kīpuka (Table 16), possibly because of a more closed canopy in the Kīpuka. Native woody plants accounted for a higher percent of cover in the East Rift forest with pigs than in the Kīpuka. Alien thimbleberry (*Rubus rosifolius*) shrubs, although not comprising a large percentage of cover, provided somewhat more cover in the pig-disturbed forest than in the Kīpuka. The Kīpuka contained fewer alien species (three) with measurable percent cover than the adjacent forest (six).

ʻŌlaʻa Tract. ʻŌlaʻa Tract in Hawaii Volcanoes National Park is primarily open canopy ʻōhiʻa rain forest with closed tree fern subcanopy and native-alien woody plant, vine, herb, and grass understory. It is

Table 15. Mean percent cover of alien and native plants in 3 x 5 m Braun-Blanquet relevés inside and outside Nāpau Exclosure, Hawaii Volcanoes National Park, 1981, 1983, and 1986 (ground - 0.5 m stratum).*

Category and Species	October 1981		November 1983		March 1986	
	Inside	Outside	Inside	Outside	Inside	Outside
Native Ferns	0.7	0.3	3.5	1.5	1.0	0.7
Native Grasses	0.2	**	1.6	0.9	0.2	**
Alien Grasses	**	**	1.1	0.5	2.7	9.5
Native Herbs		**		**		**
Alien Herbs		**		0.1		**
Native Woody Plants	0.5	0.1	1.3	2.0	0.4	0.1
Alien Woody Plants			0.1	0.1	0.3	0.4
Bryophytes	1.9	3.2	2.5	7.6	1.9	1.4
Exposed Ground	2.5	44.5	1.4	17.8		0.3
Litter	69.6	26.5	81.9	32.8	43.7	28.6
Tephra					23.8	31.1
Total Cover***	75.4	74.6	93.4	63.3	74.0	72.1
Percent Native Cover	3.3	3.6	8.9	12.0	3.5	2.2
Percent Alien Cover	0.0	0.0	1.2	0.7	3.0	9.9
Number of Native Species	15	25	12	25	10	19
Number of Alien Species	2	4	4	5	3	4

*Sample size = 4 plots inside exclosure, 10 plots outside exclosure.
**Measurable cover, but <0.1% mean.
***Because Braun-Blanquet cover estimates rely on category midpoints, percent cover does not necessarily add to 100.

Table 16. Percent cover of alien and native plants in 3 x 5 m Braun-Blanquet relevés on Boundary Kīpuka and in adjacent East Rift forest, Hawaii Volcanoes National Park, 1982 (ground to 0.5 m stratum).*

Category and Species	Kīpuka	Adjacent Forest
Native Ferns	1.6	1.4
Alien Grasses, Sedges		0.1
Native Herbs	3.3	1.2
Alien Herbs		0.2
Native Woody Plants	2.4	8.3
Alien Woody Plants	2.1	0.7
Bryophytes	15.7	20.4
Exposed Ground	0.2	2.9
Litter	65.9	66.0
Total Cover**	91.2	101.2
Percent Native Cover	23.0	31.3
Percent Alien Cover	2.1	1.0
Number of Native Species	33	34
Number of Alien Species	3	6

*Sample size = 24 plots in Kīpuka, 24 in adjacent forest.
**Because Braun-Blanquet cover estimates rely on category midpoints, percent cover does not necessarily add to 100.

underlain by fertile soils, and pig densities are probably $<20/km^2$ in the large, eastern (10,000 a or 40 km^2) section. The small, western section (320 a or 1.3 km^2) is an open canopy 'ōhi'a rain forest with closed tree fern subcanopy and largely native fern understory. The small section was fenced in 1981, with fence upgrading in August of 1983 and 1984. The small size, disjunctness, and accessibility of the area to hunters have combined to limit pig ingress over the years. Pigs were finally removed from the small section in 1983.

