

**COOPERATIVE NATIONAL PARK RESOURCES STUDIES UNIT
UNIVERSITY OF HAWAII AT MANOA**

**Department of Botany
3190 Maile Way
Honolulu, Hawaii 96822
(808) 956-8218**

Technical Report 89

**Early Succession in Pig-Disturbed Mountain Parkland
Hawaii Volcanoes National Park**

**J. Timothy Tunison¹, Rhonda K. Loh¹
Linda W. Pratt², Dina W. Kageler³**

**¹ National Park Service
P.O. Box 52
Hawaii Volcanoes National Park, Hawaii 96718**

**² National Biological Survey
P.O. Box 52
Hawaii Volcanoes Park, HI 96718**

**³ P.O. Box 411
Volcano, Hawaii 96785**

**Cooperative Agreement
CA8007-2-9004**

April 1994

TABLE OF CONTENTS

LIST OF FIGURES	ii
ABSTRACT	iii
INTRODUCTION	1
STUDY AREA	1
METHODS	2
RESULTS	3
'A'ali'i/Velvet Grass community	3
<i>Deschampsia</i> -Velvet Grass community	4
<i>Deschampsia</i> , Sweet Vernal Grass community	4
Pukiawe/ <i>Deschampsia</i> community	4
Velvet grass, <i>Deschampsia</i> community	4
DISCUSSION.....	5
Recovery of Grasses	5
Woody Plants	6
CONCLUSIONS AND RECOMMENDATIONS.....	7
LITERATURE CITED	9
Appendix 1: Changes in Percent Cover of Plant Species in Five Plant Communities	22

LIST OF FIGURES

1. Map of Hawai'i Volcanoes National Park showing study area on Mauna Loa.....	10
2. Location of study sites on Mauna Loa, Hawai'i Volcanoes National Park	11
3. Change in percent cover in the 'A'ali'i/Velvet Grass community, 1985-1992	12
4. Change in woody plant densities in the 'A'ali'i/Velvet Grass community, 1985-1992.....	13
5. Change in percent cover in the <i>Deschampsia</i> -Velvet Grass community, 1986-1992.....	14
6. Change in woody plant densities in the <i>Deschampsia</i> -Velvet Grass community, 1986-1992.....	15
7. Change in percent cover in the <i>Deschampsia</i> , Sweet Vernal Grass community, 1985-1992.....	16
8. Change in woody plant densities in the <i>Deschampsia</i> , Sweet Vernal Grass community, 1985-1992	17
9. Change in percent cover in the Pukiawe/ <i>Deschampsia</i> community, 1985-1992	18
10. Change in woody plant densities in the Pukiawe/ <i>Deschampsia</i> community, 1985-1992.....	19
11. Change in percent cover in the Velvet Grass, <i>Deschampsia</i> community, 1985-1992.....	20
12. Change in pukiawe densities in the Velvet Grass, <i>Deschampsia</i> community, 1985-1992.....	21

ABSTRACT

Prior to their eradication in 1987, feral pigs (*Sus scrofa*) were a common source of ground disturbance in the mountain parkland ecosystem of Hawai'i Volcanoes National Park, especially in grasslands. In 1985-1986, 27, 2 × 5 m plots were established in 9 open, grassy sites recently damaged by pigs. No pig digging occurred after the plots were initially established. The purpose of monitoring vegetation changes was to evaluate the efficacy of pig control in promoting community recovery and to detect any changes that might need further management intervention. Percent cover of plants was determined by point-intercept methods, and woody plants were counted in height classes in 1985, 1986, 1987, 1989, and 1992. The 27 plots were stratified into 5 plant communities based on a Braun-Blanquet analysis of surrounding vegetation, and successional changes were graphed. *Deschampsia nubigena*, a native bunchgrass, consistently increased in cover in most communities where it was originally a dominant or codominant species in surrounding vegetation. It did not increase in cover where it was initially a minor component. These trends suggest that *Deschampsia* will continue to increase in importance. Velvet grass (*Holcus lanatus*), the main competitor with *Deschampsia* in mid and upper elevation sites, recovered rapidly at first but generally declined from its maximum cover after 2-4 years. However, *Holcus* cover may be stable at upper elevation sites where it was dominant prior to disturbance. In lower and mid elevation sites, *Holcus* species may continue to decline in importance, while other alien grass species, e.g., sweet vernal grass (*Anthoxanthum odoratum*) and beardgrass (*Schizachyrium condensatum*), show signs of becoming more abundant. There was some recruitment of native shrubs in the disturbed areas, especially at lower elevations. Koa (*Acacia koa*), a root-sprouting, clonal tree in the study area, invaded many sites. The continued expansion of koa colonies may, at least locally, be more ecologically important than competition between *Deschampsia* and alien grasses.

INTRODUCTION

Feral pigs (*Sus scrofa*) are the major ungulate modifiers of Hawai'ian forests in this century (Stone 1985). Pigs selectively deplete native plant species, disturb soil, create openings, and disperse weed seeds (Stone 1985, Stone and Loope 1987). Prior to control, they were a common source of ground disturbance in the mountain parkland plant communities of Hawai'i Volcanoes National Park (HAVO), especially in grassy, open sites (Mueller-Dombois and Bridges 1981). In this environment, pigs were responsible for the displacement of native bunchgrasses and the spread of alien grasses (Spatz and Mueller-Dombois 1975). They found that alien grasses immediately invaded disturbed sites, and speculated that continued high levels of feral pig activity would result in the eventual loss of native grasses. They also hypothesized that removal of feral pigs may lead to the possible replacement of alien grasses by native grasses. The expected continued decline of native grasses and the possibility of native plant recovery motivated managers to begin control of pigs in 1984. By 1987, pigs were eradicated on Mauna Loa within the Park's Mauna Loa Strip between 1200 m and 2100 m elevation (Katahira *et al.* 1993).

Introduced ungulates have disturbed Mauna Loa since the mid-nineteenth century. Cattle (*Bos taurus*) were the main disturbance factors in the nineteenth and early twentieth century (Baldwin and Fagerlund 1943, Cuddihy 1984). With the removal of cattle in 1948, feral goats (*Capra hircus*) and pigs became important vegetation modifiers (Spatz and Mueller-Dombois 1975). Feral goat numbers were reduced by the National Park Service in the 1960's to approximately 500 individuals (Mueller-Dombois 1967), further reduced in the 1970's (Katahira and Stone 1982), and finally eradicated in the early 1980's (Katahira, pers. comm.). Cattle and goats affect woody plants, particularly regeneration of koa (*Acacia koa*), whereas feral pigs affect grasslands and do not inhibit root suckering, the most important mode of reproduction for koa on the Mauna Loa Strip (Spatz and Mueller-Dombois 1973).

This report documents 7 years of vegetation recovery in mountain parkland sites on Mauna Loa disturbed by feral pigs until 1985 but since protected. It thus addresses the capacity of these plant communities to recover, the potential benefits of feral pig control in the restoration of the native vegetation in this environment, and requirements of additional management.

STUDY AREA

The study area lies within Hawai'i Volcanoes National Park on the east flank of Mauna Loa, Island of Hawai'i, between 1400 m and 1950 m elevation (Fig. 1). Substrates are mostly pahoehoe covered by a layer of ash 1-25 cm deep. The climate is shaped by an inversion layer associated with trade wind weather and a leeward location. These factors result in decreasing rainfall upslope and a distinct summer-dry climate. Precipitation ranges from 1100-1600 mm/year. The mean air temperature is 12-17°C., and the mean daily temperature range is 10°C. (Mueller-Dombois and Fosberg 1974, Spatz and Mueller-Dombois 1973).

The vegetation has been characterized as mountain parkland (Mueller-Dombois and Fosberg 1974), a complex mosaic of koa forest, native shrublands, and grasslands, with open 'ohi'a (*Metrosideros polymorpha*) woodlands on young lava flows. Koa stands are rapidly expanding due to prolific root suckering following the removal of cattle and feral goats (Spatz and Mueller-Dombois 1973). The understory is largely grass with locally abundant native shrubs. Native shrublands are dominated with closed to open stands of pukiawe (*Styphelia tameiameia*) and 'a'ali'i (*Dodonaea viscosa*). Grasslands are dominated at lower elevations by alien grasses, but native bunchgrasses increase with elevation and dominate above 1600 m elevation (Mueller-Dombois and Bridges 1981). At lower elevations velvet grass (*Holcus lanatus*), dallis grass (*Paspalum dilatatum*), and sweet vernal grass (*Anthoxanthum odoratum*) are the primary alien grass species. *Deschampsia nubigena*, a native bunchgrass, is a minor component. *Deschampsia* increases in cover with elevation and dominates upper elevation grasslands, although velvet grass is abundant in some sites. The native bunchgrass, mountain pili (*Panicum tenuifolium*), always more abundant under tree cover, follows a pattern similar to that of *Deschampsia*.

METHODS

Pig-disturbed areas were located by Park Service hunters during control efforts in 1985 and 1986. These sites were almost always less than 25 m², and several pig-disturbed areas occurred in the same vicinity. Eighteen 2 × 5 m plots were established at 6 sites in 1985, and 9 additional plots were established at 3 other sites in 1986 (Fig. 2). Plots were not established in areas with continued pig disturbance or disturbed by pigs. All plots were located in sites in open areas dominated by grasses or grass with scattered shrubs or short koa root suckers. The plots were read within 30-60 days of disturbance, and subsequently at 1, 2, 3, 4, and 7 years. No disturbance was known to have occurred after the initial reading. One plot could not be relocated after the initial reading.

Ten, 2 m long transects were placed 0.5 m apart in each 2 × 5 m plot, and the 2 m edges of the plots were also utilized as transects. Cover along transects was sampled with a 1.25 m tall point-frame with five points per meter. Attached dead vegetation was counted as live to minimize seasonal effects. All woody plants within the 2 × 5 m plots were counted in the following height classes: 0-10 cm, 10-100 cm, 100-200 cm, and > 200 cm. Diameter at breast height (1.3 m) of trees taller than 2 m was measured.

Plots within some of the sites varied in soil depth, microtopography, and proximity to encroaching koa stands. Therefore, the plots were stratified using a Braun-Blanquet analysis of surrounding vegetation with similar site features. A synthesis table was prepared, and similar stands were subjectively grouped by the tabular comparison method (Mueller-Dombois and Ellenberg 1974). Five plant communities were derived by this method (Table 1) and used in data analysis.

Table 1. Plant communities and plot locations (also see Fig. 2).

PLANT COMMUNITY	SITE #	PLOT #	ELEVATION (M)
'A'ali'i/Velvet Grass	1	A,B,C	1400
	2	A,B,C	1450
<i>Deschampsia</i> -Velvet Grass	7	A,B,C	1475
	8	A,B,C	1450
	9	A,B,C	1450
<i>Deschampsia</i> , Sweet Vernal Grass	3	A,B,C	1500
	4	A,B,C	1550
Pukiawe/ <i>Deschampsia</i>	5	C	2000
	6	A,B	2000
Velvet Grass, <i>Deschampsia</i>	5	A,B	2000
	6	C	2000

The slash symbol between plant names separates dominant species in shrub and grass layers. The dash indicates codominants in a single vegetation stratum. The comma indicates two species in the same layer, the first as the dominant species, the second as the subdominant.

RESULTS

'A'ali'i/Velvet Grass community

This plant community, located at the lower elevational limits of the mountain parkland, is dominated by alien grasses, especially velvet grass, dallis grass, and orchard grass (*Dactylis glomerata*). *Deschampsia* is present but not abundant. The native shrubs 'a'ali'i and pukiawe are scattered to abundant, and koa has begun to invade some sites.