Exposed ground was greater in the pig-inhabited large section in 1982 and 1985 than in the protected small section, but alien plant cover in both the large and small sections was low (Table 17). Native ferns began to recover in the small section but continued to decline in large section plots. The small section plots had more native species than the large section plots, but many more small section plots (28) than large (8) were sampled. The low alien plant cover in the small section is especially low with that in mind, but in 1985, three species of *Rubus (ellipticus, argutus,* and *rosifolius)* were found in plots there that had not been present in 1982. Banana poka, yellow Himalayan raspberry, and blackberry were present in large section plots in 1982; kāhili ginger appeared in

1985. Litter and bryophyte cover seemed to be lower in 1985 than 1981 in both sections.

A recent data set from extensive transects in small section ʻŌlaʻa shows that three species of alien plants continued to increase six years after feral pig removal (Table 18). Kāhili ginger, yellow Himalayan raspberry, and banana poka all showed increases in most size classes. The smallest class (<10 cm) is perhaps not as meaningful because survival is problematical.

Table 17. Percent cover (and standard deviations) of alien and native plants in large and small sections of ʻŌlaʻa Tract, Hawaii Volcanoes National Park, 1982 and 1985 (ground-0.5 m stratum).*

Category and species	ʻŌlaʻa Large Section 1982	ʻŌlaʻa Large Section 1985	ʻŌlaʻa Small Section 1982	ʻŌlaʻa Small Section 1985
Native Ferns	3.9	3.0	2.5	3.9
Alien Ferns	**	**	**	
Native Grasses, Sedges	0.2	0.1	0.3	0.1
Alien Grasses	**		**	
Native Herbs	0.8	0.3	1.4	1.1
Alien Herbs		0.1	**	**
Native Woody Plants	0.6	0.2	1.4	1.1
Alien Woody Plants	0.1	0.5		**
Bryophytes	6.9	3.4	9.4	5.4
Exposed Ground	3.8	2.3	0.7	0.3
Litter	82.2	55.8	77.9	60.9
Logfall		5.6		5.7
Total Cover***	98.5	71.3	93.6	78.5
Percent Native Cover	12.4	7.0	15.0	11.6
Percent Alien Cover	0.1	0.6	0.0	0.0
Number of Native Species	19	27	32	39
Number of Alien Species	5	5	3	4

*Sample size = 28 plots in small section, 8 plots in large section of ʻŌlaʻa Tract.
**Measurable cover, but <0.1% mean.
***Because Braun-Blanquet cover estimates rely on category midpoints, percent cover does not necessarily add to 100.

Table 18. Number of *Hedychium gardnerianum, Rubus ellipticus*, and *Passiflora mollissima* along 30-m wide belt transects in Small Tract 'Ōla'a Tract Special Ecological Area, Hawaii Volcanoes National Park, in 1986* and 1989.

Hedychium gardnerianum (Kāhili ginger)	Height (cm) <10	10-50	50-100	100-155	
1986	820	372	54	20	
1989	324	281	75	47	
Rubus ellipticus (Yellow Himalayan raspberry)	Height (cm) <10	10-50	50-200	200-300	>300
1986	20	82	35	5	2
1989	41	78	43	10	11
Passiflora mollissima (Banana poka)	Height (cm) <10	10-200	>200		
1986	0	0	2		
1989	45	1	11		

*From J.T. Tunison, unpub. data.

Kīpahulu Valley. Anderson *et al.* (this volume) reported on distribution and spread of alien plants in Kīpahulu Valley rain forest above 2,300 ft (700 m) elevation during and subsequent to removal of feral pigs. Methodology will not be reiterated here, but some of the conclusions about alien plants and pigs bear repeating for purposes of this paper.

Based on frequency of occurrence data, the most rapid spread of weeds in the Valley during and after pig removal was a 17% increase in weeds in wet 'ōhi'a forest at 4,300 ft (1,310 m) elevation, probably resulting from a combination of factors, including increased use of newly-established trails by feral pigs, slow growth of uluhe (which had previously dominated the area), and wind and bird dispersal of the invading aliens Maui pāmakani (*Ageratina adenophora*) and thimbleberry.