Alien grasses recovered rapidly after disturbance, and their total cover increased consistently over the 7-year period of the study (Fig. 3, Appendix I). Cover of velvet grass, dallis grass, and orchard grass mostly declined after 2 years, concurrent with increasing abundance of rattail grass (*Sporobolus africanus*) and beardgrass (*Schizachyrium condensatum*). Cover of the native grasses, *Deschampsia* and 'emoloa (*Eragrostis variabilis*), varied from sampling period to sampling period with essentially no net increase in 7 years. 'A'ali'i and bracken fern (*Pteridium aquilinum*), also minor components, increased consistently in cover. Bracken fern is seasonal in cover because it dies back to rootstock in the winter months.

There was a low level of seedling recruitment of 'a'ali'i in the first year of recovery; some of these grew into juvenile shrubs (Fig. 4). Pukiawe seedlings were first detected after 2 years.

***Deschampsia*-Velvet Grass community**

This plant community consists of small grasslands dominated by *Deschampsia* and velvet grass. A wide mixture of alien grasses, primarily dallis grass, sweet vernal grass, broomsedge (*Andropogon virginicus*), and beardgrass, are also present, along with scattered native shrubs. These plots were first sampled in 1986.

Alien grasses recovered rapidly in the first 2 years (Fig. 5, Appendix 1). Velvet grass was the dominant species but had a small decline in cover after 1987. The less abundant sweet vernal grass and rattail grass, as well as *Deschampsia*, steadily increased in cover.

Koa invaded plots in Site 7 adjacent to koa stands (Fig. 6). There was little change in densities of pukiawe, small plants of which were present in very low numbers. 'A'ali'i seedlings became established in the disturbed site but disappeared by 1992.

***Deschampsia*, Sweet Vernal Grass community**

These grasslands, located in gaps in koa stands, are dominated by *Deschampsia*. The most consistently found alien grasses, sweet vernal grass and velvet grass, occur at low cover. Koa root suckers are invading many sites in this community.

Alien grasses recovered to stable levels after 2 years (Fig. 7, Appendix 1). Sweet vernal grass became the dominant alien grass species, codominant with *Deschampsia*. Velvet grass increased rapidly in the first 2 years and declined steeply thereafter. Cover of meadow ricegrass (*Ehrharta stipoides*) increased and dallis grass decreased in plots with encroaching koa. *Deschampsia* cover increased slightly and very gradually over 7 years. Mountain pili, a native bunchgrass, occurred at very low cover in Site 4.

Koa root suckers invaded almost all plots (Fig. 8). 'A'li'i became established in Site 3. There was a very low level of seedling recruitment of pukiawe in Site 4, and some recruitment from seedlings into young plants.

Pukiawe/*Deschampsia* community

This community consists of individuals and small stands of pukiawe within a matrix of *Deschampsia* at the upper elevational limits of mountain parkland. Alien velvet grass and native mountain pili are minor components.

Deschampsia recovered steadily from 1985-1989 (Fig. 9, Appendix 1). Mountain pili first appeared in 1987 and increased slightly in cover. Velvet grass was not found in the plots until 1989 and decreased slightly in cover by 1992.

Koa root suckers proliferated in the plots (Fig. 10). There was also pukiawe seedling recruitment in some years, but little recruitment of seedlings into larger size classes.

Velvet Grass, *Deschampsia* community

This community is also found at the upper elevational limits of the mountain parkland, primarily in microsites which probably have greater soil depth. Velvet grass dominates these sites, with *Deschampsia* slightly less abundant. Mountain pili is a minor component.

Velvet grass recovered rapidly to high cover values (Fig. 11, Appendix 1). *Deschampsia* cover fluctuated with probably no net increase from 1985-1992. Mountain pili appeared 2 years after disturbance and increased slightly over the next 5 years. There was almost no seedling recruitment of woody plants into the plots (Fig. 12)

DISCUSSION

Recovery of Grasses

The focus of this vegetation monitoring study was the interaction of native and alien grasses in early successional stages, anticipating the eventual recovery of native grasses. No comparable control plots (where pig disturbance continued) could be established, and predisturbance data were not available nor could they be inferred from surrounding areas. All sites with ash soil in the mountain parkland have undoubtedly been disturbed by pigs, probably many times. Therefore, vegetation surrounding the plots probably represents varying stages of recovery, rather than undisturbed or predisturbed conditions. Without comparative data and knowledge of a hypothetical successional end-point, the analysis focused on trends apparent in the first 7 years of recovery.

Grass cover generally stabilized after 1-2 years in communities dominated by alien grasses and after 2-4 years in communities dominated by native grasses. This finding is consistent with the perception that some alien species are relatively fast growing and aggressive colonizers of disturbed sites (Baker 1965). In 1992, there was a slight decline in percent cover for many species relative to 1989. The years 1988 and 1989 were average to wet years; late 1991 and early 1992 were very dry. The plots were last sampled during this dry period.

Based on one year's observation of natural and artificially disturbed sites, mostly in the upper mountain parkland where *Deschampsia* and velvet grass are the main competitors, Spatz and Mueller-Dombois (1975) hypothesized the eventual displacement of *Deschampsia*, given continued high levels of pig disturbance. They also speculated about the possible replacement of velvet grass by *Deschampsia*, following control of pigs. They observed that velvet grass appeared to establish more readily in disturbed and open soil, especially during wet, cool periods. Velvet grass rapidly invaded artificially disturbed sites where it was previously dominant, and velvet grass and *Deschampsia* equally invaded sites where hairgrass was previously dominant. Jacobi (1981 and pers. comm. in Stone et al. 1992) found some confirmation of these predictions in subalpine *Deschampsia* grasslands in Haleakala National Park. *Deschampsia* cover was slightly greater inside an enclosure after 11 years, and velvet grass cover was slightly greater outside. In extensive belt transects outside the enclosure, Jacobi found stable levels of *Deschampsia* but increasing cover of velvet grass.

The study sites in the current investigation were distributed throughout the mountain parkland zone. *Deschampsia* and velvet grass were present in all sites, abundant in most, and were the main competitors at high elevation. However, alien grasses other

than velvet grass were abundant at lower and mid elevation sites, confounding an interpretation of *Deschampsia*/velvet grass competition throughout the mountain parkland.

The recovery patterns of native grass and alien grass after pig eradication are consistent in most sites with the hypotheses of Spatz and Mueller-Dombois (1975) about long term succession. However, *Deschampsia* appears to increase in cover in a consistent manner only in communities where its cover was apparently high prior to disturbance, as suggested by high cover in the surrounding plant community. In the highest elevation sites similar to those studied by Spatz and Mueller-Dombois (1975) and Jacobi (1981), *Deschampsia* increased where it was the dominant grass species, in the pukiawe/*Deschampsia* community (Fig. 9). Velvet grass unexpectedly became established in the protected site after 4 years. *Deschampsia* cover changed little where velvet grass was the dominant species in the Velvet Grass, *Deschampsia* community (Fig. 11). Velvet grass increased uniformly but *Deschampsia* cover varied over time without a consistent trend.

Cover of *Deschampsia* increased in some mid-elevation sites (*Deschampsia*-Velvet Grass community) (Fig. 5). However, it increased only slightly, if at all, in other mid-elevation sites (*Deschampsia*, Sweet Vernal Grass community), even though it was the single most abundant grass species (Fig. 7). In this plant community, recovery of *Deschampsia* may have been inhibited by the encroachment of koa, which appears to favor the more shade-tolerant meadow ricegrass, sweet vernal grass, and mountain pili (Tunison, unpublished data). Total alien grass cover is stable or declining slightly in recovering mid-elevation plant communities, with a complex pattern of increasing and decreasing cover of several alien grass species.

Deschampsia did not increase in the lowest elevation sites ('A'ali'i/Velvet Grass community) where it was a relatively minor component (Fig. 3). Spatz and Mueller-Dombois (1975) found that pig digging had little effect on native grass abundance in their low elevation site.

Increasing cover of *Deschampsia* in communities in which *Deschampsia* is a dominant, codominant, or abundant plant is understandable. Pig digging may leave vestigial bunches that can recover vegetatively, and *Deschampsia* seed sources are available in the surrounding areas. The proportion of *Deschampsia* attributable to vegetative recovery versus seedling recruitment was not determined in this study. However, Spatz and Mueller-Dombois (1975) report numerous *Deschampsia* seedlings after scalping and digging.

Woody Plants

Pukiawe, 'a'ali'i, and koa became established in all plant communities. Pukiawe was the least invasive of the three species, with only a very low level of seedling recruitment in 2 plant communities and possibly relictual young plants in 2 others. There was relatively modest seedling establishment of 'a'ali'i in 4 of the 5 plant communities, with recruitment into juvenile stages in 3 of these communities. Establishment of these shrubs was greatest at lower elevation in the 'A'ali'i/Velvet Grass community. Shrubs were less successful in becoming established in the upper elevation communities.

Koa suckers invaded all but the velvet grass-dominated community at higher elevations. Grasslands tend to be small in the mountain parkland, and many plots were located adjacent to expanding koa colonies. Root suckering is viewed by Spatz and Mueller-Dombois (1973) to be at unnaturally high levels due to the past disturbance of feral goats and their removal. Mueller-Dombois and Krajina (1968) found koa stands to be expanding at the rate of 0.5-2.5 m/yr. The expansion of koa will undoubtedly affect the composition of grasslands, possibly more than recovery from feral pig damage. At lower elevation, koa understories tend to be dominated by meadow ricegrass. At mid and upper elevations, mountain pili and *Carex wahuensis* appear to be correlated with koa, whereas *Deschampsia* is eliminated by expanding colonies (Tunison unpublished data).

CONCLUSIONS AND RECOMMENDATIONS

Based on recovery patterns of the last seven years, some tentative predictions may be offered.

- 1) *Deschampsia* will continue to recover in sites where it was apparently a dominant or codominant plant species prior to disturbance. This trend indicates the effectiveness of pig control in stimulating the recovery of native grassland communities. However, *Deschampsia* shows little sign of becoming more important in sites in which it is a minor component of the surrounding plant community, such as lower elevation mountain parkland or upper elevation sites dominated by velvet grass. On the other hand, *Deschampsia* does not appear to be in a danger of being displaced where it is a minor component.
- 2) There is no indication that velvet grass and other alien grasses will be eliminated by pig removal. Although velvet grass is declining in some sites at mid and lower elevations, other alien grasses, e. g. sweet vernal grass, meadow ricegrass, appear to be spreading. Velvet grass shows little signs of declining in high elevation sites where it was abundant prior to disturbance.
- 3) The continued spread of koa colonies will, at least locally, be more ecologically important than the competition between *Deschampsia* and alien grasses.

The plots should be monitored in the future at 2-5 year intervals. Grass populations in the monitoring plots have not reached a stable state. Many species continue to show clear upward or downward trends. Native shrubs are showing increasing signs of becoming established, and koa is noticeably encroaching most sites.

No weed management actions are recommended, largely for practical considerations. Possible candidates for management are velvet grass, meadow ricegrass, and sweet vernal grass. These species are widespread and abundant, making control over broad areas impractical or unfeasible. Even if limited control were implemented, managers must be certain about the successional role of these species and their impacts on the dynamics of native plant communities. The current study provides only a short-term understanding.

Although control of velvet grass at upper elevations may permit reestablishment of *Deschampsia*, this action is not needed. *Deschampsia* is the dominant grass at upper elevations, and although velvet grass is stable in the sites it dominates, it does not appear to be expanding at upper elevations. Longer term successional trends may favor the eventual reestablishment of *Deschampsia* which is very abundant at upper elevations and recovered well in pig disturbed sites in which it was formerly dominant. Meadow ricegrass and sweet vernal grass appeared to be continuing to expand in mid-elevation sites, a process possibly associated with the spread of koa colonies. The effects of these species on the dynamics of native plant communities are not understood. Native grasses appear to be holding their own so far, at least in the relatively open sites investigated in the current study.