Lowest weed frequencies were found in areas least disturbed by pigs, mostly at higher elevations. Removal or reduction of pigs did not result in decreased weed occurrence in koa forests at lower elevations that had been considerably disturbed, where sunlight needed for proliferation of alien plants was available, and where propagules of invasive weed species were numerous. Numbers of weed species, and percentage of weed cover in general, increased with decreasing elevation in the Valley.

Life forms of weeds seemed related to elevation, with alien grasses and sedges comprising most of the alien plant cover at lower elevations (3,600 ft or 1,100 m), but alien herbs (less invasive and lower percentage

of cover than grasses) at higher elevations. The native matted fern, uluhe, inhibited alien plant invasions where undisturbed in the Valley, but the native fern hō'i'o (*Diplazium sandwichianum*) was preferred by pigs. Alien plants such as strawberry guava and Hilo grass often invaded pig-disturbed areas once dominated by this fern (Anderson *et al.*, this volume).

Feral pig disturbance was definitely not a prerequisite for invasions of kāhili ginger and strawberry guava in the Valley. Each was found in undisturbed areas, and all continue to spread at present (1989). That recovery of native plants after pig removal is not assured is demonstrated by alien grasses and sedges that still dominate in an exclosure at about 3,000 ft (915 m) elevation, which had been free of pigs for 10 years when last observed. Native shrubs and ground cover have not regenerated in the exclosure (Anderson *et al.*, this volume).

INTACTNESS AND MANAGEABILITY

"Intactness" of a native plant community in Hawai'i can potentially be indexed by the prevalence of invasive alien plants in it. Primary emphasis on alien plants rather than natives is useful, because aliens are the primary targets of management subsequent to feral ungulate removal. Native species richness is an additional piece of information important in setting management priorities. Although such indices are useful, other information is also used in decision-making. Knowledge of rare plant abundance and distribution and community rarity are valuable in making judgements; funding, personnel, and size of an area must be considered; and potential threats posed by particularly invasive alien plant species must also be evaluated and given considerable weight in decision-making.

Percent alien plant cover and native/alien species ratios of some areas considered in this paper are summarized in Table 19 (for grasslands and shrublands) and Table 20 (for rain forests). These intactness indices suggest that low elevation grasslands and at least some accessible (to humans and alien plant propagules) and long-damaged rain forests provide the greatest restoration challenges after ungulate removal. The Fern Jungle rain forest data (14 years without pigs inside the exclosure) suggest that simple protection from pigs may eventually result in near-native forest, but that native species richness may be low after considerable disturbance. Remote, subalpine grasslands and montane parklands may also show important alien components and/or decreased native plant richness with continual disturbance by feral ungulates, as well as higher alien plant cover indefinitely, especially at the lower elevational limits of these types. Adequate recovery of many Hawaiian ecosystems disturbed by ungulates will likely require protection, aggressive and continual alien plant management, considerable recovery time, and some reintroduction of missing native plant species. Long-term damage by ungulates can eliminate native plant species and deplete seed beds, change microclimates as well as water and nutrient systems, and slow growth of many natives. Tolerance of an alien species component in otherwise native communities will also be necessary.

Table 19. Grassland and shrubland intactness as measured by percent cover of alien plants and native/alien species ratios.

Vegetation Type (Locality)	Years w/out Goats*	% Alien Cover	Native/Alien Species Ratio
Scaevola strand (Hawaii Volcanoes Lowlands)	4	0.0	4.0+
Metrosideros/Native shrub (Mauna Loa)	2	0.3	6.0
Metrosideros/Native shrub (Mauna Loa)	2	0.3	9.0+
Subalpine shrub (Mauna Loa)		0.8-6	0.9-3.3
Subalpine shrub (Mauna Loa)	6	1.6-3.6	2.3-2.5
Subalpine shrub (Manawainui)	10	2.0-6.7	3.0-11.0
Deschampsia/Native shrub (Mauna Loa)	2	7.0	1.7
Metrosideros/Native shrub (Hawaii Volcanoes Lowlands)	4	9.0	0.3
Deschampsia grassland (Kalapawili Exclosure)	13	12-17	--
Heteropogon/Rhynchelytrum (Hawaii Volcanoes Lowlands)	4	13.0	0.3
Metrosideros/Native shrub (Hawaii Volcanoes Lowlands)	4	16.0	0.8
Lowland shrub (Hawaii Volcanoes Lowlands)	4	20.6	0.9
Mixed grass (Hawaii Volcanoes Lowlands)	4	29.2	0.4
Lowland shrub (Hawaii Volcanoes Lowlands)	4	39.6	0.7
Rhynchelytrum grassland (Hawaii Volcanoes Lowlands)	4	36.7	0.2
Rhynchelytrum grassland (Hawaii Volcanoes Lowlands)	4	45.3	0.1
Schizachyrium condensatum (Hawaii Volcanoes Lowlands)	4	64.4	0.3
Rhynchelytrum grassland (Hawaii Volcanoes, Kūkalau'ula)	13	71.0-77.4	0.4-0.5
Melinis/Rhynchelytrum (Hawaii Volcanoes Lowlands)	4	73.7	0.2
Hyparrhenia grassland (Hawaii Volcanoes Lowlands)	4	75.0	1.0
Hyparrhenia grassland (Hawaii Volcanoes, Kaone)	15	77.4-81.6	0.3

*See text for ungulate history.

Table 20. Rain forest intactness as measured by percent cover of alien plants and native/alien species ratios in pig-free plots in Hawaii Volcanoes National Park.

Vegetation Type (Locality)	Years w/out Pigs*	Mean % Alien Cover	No. of Native Species (n)	Native/Alien Species Ratio
ʻŌlaʻa (Small Tract)	3	0.0	39 (28)	9.8
Fern Jungle	14	0.8	15 (15)	1.7
Boundary Kīpuka	20?	2.1	33 (24)	11
Nāpau	11	3.0	10 (4)	3.3
Thurston I	4	5.3	17 (7)	1.9
Thurston II	4	22.8**	11 (5)	1.8

*See text for ungulate history.
**Largely meadow ricegrass invasion.

CONCLUSIONS

Feral pigs and goats are major stresses for many Hawaiian ecosystems, and their elimination usually produces beneficial responses, including recovery of native species. However, communities may be considerably simplified through years of ungulate damage, a significant alien component may remain, key alien species may continue to spread, and continued plant management may be required after ungulate removal. Many lowland grasslands subjected to over a century of stress from goats have responded to goat removal with an increase in percent cover of flammable alien grasses, including bush beardgrass (*Schizachyrium condensatum*), broomsedge, molasses grass, and *Hyparrhenia rufa*. Little hope exists that native plants will eventually dominate without more intensive management or biological control. Reintroduction of native species to these areas is a costly but perhaps necessary method to restore them in the future. Lowland shrublands seem less damaged by long-term goat use and retain reasonably low percentages of alien cover; however, native/alien plant species ratios may remain low (< 1.0) even after up to 13 to 15 years of recovery from goat damage. Williams (1990) similarly found rapid recovery of native woody species within a few years after removal of goats in the eastern lowlands of Hawaii Volcanoes National Park.

In subalpine grassland and shrubland where native plant propagules are present and where the still-dominant native bunch grass *Deschampsia* can overtop and crowd out alien grasses and herbs, recovery progresses slowly, but stasis may prevail for the foreseeable future. Velvet grass is perhaps of primary concern after ungulate removal, although stabilization or even decline of this species is known to occur in some areas. Blackberry may also increase in some areas. Subalpine shrublands seem less affected by feral goats in some areas than in others, perhaps because goat densities vary greatly and because, where human access is good, hunting can provide

effective protection for an area from this social ungulate. In montane woodlands, velvet grass and some other alien grasses (*e.g.*, meadow ricegrass) may continue to expand after pig or goal removal.

Responses of vegetation to release from goat damage can be rapid in terms of increased numbers of woody plant seedlings and vegetative reproduction (*e.g.*, koa, *Vaccinium*). However, exposed soil, continuing erosion, and alien grasses will undoubtedly remain in some subalpine and montane parkland areas long after goat removal. Restoring native components that are missing after long abuse may also be a problem.