LITERATURE CITED

- Baker, H. G. 1965. Characteristics and modes of origin of weeds. *In* the genetics of colonizing species, H.G Baker and G.L. Stebbins (editors), pp. 147-172. Academic Press, Inc. New York.
- Baldwin, P. H. and G.O. Fagerlund. 1943. The effects of cattle grazing on koa reproduction in Hawai'i National Park. *Ecology* 24:118-122.
- Cuddihy, L. J. 1984. Effects of cattle grazing on the mountain parkland ecosystem, Mauna Loa, Hawai'i. Technical Report No. 51 University of Hawai'i, Cooperative National Park Resources Studies Unit. 135 pp.
- Jacobi, James D. 1981. Vegetation changes in a subalpine grassland in Hawai'i following disturbance by feral pigs. Technical Report No. 41. University of Hawai'i, Cooperative National Park Resources Studies Unit. 23 pp.
- Katahira, L. K., P. Finnegan, and C. P. Stone. 1993. Eradicating feral pigs in montane mesic habitat at Hawai'i Volcanoes National Park. *Wildlife Society Bulletin* 21:269-274.
- Katahira, L. K., and C. P. Stone. 1982. Status of management of feral goats in Hawai'i Volcanoes National Park. *In* Proceedings of the fourth conference in natural sciences, Hawai'i Volcanoes National Park, pp. 102-108.
- Mueller-Dombois, D. and F. R. Fosberg. 1974. Vegetation map of Hawai'i Volcanoes National Park. Technical Report No. 4. University of Hawai'i, Cooperative National Park Resources Studies Unit. 44 pp.
- Mueller-Dombois, D. and K. W. Bridges. 1981. Spatial distribution of island biota. *In* D. Mueller-Dombois, K. W. Bridges, and H. L. Carson (editors) *Island ecosystems: biological organization in selected Hawaiian communities*, pp. 35-59. Hutchinson Ross Pub. Co.
- Mueller-Dombois, D. and H. Ellenberg. 1974. *Aims and Methods of Vegetation Ecology*. John Wiley & Sons. 547 pp.
- Mueller-Dombois, D., and V. J. Krajina. 1968. Comparison of east flank vegetation on Mauna Loa and Mauna Kea, Hawai'i. *In* Proceedings of the symposium on recent advances in tropical ecology. pp. 508-520.
- Spatz, G. and D. Mueller-Dombois. 1973. The influence of feral goats on koa tree reproduction in Hawai'i Volcanoes National Park. *Ecology* 54 (4):870-876.
- Spatz, G. and D. Mueller-Dombois. 1975. Succession patterns after pig digging in grassland communities on Mauna Loa, Hawai'i. *Phytocoenologia* 3(2/3):346-373.
- Stone, C. P. 1985. Alien animals in Hawai'i's native ecosystems: toward controlling the adverse effects of introduced vertebrates. *In* C.P. Stone and J.M. Scott (editors) *Hawai'i's terrestrial ecosystems: preservation and management*, pp. 251-288. University of Hawai'i Cooperative National Park Resources Studies Unit. Univ. Hawai'i Press, Honolulu.
- Stone, C. P., and L. L. Loope. 1987. Reducing negative effects of introduced animals on native biotas in Hawai'i: what is being done, what needs doing, and the role of national parks. *Environmental Conservation* 14(3):245-257.
- Stone, C. P., L. W. Cuddihy, and J. T. Tunison. 1992. Responses of Hawai'iian ecosystems to removal of feral pigs and goats. *In* C.P. Stone, C.W. Smith, and J.T. Tunison (editors) *Alien plant invasions in native ecosystems of Hawai'i: management and research*, pp. 666-704. University of Hawai'i Cooperative National Park Resources Studies Unit. University of Hawai'i Press, Honolulu.

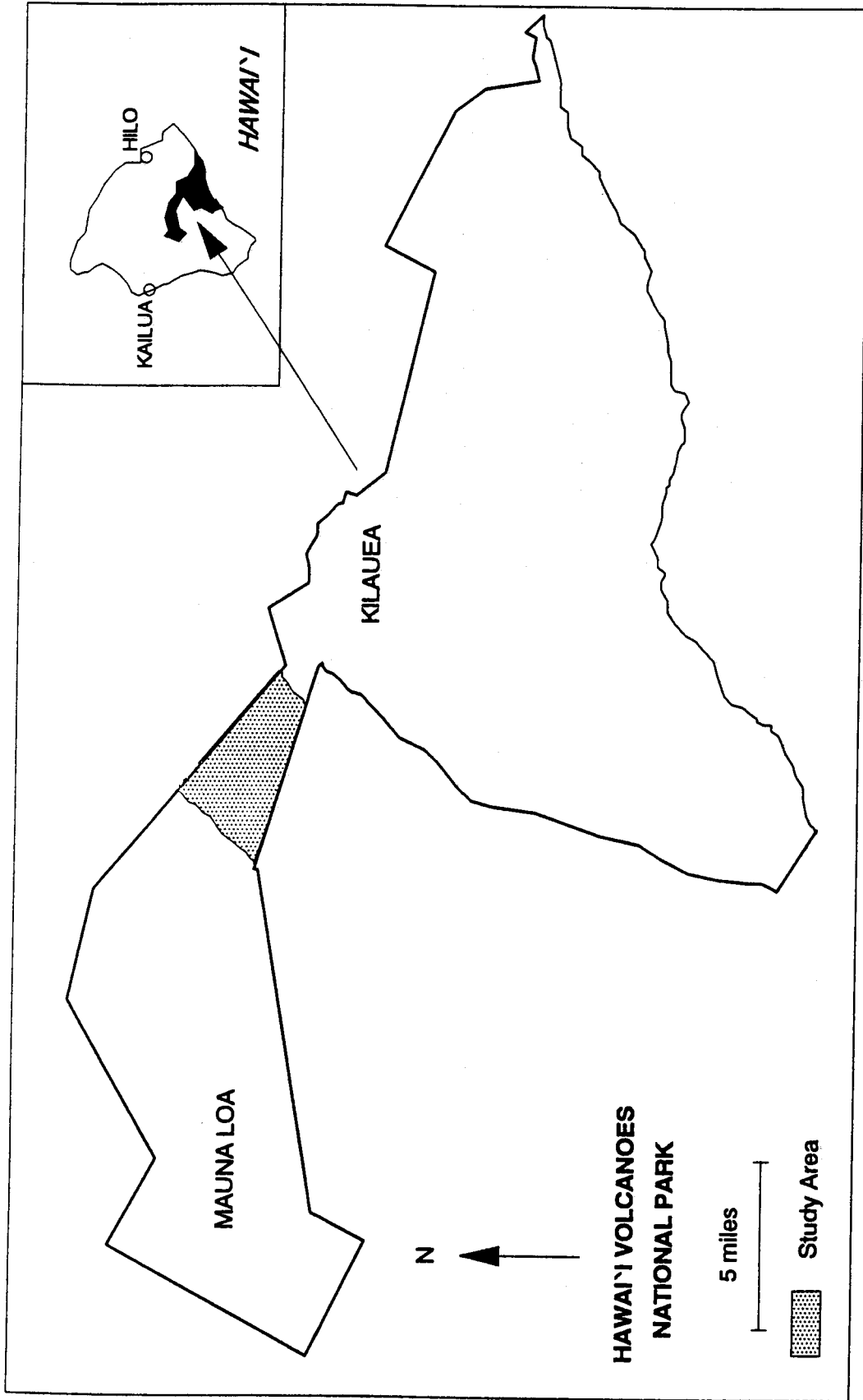


Figure 1. Map of Hawaii's Volcanoes National Park showing the study area on Mauna Loa.

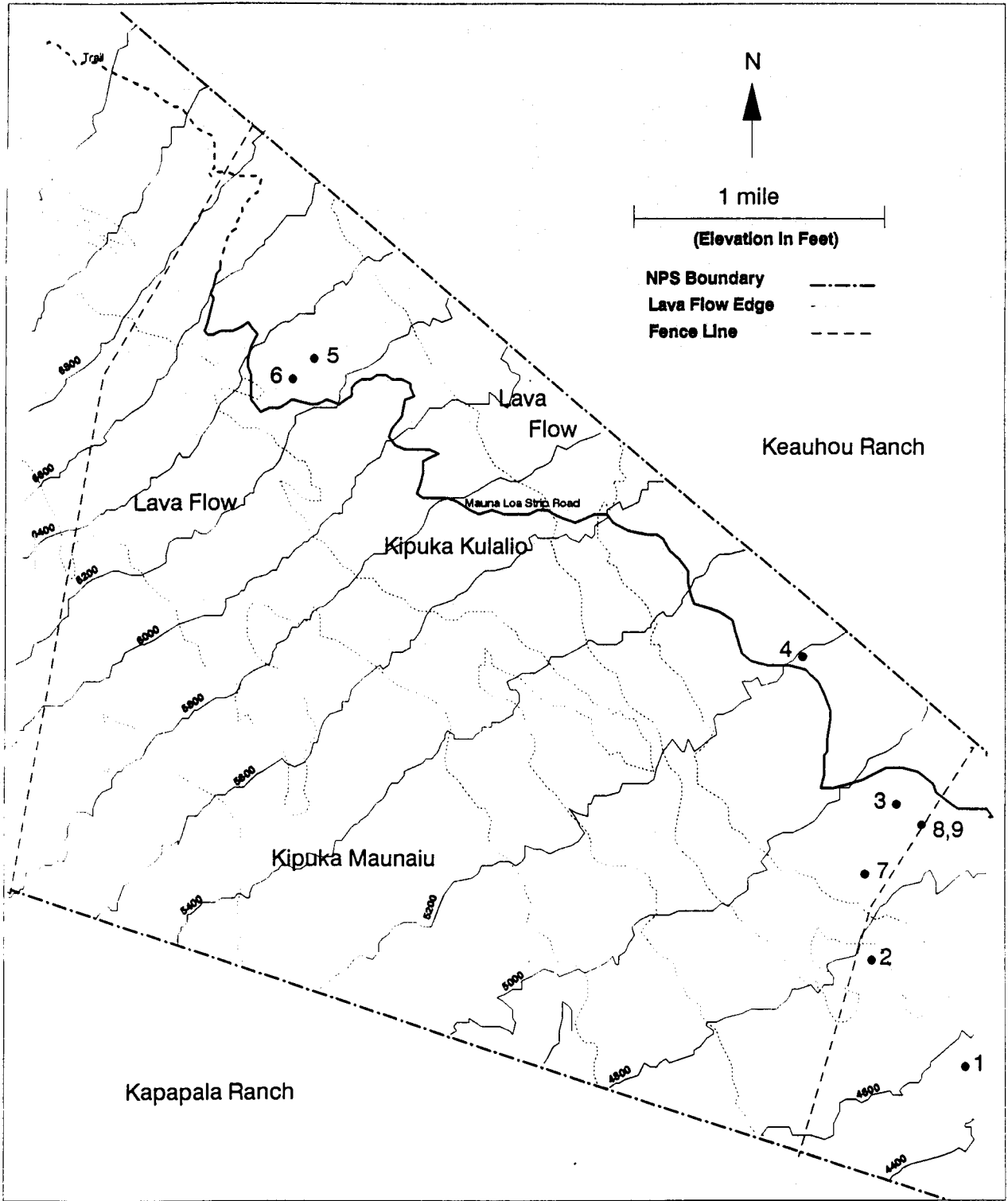
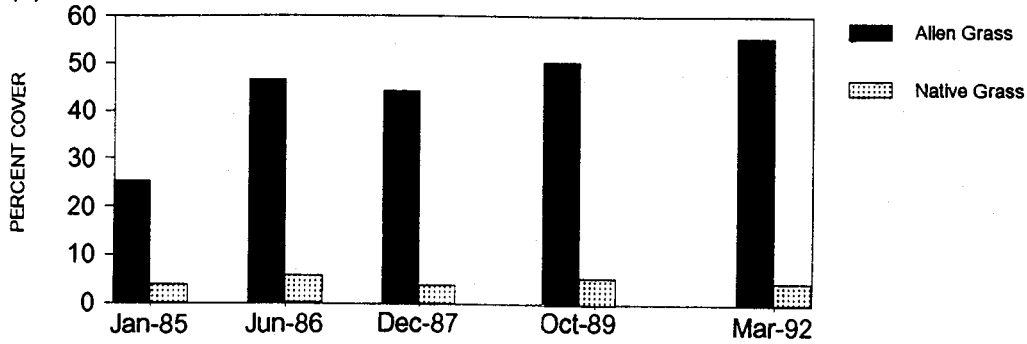
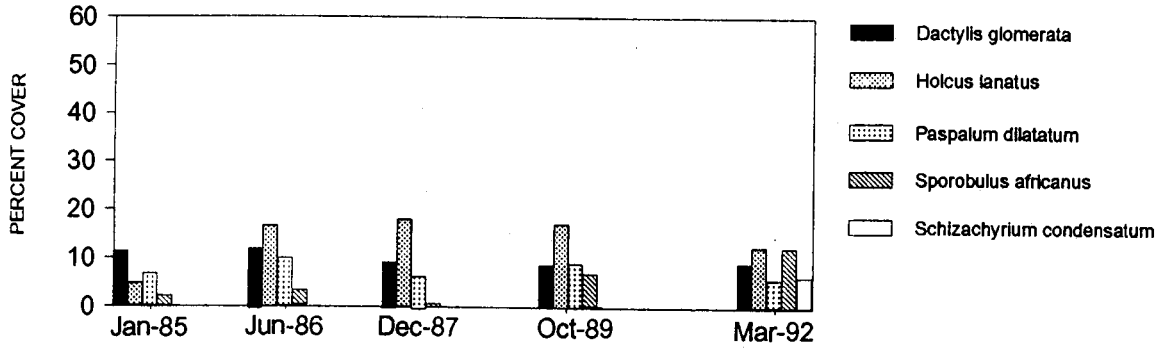


Figure 2. Study sites on Mauna Loa, Hawaii Volcanoes National Park.

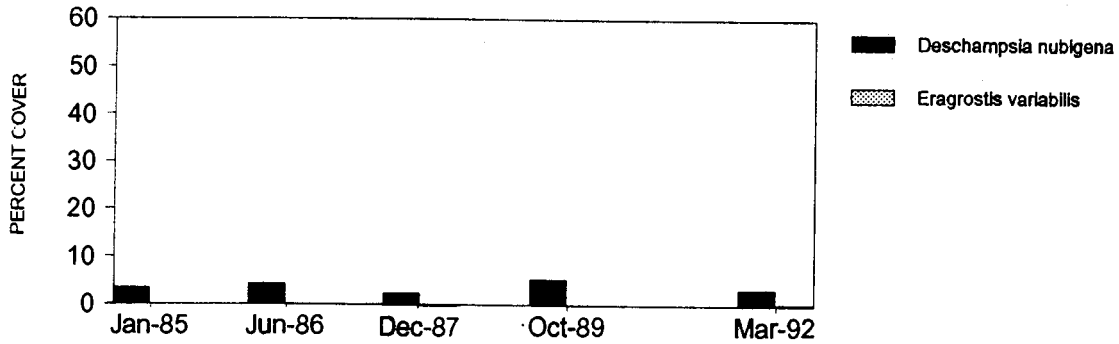
(a) Alien and Native Grasses



(b) Alien Grasses



(c) Native Grasses



(d) Native Herbs and Shrubs

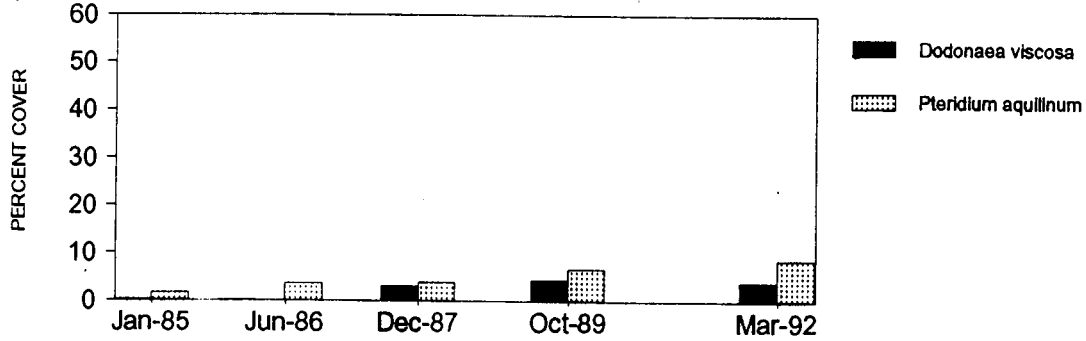


Figure 3. Change in percent cover in the 'A'ali'i/Velvet Grass community, 1985-1992.

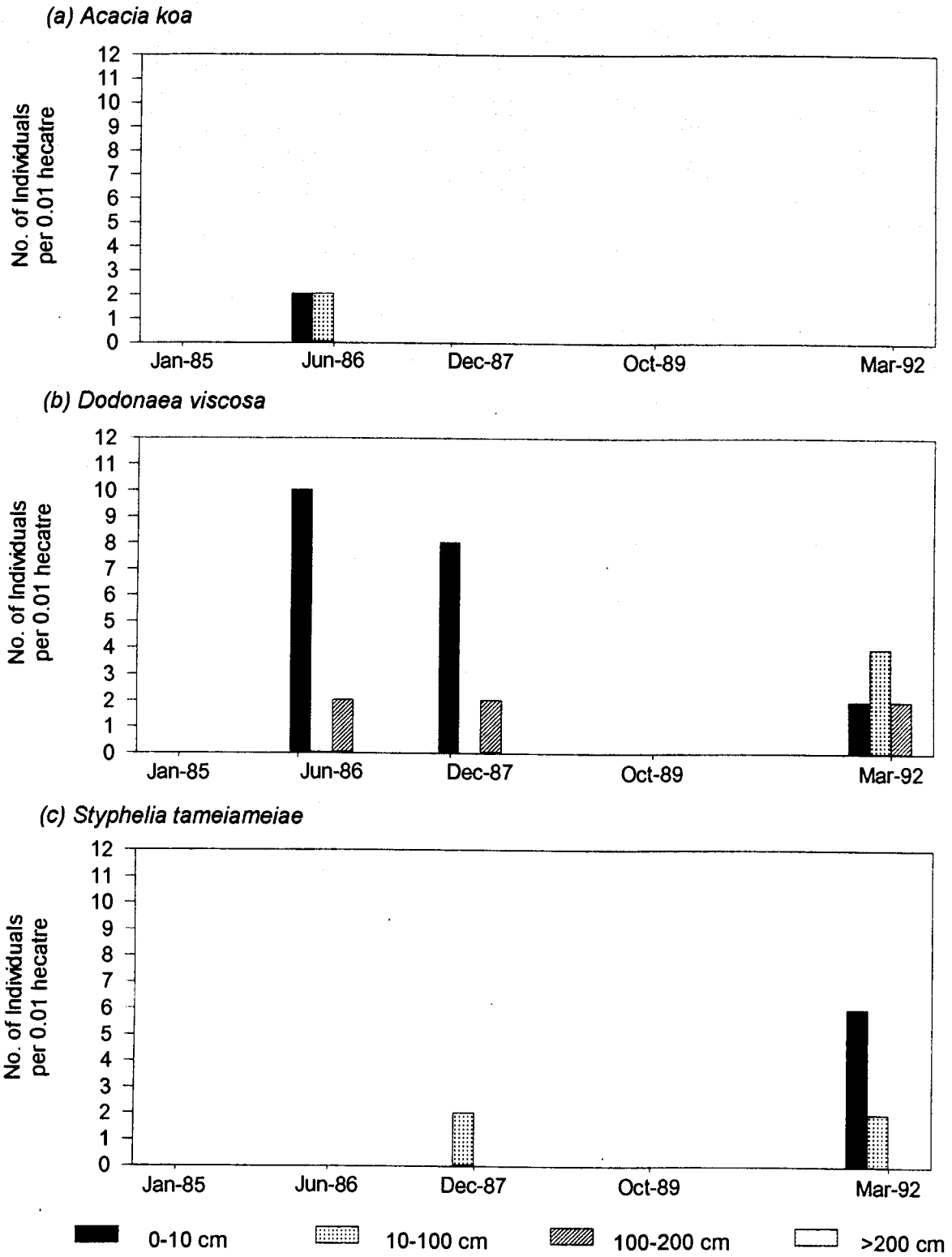
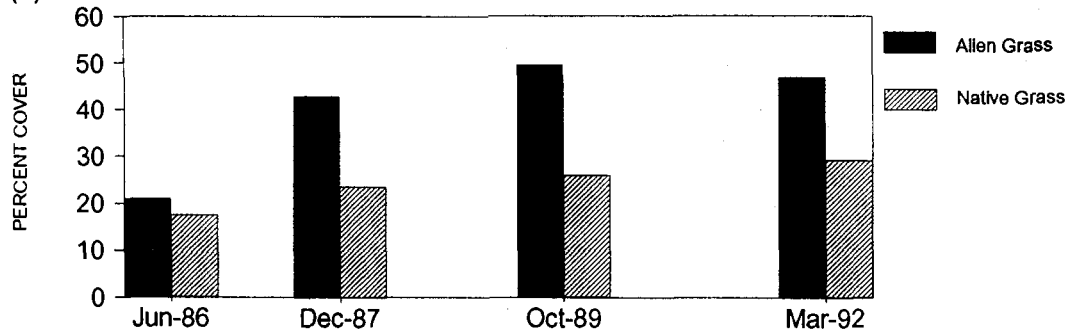
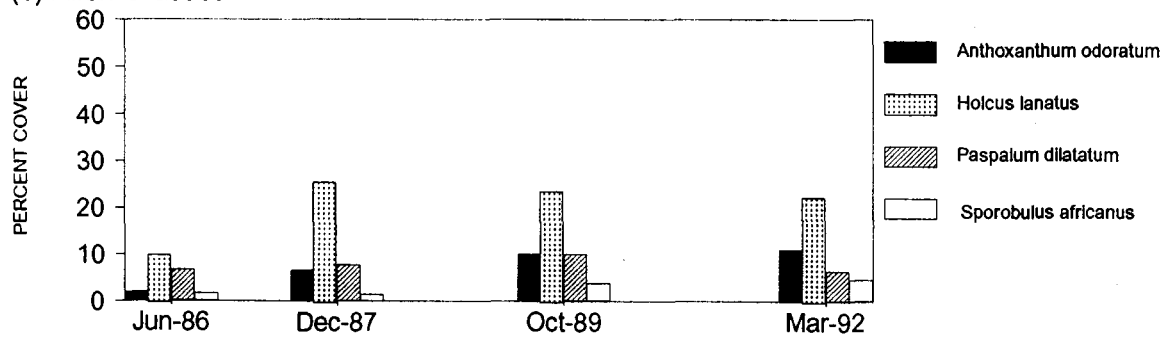


Figure 4. Change in Woody plant densities in the 'A`ali`i/Velvet Grass community, 1985-1992.