In Hawaiian rain forests, responses of vegetation to pig removal are varied according to remoteness and presence of especially disruptive alien plants. The most intact (lowest alien cover and numbers of alien plants) rain forests are those rarely or never invaded by pigs and people. Lack of such disturbance may result from remoteness, rugged topography, restricted legal access by humans, or difficulty of penetration into the area. The small section of ʻŌlaʻa Tract and the East Rift zone in Hawaii Volcanoes National Park, together with Kīpahulu Valley in Haleakala National Park, were the most species-rich and least invaded of the rain forest areas considered in this paper. However, some aggressive alien plants remained and/or increased in these and other areas in the absence of feral pigs, over time intervals of 4 to 10 years.

Rain forest areas most accessible to humans and aliens in this study have been much disturbed by feral pigs and much invaded by alien plants. Recovery after four to six years without pigs is not marked. Aggressive alien plants can increase in such areas, especially near ranches or other weedy areas, and adequate forest recovery where weeds have become dominant will probably require active, enduring, and well-supported alien plant management programs.

Further studies of population structures, successional patterns, and competitive advantages of aggressive alien plants in different areas and different climates may eventually help prediction of long-term ecosystem recovery and establishment of effective management strategies for different areas. However, a number of variables influence the recovery of vegetation after feral ungulate removal from an area. These include: the duration, intensity, and frequency of previous ungulate disturbance; the intervals between disturbance events; the vulnerability and palatability of key native plant species in the community; the reproductive mode and dispersability of native plants in the area; the size of the affected area and the proximity to other similar areas; the sources and types of alien plant propagules available; the soil type and condition prior to and after ungulate disturbance; climatic cycles favorable and unfavorable to temporary alien and native plant establishment; ancillary disturbance; and alien and native plant propagule distribution by humans, birds, and other animals.

The variables are too numerous and too uncontrollable to allow definitive cause and effect statements about responses of vegetation due entirely to feral ungulate removal. They also defy predictive approaches,

especially with currently limited databases. Not the least of the problems is lack of knowledge about what plant communities looked like in detail before a century or more of foraging by goats, sheep *(Ovis aries),* and cattle (*Bos taurus*), confounded with more recent impacts caused by pigs, horses (*Equus caballus*), deer (*Odocoileus hemionus* and *Axis axis*), and other ungulates. We conclude that different areas are unique and will continue to require different monitoring and management strategies for alien plants long after ungulate removal.

RECOMMENDATIONS

Increasing our knowledge about the recovery and management potential of Hawaiian ecosystems after feral ungulate removal should receive more emphasis. We need to avoid costly efforts to remove ungulates from heavily invaded areas subject to further deterioration not readily amenable to management. In all vegetation types, losses of native components over time and gain of aliens through the usual colonization/extinction equilibria and through successional stages should be better documented and increasingly considered in management decisions. Size and proximity of vegetation types and dispersal and reproductive capabilities of alien and native plants are also relevant.

More emphasis should also be placed on determining alien plant distribution over wide areas within key ecosystems. We need to better understand the extensive dynamics of aliens for long periods. Exclosures and vegetation plots confined to small areas should be continued but enhanced with more extensive frequency of occurrence and percent cover data.

Continued research and management efforts on monitoring responses of vegetation to release from ungulate damage is needed. More areas should be studied to determine how released areas function with respect to alien plant invasion over time. Generalizations from a few areas are difficult because communities are variable and the complexity of determining factors are numerous and unpredictable. The fact that generalizations may not be possible should not preclude systematic data collection and long-term "management experiments."

Potentially generalizable measures such as "intactness" and "manageability" of invaded ecosystems should be considered further. Although they are no substitute for management judgments, such abstractions can serve as guides and be grasped by administrators. Increased predictability is needed for vegetation responses in relation to proximity of aggressive alien plants, sizes of areas, and other preserve design considerations (Franklin 1985). Cooperative and interactive efforts by natural resource managers and researchers, particularly in obtaining and interpreting monitoring data, will be necessary for a long period to understand the ecology of alien plants and their invasions subsequent to ungulate removal. The elimination of ungulates is but one of a number of important steps in active ecosystem restoration in Hawai'i.

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