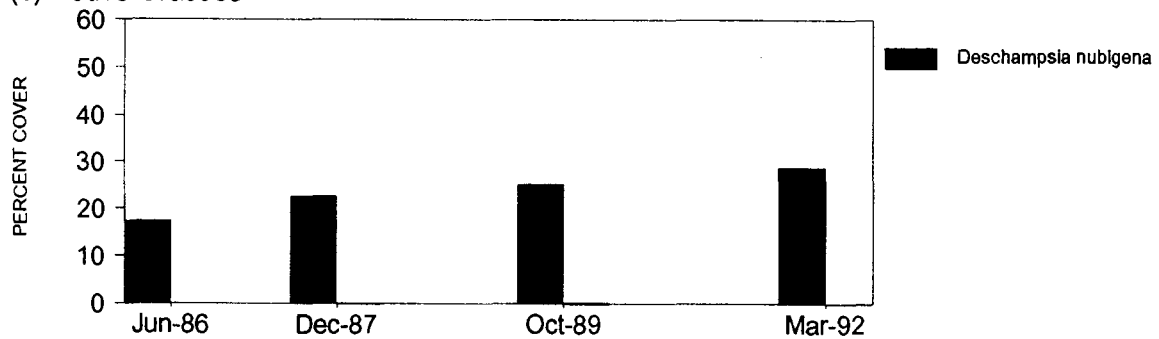
(a) Alien and Native Grasses



(b) Alien Grasses



(c) Native Grasses



(d) Native Herbs and Shrubs

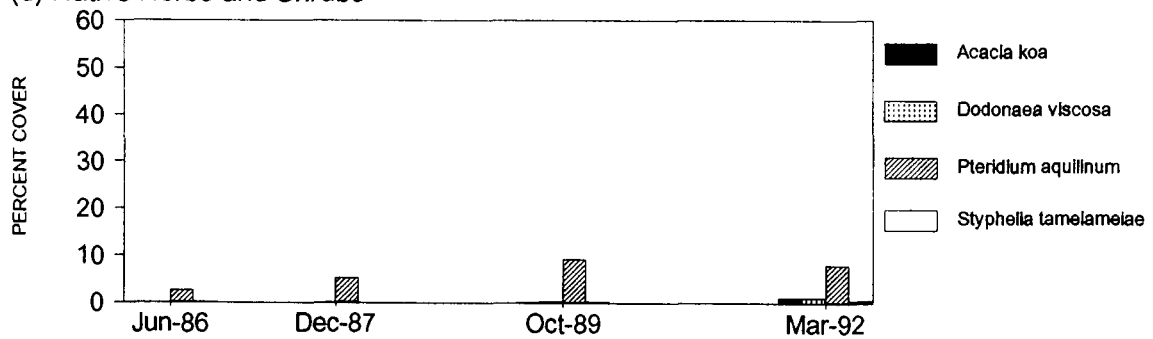


Figure 5. Change in percent cover in the *Deschampsia*-Velvet Grass community, 1985-1992.

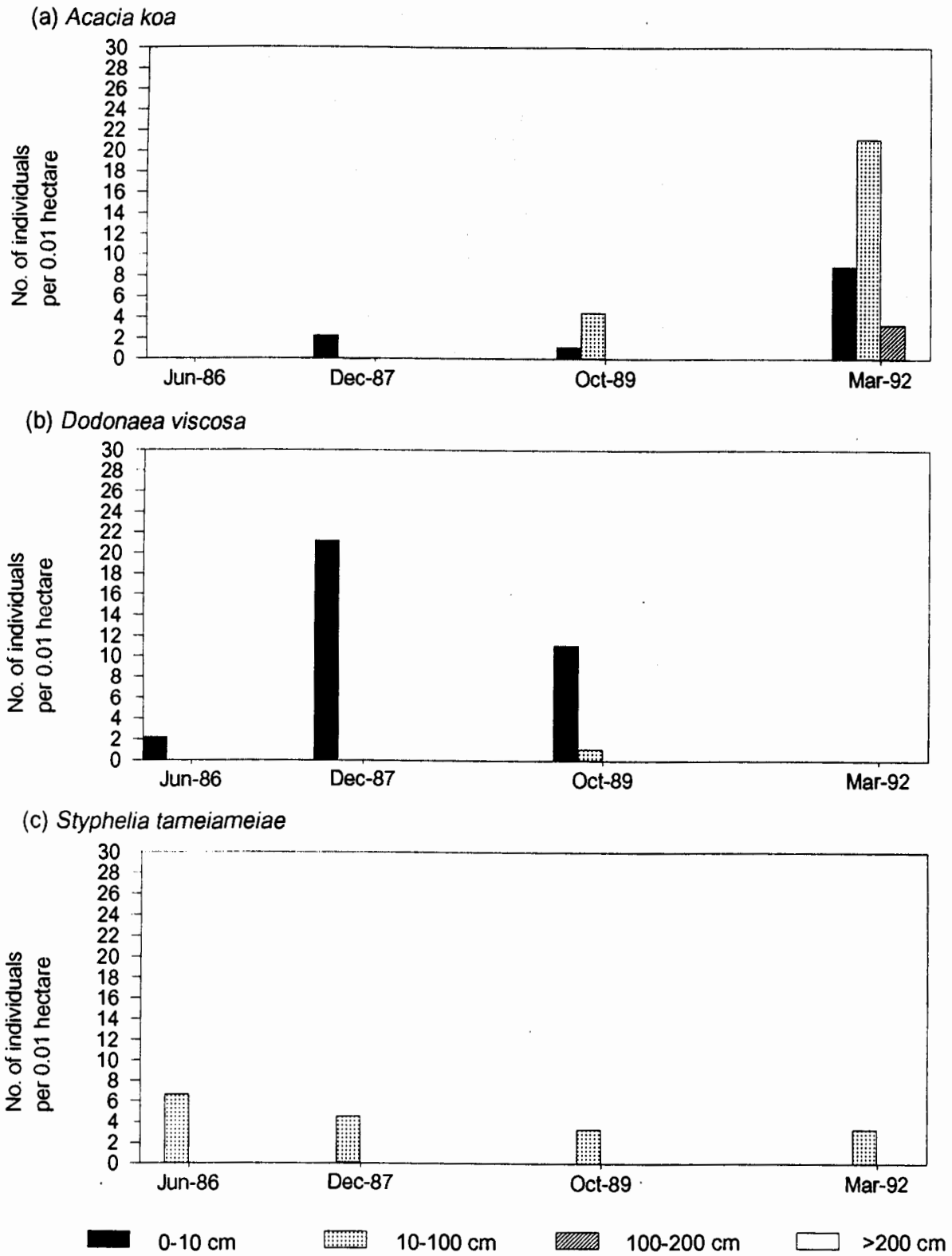
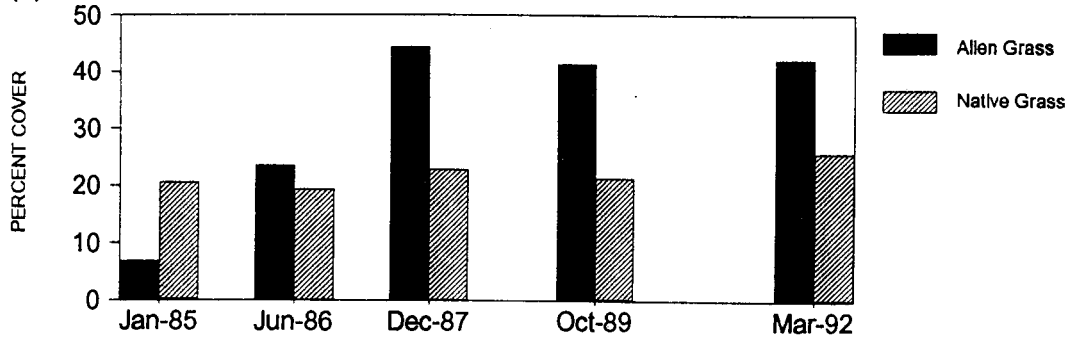
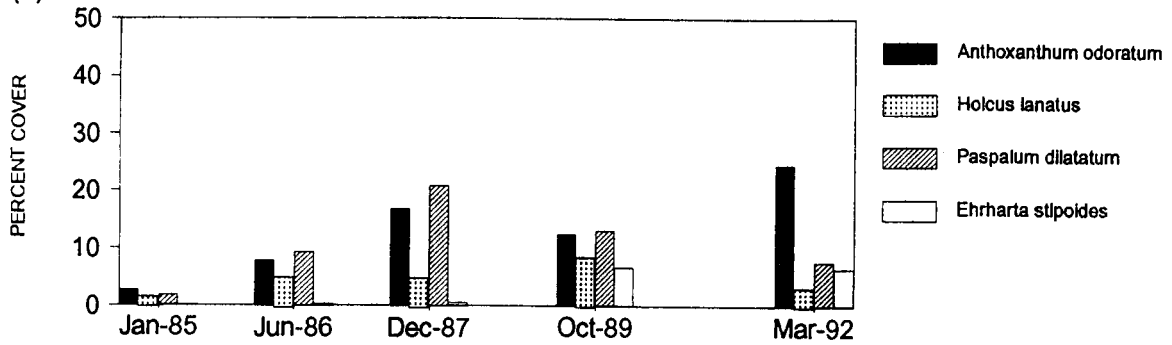


Figure 6. Change in woody plant densities in the *Deschampsia*-Velvet Grass community, 1986-1992.

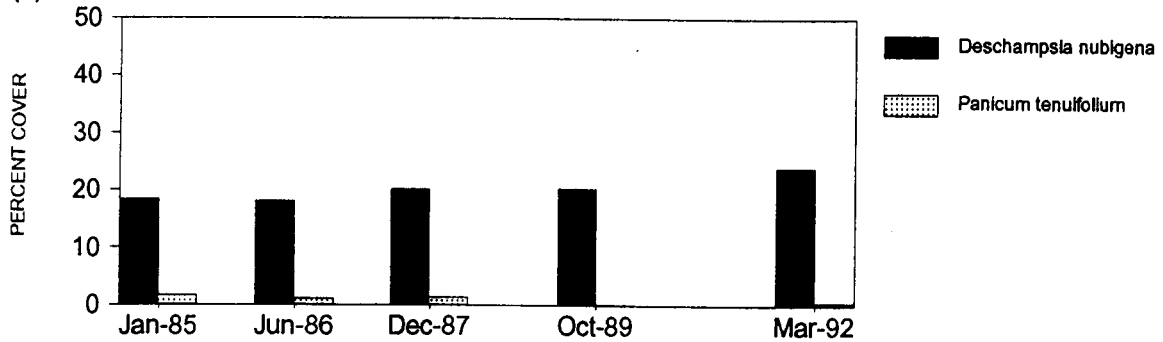
(a) Alien and Native Grasses



(b) Alien Grasses



(c) Native Grasses



(d) Native Herbs and Shrubs

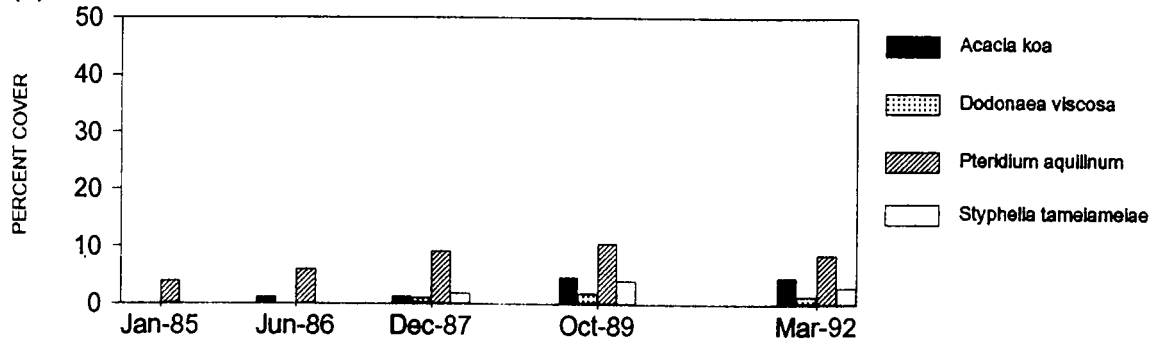


Figure 7. Change in percent cover in the *Deschampsia*, Sweet Vernal Grass community, 1985-1992.

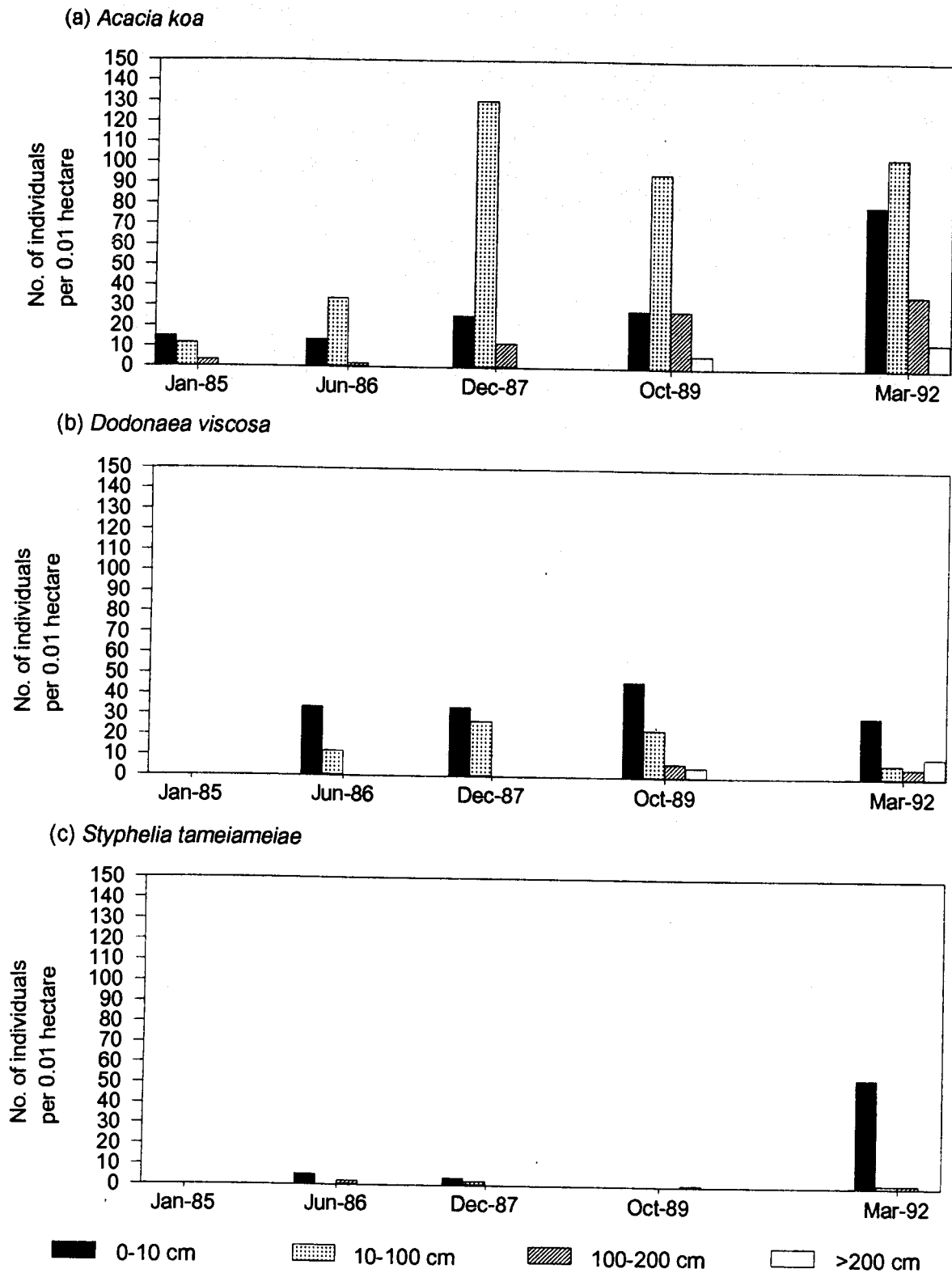
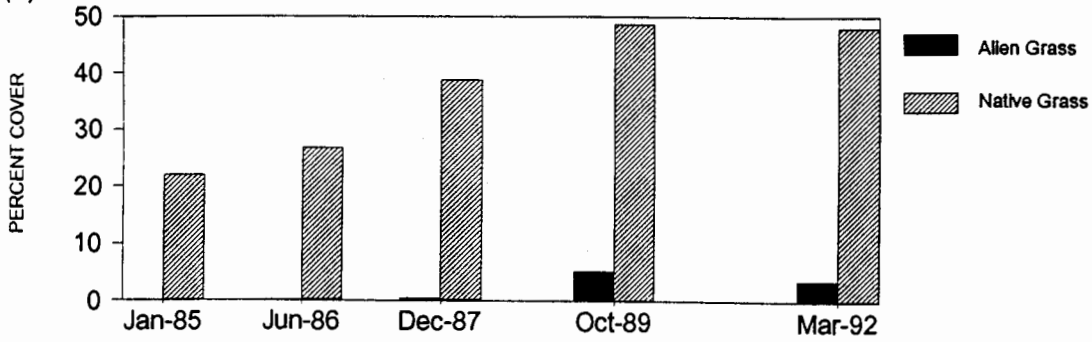
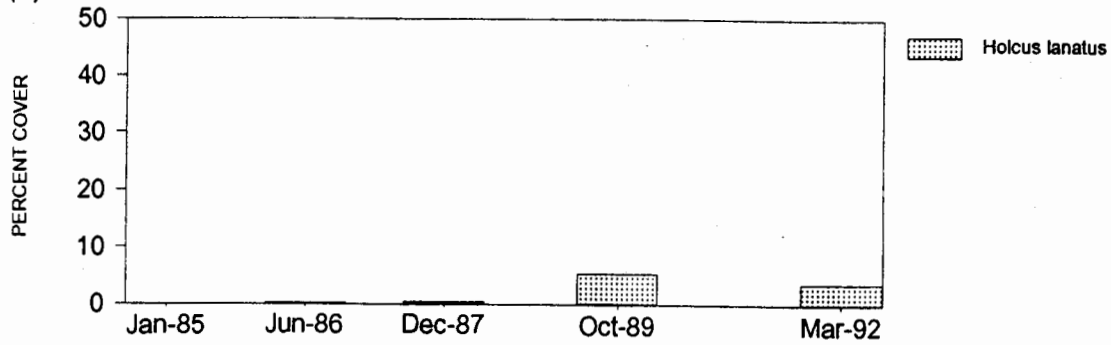


Figure 8. Change in woody plant densities in the *Deschampsia*, Sweet Vernal Grass community, 1985-1992.

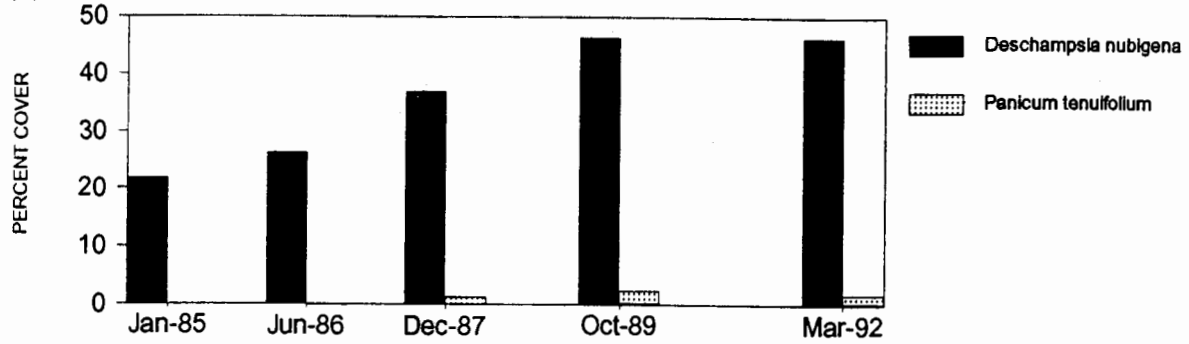
(a) Alien and Native Grasses



(b) Alien Grasses



(c) Native Grasses



(d) Native Herbs and Shrubs

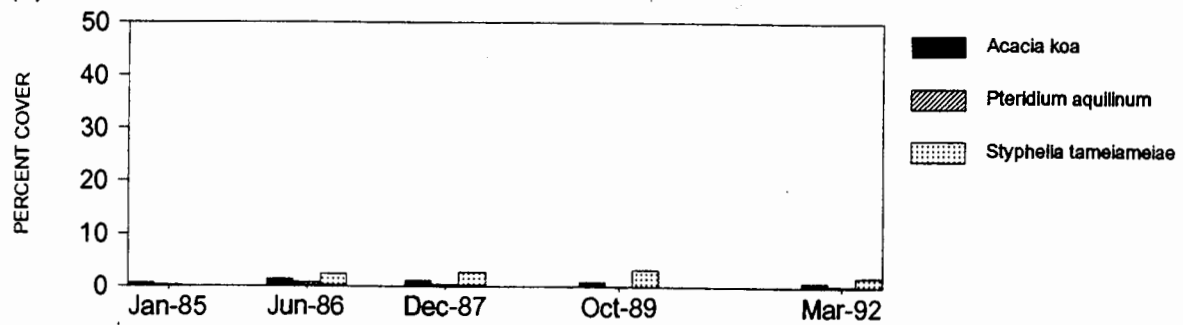


Figure 9. Change in percent cover in the Pukiawe/*Deschampsia* community, 1985-1992.

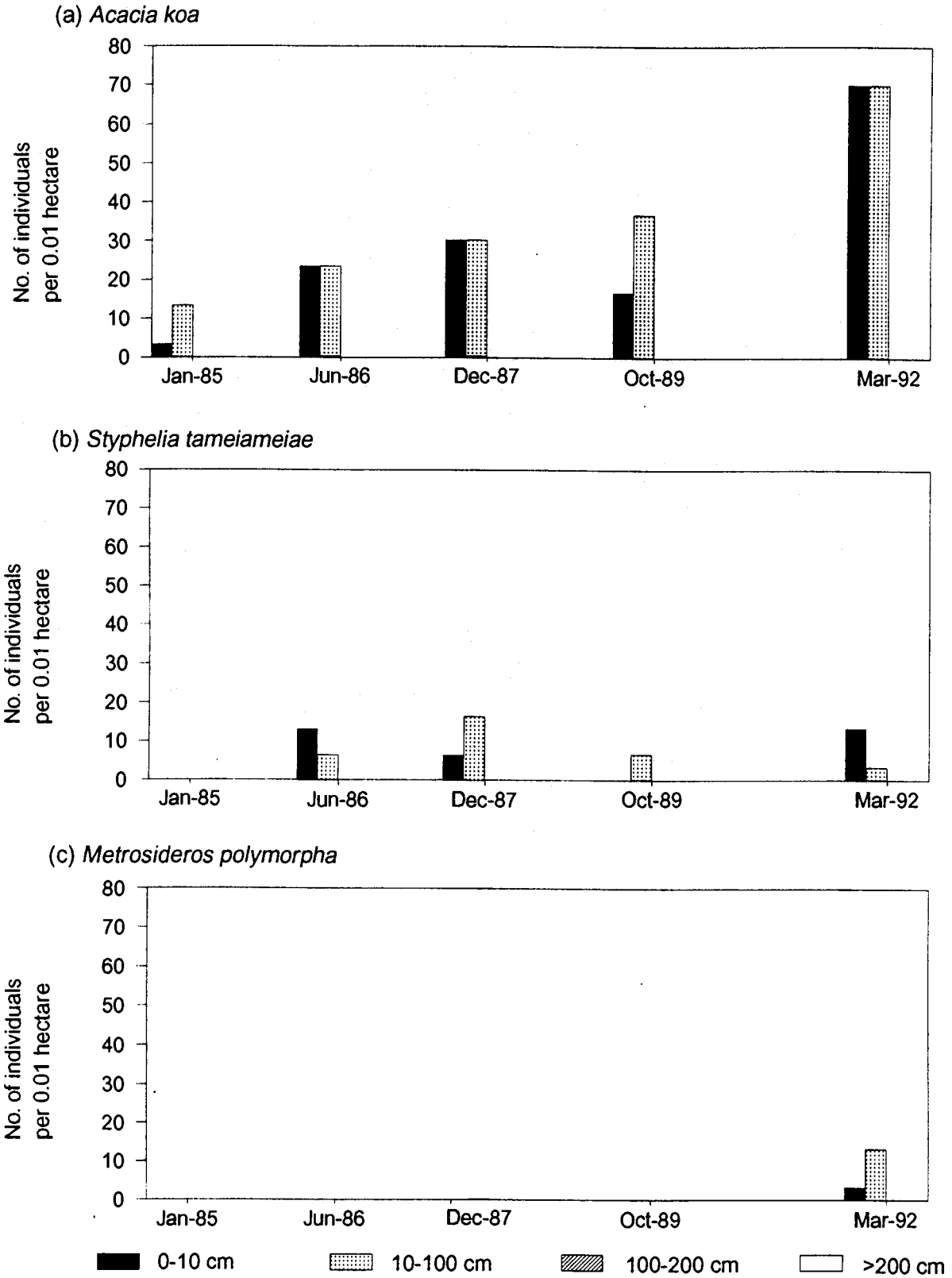
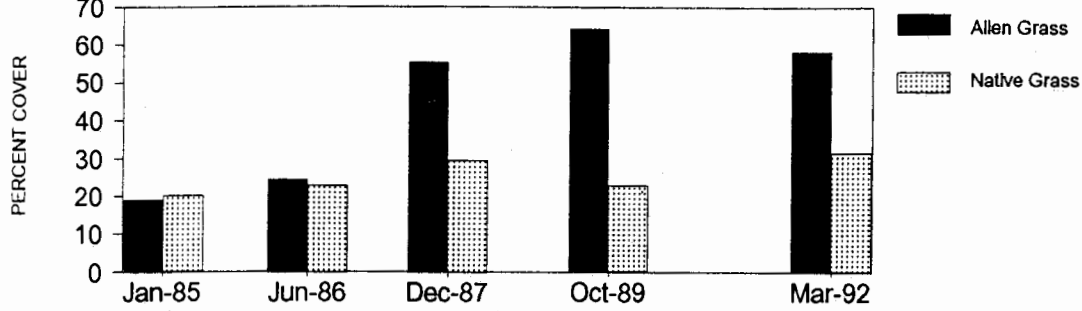
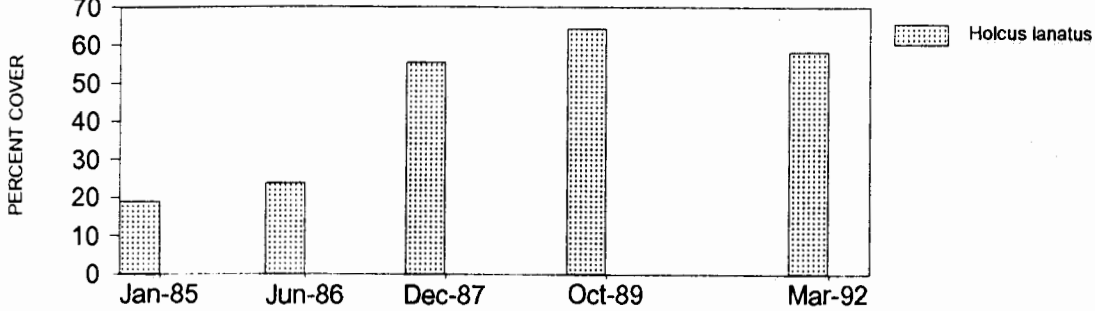


Figure 10. Change in woody plant densities in the Pukiawe/*Deschampsia* community, 1985-1992.

(a) Alien and Native Grasses



(b) Alien Grasses



(c) Native Grasses

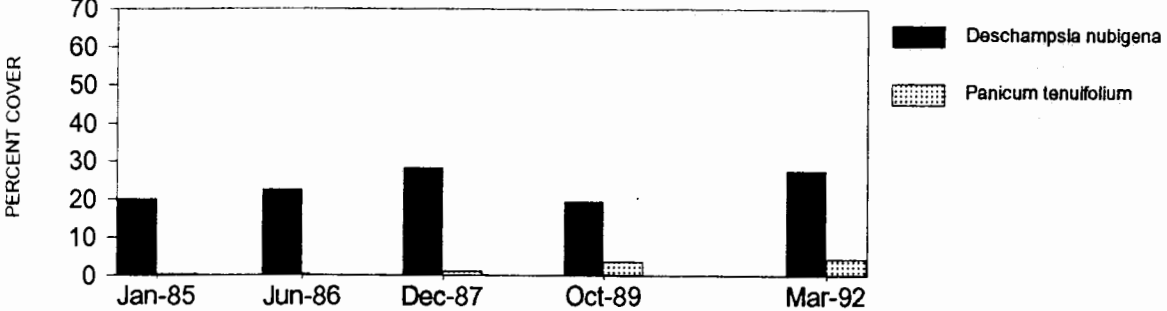


Figure 11. Change in percent cover in the Velvet Grass, *Deschampsia* community, 1985-1992,

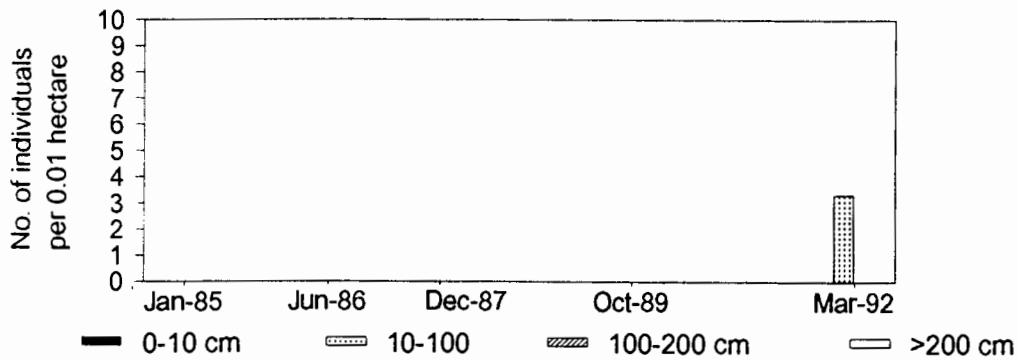


Figure 12. Change in pukiawe densities in the Velvet Grass, *Deschampsia* community, 1985-1992

Appendix I. Change in percent cover of plant species in five plant communities.

Table 1. Change in percent cover in the 'A'ali'i/Velvet Grass community, 1985-1992.

	Mean %Cover				
	1985	1986	1987	1989	1992
<i>Andropogon virginicus</i>	0.0	0.0	0.0	1.2	1.0
<i>Anthoxanthum odoratum</i>	0.2	3.2	8.4	5.6	5.6
<i>Dactylis glomerata</i>	11.3	12.5	9.4	9.0	9.2
<i>Holcus lanatus</i>	4.7	16.8	18.2	17.4	12.6
<i>Microlaena stipoides</i>	0.0	0.0	0.0	0.0	0.0
<i>Paspalum dilatatum</i>	6.8	10.2	6.8	9.2	5.8
<i>Rynchelytrum repens</i>	0.2	0.5	0.6	1.2	2.6
<i>Schizachyrium condensatum</i>	0.0	0.2	0.2	0.2	6.4
<i>Sporobolus africanus</i>	2.2	3.2	0.8	6.8	12.4
Total Alien Grasses	25.3	46.5	44.4	50.6	55.6
<i>Anagallis arvensis</i>	0.0	0.3	0.0	0.0	0.0
<i>Centaureum erythraea</i>	0.0	0.0	0.0	0.4	0.0
<i>Hypochoeris radicata</i>	1.2	5.0	3.8	2.4	1.4
<i>Plantago lanceolata</i>	2.8	6.5	4.8	11.8	6.0
<i>Rumex acetosella</i>	0.0	0.7	0.0	0.0	0.0
<i>Veronica plebeia</i>	0.2	0.2	0.0	0.0	0.0
Total Alien Herbs	4.2	12.7	8.6	14.6	7.4
<i>Lythrum maritimum</i>	0.0	0.3	0.4	2.2	3.2
<i>Rubus argutus</i>	0.0	0.0	0.0	0.0	0.0
Total Alien Shrubs	0.0	0.3	0.4	2.2	3.2
Total Alien Plants	29.5	59.5	53.4	67.4	66.2
<i>Carex wahuensis</i>	0.2	0.0	0.6	0.2	0.8
<i>Deschampsia nubigena</i>	3.5	4.3	3.4	5.4	3.4
<i>Eragrostis grandis</i>	0.0	0.0	0.0	2.0	0.4
<i>Luzula hawaiiensis</i>	0.2	1.3	0.0	0.0	0.0
<i>Panicum tenuifolium</i>	0.0	0.0	0.0	0.0	0.0
Total Native Grasses	3.8	5.7	4.0	5.6	4.6
<i>Cocculus ferrandianus</i>	0.2	0.0	0.0	0.0	0.2
<i>Pteridium aquilinum</i>	1.7	3.7	4.0	6.8	8.6
Total Native Herbs	1.8	3.7	4.0	6.8	8.8
<i>Dodonaea viscosa</i>	0.3	0.2	3.2	4.4	4.0
<i>Styphelia tameiameia</i>	0.0	0.0	0.0	0.0	0.0
<i>Vaccinium reticulatum</i>	0.0	0.0	0.0	0.0	0.0
Total Native Shrubs	0.3	0.2	3.2	4.4	4.0
Acacia koa	0.0	0.2	0.0	0.0	0.0
Total Native Trees	0.0	0.2	0.0	0.0	0.0
Total Native Plants	6.0	9.7	11.2	16.8	17.4
Litter	32.0	14.3	25.0	9.0	10.8
Soil	28.3	17.8	7.8	5.8	4.6
Rock	1.7	1.2	1.6	1.0	1.0

Table 2. Change in percent cover in the *Deschampsia*-Velvet Grass community, 1985-1992.

	Mean %Cover			
	1986	1987	1989	1992
<i>Andropogon virginicus</i>	0.1	0.0	1.1	0.7
<i>Anthoxanthum odoratum</i>	2.0	6.8	10.1	11.1
<i>Dactylis glomerata</i>	0.0	0.0	0.0	0.0
<i>Holcus lanatus</i>	10.2	26.0	24.0	22.7
<i>Microlaena stipoides</i>	0.0	0.0	0.0	0.0
<i>Paspalum dilatatum</i>	6.8	7.8	10.0	6.6
<i>Rynchelytrum repens</i>	0.0	0.0	0.0	0.0
<i>Schizachyrium condensatum</i>	0.2	1.0	0.3	1.2
<i>Sporobolus africanus</i>	1.7	1.4	3.9	4.7
Total Alien Grasses	21.0	43.0	49.6	46.9
<i>Centaureum erythraea</i>	0.0	0.0	0.0	0.0
<i>Erigeron canadense</i>	0.0	0.1	0.0	0.0
<i>Hypochoeris radicata</i>	1.6	2.6	1.9	0.7
<i>Plantago lanceolata</i>	0.3	0.8	1.7	1.2
<i>Rumex acetosella</i>	0.0	1.0	0.3	0.0
Total Alien Herbs	1.9	4.4	3.9	1.9
<i>Lythrum maritimum</i>	0.0	0.0	0.0	0.0
<i>Rubus argutus</i>	0.0	0.0	0.0	0.0
Total Alien Shrubs	0.0	0.0	0.0	0.0
Total Alien Plants	22.9	47.4	53.4	48.8
<i>Carex wahuensis</i>	0.1	0.4	0.4	0.3
<i>Deschampsia nubigena</i>	17.4	22.8	25.3	28.8
<i>Eragrostis grandis</i>	0.0	0.0	0.0	0.0
<i>Luzula hawaiiensis</i>	0.0	0.0	0.1	0.0
<i>Panicum tenuifolium</i>	0.0	0.4	0.1	0.2
Total Native Grasses	17.6	23.7	26.0	29.3
<i>Cocculus ferrandianus</i>	0.0	0.0	0.0	0.0
<i>Pteridium aquilinum</i>	2.7	5.1	9.3	8.0
Total Native Herbs	2.7	5.1	9.3	8.0
<i>Dodonaea viscosa</i>	0.0	0.1	0.3	1.2
<i>Styphelia tameiameia</i>	0.2	0.1	0.3	0.7
<i>Vaccinium reticulatum</i>	0.0	0.0	0.0	0.0
Total Native Shrubs	0.2	0.2	0.7	1.9
<i>Acacia koa</i>	0.0	0.0	0.2	1.1
Total Native Trees	0.0	0.0	0.2	1.1
Total Native Plants	20.4	29.0	36.2	40.3
Litter	30.4	16.7	7.3	7.2
Soil	25.3	5.0	2.7	3.4
Rock	0.3	0.3	0.3	0.2

Table 3. Change in percent cover in the Sweet Vernal Grass community, 1985-1992.

	Mean %Cover				
	1985	1986	1987	1989	1992
<i>Andropogon virginicus</i>	0.0	0.0	0.0	0.0	0.0
<i>Anthoxanthum odoratum</i>	2.8	8.0	17.0	12.5	24.5
<i>Dactylis glomerata</i>	0.2	0.2	0.5	0.0	0.0
<i>Holcus lanatus</i>	1.8	5.3	5.2	8.8	3.5
<i>Microlaena stipoides</i>	0.2	0.5	0.7	6.8	6.5
<i>Paspalum dilatatum</i>	1.8	9.5	21.0	13.2	7.7
<i>Rynchelytrum repens</i>	0.0	0.0	0.0	0.0	0.0
<i>Schizachyrium condensatum</i>	0.0	0.0	0.0	0.0	0.0
<i>Sporobolus africanus</i>	0.0	0.0	0.0	0.0	0.0
Total Alien Grasses	6.8	23.5	44.3	41.3	42.2
<i>Centaureum erythraea</i>	0.0	0.0	0.0	0.0	0.0
<i>Hypochoeris radicata</i>	0.0	3.0	0.8	1.3	0.3
<i>Plantago lanceolata</i>	0.0	0.0	0.0	0.0	0.0
<i>Rumex acetosella</i>	0.0	0.2	0.0	0.0	0.0
Total Alien Herbs	0.0	3.2	0.8	1.3	0.3
<i>Lythrum maritimum</i>	0.0	0.0	0.0	0.0	0.0
<i>Rubus argutus</i>	0.0	1.2	0.3	1.0	0.8
Total Alien Shrubs	0.0	1.2	0.3	1.0	0.8
Total Alien Plants	6.8	27.8	45.5	43.7	43.2
<i>Carex wahuensis</i>	0.3	0.2	1.5	1.0	1.5
<i>Deschampsia nubigena</i>	18.3	18.0	20.0	20.2	23.8
<i>Eragrostis grandis</i>	0.0	0.0	0.0	0.0	0.0
<i>Luzula hawaiiensis</i>	0.0	0.0	0.0	0.0	0.0
<i>Panicum tenuifolium</i>	1.8	1.2	1.3	0.2	0.5
Total Native Grasses	20.5	19.3	22.8	21.3	25.8
<i>Cocculus ferrandianus</i>	0.0	0.0	0.0	0.0	0.0
<i>Pteridium aquilinum</i>	3.8	6.0	9.2	10.5	8.5
Total Native Herbs	3.8	6.0	9.2	10.5	8.5
<i>Dodonaea viscosa</i>	0.0	0.0	1.0	1.7	1.3
<i>Styphelia tameiameia</i>	0.8	1.2	1.8	4.0	2.8
<i>Vaccinium reticulatum</i>	0.0	0.0	0.0	0.0	0.0
Total Native Shrubs	0.8	1.2	2.8	5.7	4.2
<i>Acacia koa</i>	0.0	1.2	1.3	4.5	4.5
<i>Metrosideros polymorpha</i>	0.0	0.0	1.5	0.0	0.0
Total Native Trees	0.0	1.2	2.8	4.5	4.5
Total Native Plants	25.2	27.7	37.7	42.0	43.0
Litter	32.5	29.0	12.7	12.3	12.7
Soil	22.8	9.0	3.0	1.8	0.8
Rock	1.3	1.5	1.0	0.2	0.2

Table 4. Changes in percent cover in the Pukiawe/*Deschampsia* community, 1985-1992.

	1985	1986	Mean %Cover		
			1987	1989	1992
<i>Andropogon virginicus</i>	0.0	0.0	0.0	0.0	0.0
<i>Anthoxanthum odoratum</i>	0.0	0.0	0.0	0.0	0.0
<i>Dactylis glomerata</i>	0.0	0.0	0.0	0.0	0.0
<i>Holcus lanatus</i>	0.0	0.0	0.3	5.3	3.7
<i>Microlaena stipoides</i>	0.0	0.0	0.0	0.0	0.0
<i>Paspalum dilatatum</i>	0.0	0.0	0.0	0.0	0.0
<i>Rynchelytrum repens</i>	0.0	0.0	0.0	0.0	0.0
<i>Schizachyrium condensatum</i>	0.0	0.0	0.0	0.0	0.0
<i>Sporobolus africanus</i>	0.0	0.0	0.0	0.0	0.0
Total Alien Grasses	0.0	0.0	0.3	5.3	3.7
<i>Centaureum erythraea</i>	0.0	0.0	0.0	0.0	0.0
<i>Hypochoeris radicata</i>	3.7	6.0	5.7	6.3	5.3
<i>Plantago lanceolata</i>	0.0	0.0	0.0	0.0	0.0
<i>Rumex acetosella</i>	0.0	0.0	0.0	0.0	0.0
Total Alien Herbs	3.7	6.0	5.7	6.3	5.3
<i>Lythrum maritimum</i>	0.0	0.0	2.0	0.0	0.0
<i>Rubus argutus</i>	0.0	0.0	0.0	0.0	0.0
Total Alien Shrubs	0.0	0.0	2.0	0.0	0.0
Total Alien Plants	3.7	6.0	8.0	11.7	9.0
<i>Carex wahuensis</i>	0.3	0.3	0.0	0.0	0.0
<i>Deschampsia nubigena</i>	21.7	26.3	37.0	46.3	46.3
<i>Eragrostis grandis</i>	0.0	0.0	0.0	0.0	0.0
<i>Luzula hawaiiensis</i>	0.0	0.0	0.3	0.0	0.0
<i>Panicum tenuifolium</i>	0.0	0.0	1.3	2.3	1.7
Total Native Grasses	22.0	26.7	38.7	48.7	48.0
<i>Cocculus ferrandianus</i>	0.0	0.0	0.0	0.0	0.0
<i>Pteridium aquilinum</i>	0.3	0.7	0.3	0.0	0.3
Total Native Herbs	0.3	0.7	0.3	0.0	0.3
<i>Dodonaea viscosa</i>	0.0	0.0	0.0	0.0	0.0
<i>Styphelia tameiameia</i>	0.0	2.3	2.7	3.3	2.0
<i>Vaccinium reticulatum</i>	0.0	0.0	0.0	0.3	0.0
Total Native Shrubs	0.0	2.3	2.7	3.7	2.0
<i>Acacia koa</i>	0.7	1.3	1.0	1.0	1.0
<i>Metrosideros polymorpha</i>	0.0	0.0	0.3	0.0	0.0
Total Native Trees	0.7	1.3	1.3	1.0	1.0
Total Native Plants	23.0	31.0	43.0	53.3	51.3
Litter	33.3	21.7	12.7	7.3	14.0
Soil	22.7	26.0	19.0	14.0	12.3
Rock	9.7	14.7	15.3	13.3	13.3

Table 5. Change in percent cover in the Velvet Grass, *Deschampsia* community, 1985-1992.

	Mean %Cover				
	1985	1986	1987	1989	1992
<i>Andropogon virginicus</i>	0.0	0.0	0.0	0.0	0.0
<i>Anthoxanthum odoratum</i>	0.0	0.0	0.0	0.0	0.0
<i>Dactylis glomerata</i>	0.0	0.0	0.0	0.0	0.0
<i>Festuca spp</i>	0.0	0.7	0.0	0.0	0.0
<i>Holcus lanatus</i>	19.0	24.0	55.7	64.3	58.3
<i>Microlaena stipoides</i>	0.0	0.0	0.0	0.0	0.0
<i>Paspalum dilatatum</i>	0.0	0.0	0.0	0.0	0.0
<i>Rynchelytrum repens</i>	0.0	0.0	0.0	0.0	0.0
<i>Schizachyrium condensatum</i>	0.0	0.0	0.0	0.0	0.0
<i>Sporobolus africanus</i>	0.0	0.0	0.0	0.0	0.0
Total Alien Grasses	19.0	24.7	55.7	64.3	58.3
<i>Centaureum erythraea</i>	0.0	0.0	0.0	0.0	0.0
<i>Cirsium vulgare</i>	0.3	0.0	0.0	0.0	0.0
<i>Epilobium cinereum</i>	0.0	0.3	0.0	0.0	0.0
<i>Hypochoeris radicata</i>	1.7	2.7	1.7	6.0	0.3
<i>Plantago lanceolata</i>	0.0	0.0	0.0	0.3	0.0
<i>Rumex acetosella</i>	0.0	1.0	0.0	0.0	0.0
Total Alien Herbs	2.0	4.0	1.7	6.3	0.3
<i>Lythrum maritimum</i>	0.3	0.0	0.7	0.0	0.3
<i>Rubus argutus</i>	0.0	0.0	0.0	0.0	0.0
Total Alien Shrubs	0.3	0.0	0.7	0.0	0.3
Total Alien Plants	21.3	28.7	58.0	70.7	59.0
<i>Carex wahuensis</i>	0.0	0.0	0.0	0.0	0.0
<i>Deschampsia nubigena</i>	20.0	22.7	28.3	19.3	27.3
<i>Eragrostis grandis</i>	0.0	0.0	0.0	0.0	0.0
<i>Luzula hawaiiensis</i>	0.0	0.0	0.0	0.0	0.0
<i>Panicum tenuifolium</i>	0.3	0.3	1.3	3.7	4.3
Total Native Grasses	20.3	23.0	29.7	23.0	31.7
<i>Cocculus ferrandianus</i>	0.0	0.0	0.0	0.0	0.0
<i>Pteridium aquilinum</i>	0.0	0.0	0.0	0.0	0.0
Total Native Herbs	0.0	0.0	0.0	0.0	0.0
<i>Dodonaea viscosa</i>	0.0	0.0	0.0	0.0	0.0
<i>Styphelia tameiameia</i>	0.0	0.0	0.0	0.0	0.3
<i>Vaccinium reticulatum</i>	0.0	0.0	0.0	0.0	0.7
Total Native Shrubs	0.0	0.0	0.0	0.0	1.0
<i>Acacia koa</i>	0.0	0.0	0.0	0.0	0.0
Total Native Trees	0.0	0.0	0.0	0.0	0.0
Total Native Plants	20.3	23.0	29.7	23.0	32.7
Litter	34.7	29.0	10.3	6.3	8.0
Soil	19.3	18.7	1.0	0.0	0.3
Rock	0.7	0.7	0.0	0.0	0.0